The quantification of the online control of goal-directed movement using frequency domain analysis

by

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Abstract

The field of motor control has devoted a lot of attention to the use of sensory information during movements for the maintenance of accuracy. This sensorimotor processing has been colloquially termed online control. Its accurate quantification and identification has posed a continual challenge to motor control researchers. Consequently, many measures of online control have been developed and have shaped the concurrent state of the field. Recent theories of online control have posited the existence of multiple distinct feedback processes. The current dissertation sought to gain insights into the multi-faceted nature of online control by evaluating the utility of frequency domain analyses as a tool for its quantification. Frequency domain analyses were hypothesized to be sensitive to the aforementioned distinct feedback processes given the assumption that they operate at unique timescales. Four experiments were conducted and evidence was obtained in favour of the utility of frequency domain analyses for the quantification of online control. Specifically, frequency domain analyses were found to be both one of the most sensitive measures to online control and the most robust measure to offline contamination. Thus frequency domain analyses represent an excellent choice for the evaluation of online control processes. Additionally, theoretical insights were attained through the sensitivity of frequency domain analyses to the contribution of two distinct processes contributing to reaching performance. The first was an iterative visuomotor process that influenced reaching performance at relatively stable rates. Notably, the specific rate of influence was found to be flexible based on the spatio-temporal requirements of reaching movements. Additionally, frequency domain analyses were found to be sensitive to a second, non-visual
process. This process was promoted in the absence of online vision and likely represented the contribution of a peripheral proprioceptive process. Importantly, contemporary alternative methodologies for the quantification of online control were not sensitive to the unique contributions of this secondary process. Altogether, the current dissertation reaffirmed and expanded upon the multi-faceted nature of online feedback utilization and provided a novel approach to its quantification.
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1 Introduction

1.1 Overview of the dissertation

The current dissertation had two core aims: 1) to develop a novel approach for the quantification of feedback utilization during movement using frequency domain analyses; and 2) to expand the current theoretical understanding of online control. These aims were reached by examining the rates at which sensorimotor feedback loops operate during goal-directed reaching movements by assessing limb trajectories in the frequency domain.

The main research direction of the current dissertation was to apply frequency domain analyses to trajectories to determine if it could detect the use of sensory information during goal-directed upper-limb reaching movements. Based on the theoretical assumption that the use of online feedback is an iterative process, which has been presumed to act at a particular latency, the contributions of distinct feedback loops functioning at different oscillatory latencies (i.e., frequencies) were hypothesized to be measurable using frequency domain analyses. Importantly, sensory information may be utilized at different rates for different processes. That is, separable processes invariably require a unique set of computations resulting in specific minimum latencies at which they can act. If the latencies of such processes (in ms) are relatively stable, then they can be represented as a frequency (in Hz).

The four manuscripts included in the current dissertation include five experiments, which sought to isolate and measure the distinct feedback processes contributing to the performance of goal-directed reaching movements. The primary focus of these experiments was an evaluation of visually-mediated feedback processes in particular. Specifically, the potential contributions of visual feedback processes were examined through manipulations of the availability of online vision during reaching performance. Given the expected distinct latencies for unique processes contributing to reaching performance, conditions were tested wherein differential contributions of unique processes were expected. Thirdly, because offline changes in limb trajectories are difficult to isolate from online control, the robustness of both frequency domain analyses and conventional measures of online control to experimentally induced trial-to-trial changes in
movement planning were examined. And lastly, the association between the frequency domain findings and online control processes were further evaluated through the implementation of both blocked/randomized feedback scheduling and instructions to adopt an accuracy-based movement focus.

The included experiments allowed for the quantification of feedback utilization of movement in a manner that overcame difficulties of trajectory analysis in the time domain. For example, the frequency analyses employed in this dissertation succeeded in the inherently difficult task of identifying the contributions of temporally overlapping processes (e.g., Elliott, Carson, Goodman & Chua, 1991; Elliott et al., 2010). Ultimately, contribution of the current dissertation to the research literature was thus both methodological and theoretical. First, methodologically speaking, frequency domain analyses were found to be a suitable measure for the quantification of online feedback utilization. Further, this sensitivity to online processes was also relatively more robust to performance differences associated with of trial-to-trial influences induced by the provision of optical prisms and terminal feedback, than traditional online control measures. Second, the theoretical implications of the current dissertation include direct evidence for an iterative control process, which contributed online to reaching performance. Such iterative online feedback utilization was found to be flexible in its rate of operation. Also, distinct visual and non-visual processes separately influence performance at markedly different latencies.
2 Review of the Literature

2.1 Overview of the literature to be reviewed

The current chapter reviewed the literature associated with the processes mediating the accurate performance of ongoing goal-directed, upper-limb movements. First, the general organization of goal-directed upper-limb movements was completed. Second, an overview of the different types of limb trajectory corrections was completed. This was followed by a review of the commonly used methodologies for the quantification of online feedback utilization. Next, the durations required for online feedback to operate were assessed. Fourth, an examination was completed of the evidence in favour of the use of multiple parallel feedback loops during action. Fifth, the evidence for a single multisensory feedback controller of action was reviewed. Sixth, the basic principles of frequency domain analyses and their applications for the quantification of feedback utilization in simple movements were reviewed. Seventh and last, potential sources of limb oscillations were reviewed. As a result, this review of literature provides a series of rationales as to why frequency analyses may prove useful to assess and understand the control of ongoing voluntary movements.

2.2 The two component model of voluntary goal-directed upper-limb movements

Accurately interacting with the world is something that is often taken for granted. Although many may have pondered about how we accomplish such feats, the work of R. S. Woodworth (1899) provided seminal and empirical examinations and explanations of the processes involved. Part of Woodworth`s examination focused on the influences of movement speed and the availability of vision on the accuracy of voluntary movement. Woodworth found that movements were more accurate when they were completed with the eyes opened as compared to movements completed with the eyes closed. Additionally, differences between eyes-open and eyes-closed conditions became more apparent at longer movement durations. Thus, longer movements benefited from sensory feedback and adjustments to these movements improved accuracy. This adjustment phase of the movement was operationally defined as the
current-control phase. Movements of all durations were also thought to be first influenced by an additional, initial phase not directly reliant upon online sensory feedback, which was labelled the initial impulse phase. In summary, Woodworth (1899) proposed that voluntary reaching movements performed by individuals thus consist of two distinct phases: 1) the initial impulse phase, which is not directly reliant on concurrent visual feedback; and can be used to move the limb with a certain degree of accuracy to a target, and 2) the current-control phase, which utilizes feedback when there is sufficient time to correct an ongoing movement to improve accuracy.

Many years later, Howarth, Beggs, and Bowden (1971) developed a quantification of the relationship between the error and the speed of a voluntary goal-directed upper-limb movement. The amount of error for a given movement was proposed to increase linearly with the amount of distance travelled since the last feedback-based correction. When individuals moved rapidly, the increased distance travelled since the last corrective process did increase the likelihood of an error. Therefore, the effectiveness of the current-control phase of a goal-directed movement was hypothesized to be dependent upon the distance travelled since the last feedback-based corrective process. Howarth et al. (1971) estimated that the corrective reaction time to utilize feedback was approximately 290 ms. Because discrete movements often do not extend beyond more than one corrective reaction time (i.e., movement times of <= 580 ms), typical goal-directed actions would have time for only a single correction from which to maximize accuracy. Thus, optimizing the timing of this correction to a constant time relative to the end of the movement would be advantageous.

In a similar vein, Crossman and Goodeve (1963/1983) examined the nature of the corrective processes in the control of voluntary limb movements. Specifically, the possibility of the continuous utilization of sensory information was compared to the possibility of intermittent utilization of sensory information. Evidence was attained primarily for the latter possibility, namely the intermittent utilization model of feedback utilization. This was determined by the examination of velocity profiles of goal-directed wrist rotations (see Crossman & Goodeve, 1963/1983; Experiment 2). These profiles exhibited a sequence of discrete impulses, which were
characteristically stereotyped in form (i.e., Gaussian velocity impulses). Crossman and Goodeve also considered their data with a continuous velocity control model in which impulses would not have been apparent in the trajectories. The utilization of feedback for the attainment of accuracy during goal-directed movement was proposed to occur as series of discrete adjustments (i.e., an iterative process) whereby stereotyped corrections are utilized based on the accuracy of the ongoing movement. The authors proposed that these discrete corrections emerging from feedback utilization were made at a fixed rate. Each corrective iteration reduced the error of an ongoing goal-directed movement by a fixed proportional amount. This point of view has been referred to as the deterministic iterative-correction model (see Meyer, Abrams, Kornblum, Wright, & Smith, 1988). Thus, given sufficient time, more than a single correction likely influences online reaching performance. Nevertheless, subsequent research argued that the iterative-correction model did not account for all aspects of reaching performance.

Meyer et al. (1988) developed a statistical model to attempt to explain the relationship between speed and accuracy of goal-directed voluntary movements. They made the argument that the model proposed by Crossman and Goodeve (1963/1983) failed to describe a large body of experimental research. Specifically, the predictions of the iterative-corrections model of Crossman and Goodeve were incompatible with experimental findings relating to the rate and prevalence of secondary submovements, error rates, and the influence of the removal of vision. Meyer et al. (1988) suggested that online visual feedback is instead utilized in a statistically optimal manner, meaning that submovements are initiated in a manner that minimizes their necessity. This model was dubbed the stochastic optimized-submovement model. Within this model, movements were thought to be generated as a primary submovement. If the endpoint of this submovement fell within the target area, then no secondary submovements were required or produced. Conversely, if the primary submovement failed to attain the target location, a secondary submovement was thought to be utilized to acquire the target. Under this model, feedback utilization is iterative only when necessary. This model can be contrasted with the iterative submovement model of Crossman and Goodeve (1983) in that the iterative submovement model posits that all movements are made up of iterative corrective processes
whereas the stochastic optimized submovement model posts corrective processes on an as-needed basis. Nevertheless, further evidence for iterative control mechanisms have since been reported.

Elliott, Carson, Goodman, and Chua (1991) extended the above ideas and examined the performance of individuals performing voluntary limb movements under a range of sensory conditions to evaluate the ability of existing models to explain performance based on kinematic profiles. Previous models of voluntary movement often explained the presence of discrete discontinuities in kinematic profiles as error-reducing corrective processes (i.e., discrete corrections: Jeannerod, 1988; Meyer et al., 1988). Elliott et al. (1991) computed correlations between the number of zero-crossings in the acceleration profiles with endpoint accuracy. Importantly, the number of discrete corrections in the profile did not correlate highly with the accuracy of the movement. Additionally, the greatest number of zero-crossings in the acceleration profile came from a condition where visual information had been extinguished for 2 s prior to movement initiation. Therefore, some discontinuities inherently did not come about via online visual feedback mechanisms. It was hypothesized that discontinuities measured in conditions without real-time visual feedback could have to come about via corrective mechanisms from other sensory modalities (i.e., proprioception as a prime candidate).

Additionally, to reconcile the apparent lack of a correlation between number of zero-crossings in the acceleration profile and the accuracy of the movement, the authors proposed that feedback-based adjustments must be implemented in a pseudocontinuous/overlapping fashion (see also Flash & Henis, 1991). In such a framework, successive adjustments would begin within a short time interval, prior to the completion of the previous corrective submovement. Ultimately, a series of such overlapping submovements could thus elicit a smooth kinematic profile.

Overall, the accurate completion of goal-directed action typically requires the use of online feedback (e.g., Woodworth, 1899). The use of such feedback has then been thought to be iterative in nature (e.g., Meyer et al., 1988). However, because discrete corrective processes evident in kinematic profiles of voluntary action are not always tightly linked to the accuracy of the involved movements, additional control processes must also contribute to movement
accuracy (e.g., Elliott et al., 1991). Further, the presence of discrete submovements in the absence of visual feedback indicates that in these cases, sensory information from alternative sources such as proprioception may be functioning in addition to, or instead of, visual processes (Elliott et al., 1991). Therefore, the control of ongoing voluntary goal-directed action may come about through a series of sub-processes governing discrete and/or pseudocontinuous corrections.

2.3 Multiple ways to correct a trajectory

Although much of the online control literature has focused on the quantification of the relative reliance on feedback-based processes, an important topic worth visiting is the manner in which these processes ultimately exert their influence. Woodworth (1899) first described corrective processes through an increase in trajectory discontinuities following an initial impulse. This initial impulse later became known colloquially as the primary submovement and the subsequent discontinuities as secondary submovements (e.g., Meyer et al., 1988). Although quantitative routines to discern the primary from secondary submovements have been developed (e.g., Langolf, Chaffin, & Foulke, 1976), Meyer et al. (1988) popularized a relatively exhaustive and multifaceted approach to identifying the presence of secondary submovements. Three main criteria were set for the identification of submovements: Type-1) zero-crossings in the velocity profile, changing from positive to negative; Type-2) zero-crossings in the acceleration profile, changing from negative to positive; and Type-3) the presence of a relative minimum in the acceleration profile while the acceleration values remained negative. More recently, Dounskaia and colleagues (Dounskaia, Wisleder, & Johnson, 2005; Fradet, Lee, & Dounskaia, 2008; Wisleder & Dounskaia, 2007) utilized these three criteria to classify submovements into distinct types. Type-1 submovements were deemed to represent movement reversals due to target overshoots. Type-2 submovements were deemed to represent reaccelerations due to target undershoots. Type-3 submovements were deemed to represent subtle/graded changes in the deceleration of the movement (i.e., zero-crossings in the jerk profile). Thus, discrete corrections have been described as reflecting a number of different response types.
Beyond the contribution of discrete secondary submovements, there is also some evidence for another, more continuous online control process. Initially, Crossman and Goodeve (1963/83) argued that corrections operated throughout a trajectory in a serial and continuous manner. Although some argued against the possibility of a continuous control process (e.g., Cruse, Dean, Heuer, & Schmidt, 1990; Meyer et al., 1988), evidence for such a control process has been reported (e.g., Knill & Saunders, 2003). A conceptually similar mode of control was proposed by Elliott et al. (1991), which became known as pseudocontinuous control. In pseudocontinuous control, serially organized movement corrections exert their influence in an overlapping fashion, which tends to minimize their apparent contribution to ongoing trajectories because they often result in relatively smooth trajectories.

Lastly, a third manner in which control is thought to be exerted upon ongoing trajectories was formalized in the multiple processes model of Elliott et al. (2010; 2017). The idea was that corrective processes could also directly influence the initial impulse (e.g., Woodworth, 1899) or primary submovement (e.g, Meyer et al., 1988). The manner in which these corrective processes influence the trajectory was proposed to be graded adjustments to this impulse and was called impulse regulation. Corrections of this type were argued to come about through a comparison of expected vs. actual sensory consequences of the unfolding movement, such as perceived limb velocity. As such, the majority of the evidence for this type of control came from studies employing illusion-inducing moving background manipulations (e.g., Grierson & Elliott, 2008), which have been replicated many times (e.g., Brenner & Smeets, 1997; Gomi, 2008; Proteau & Masson, 1997; Whitney, Westwood, & Goodale, 2003). Nonetheless, there is evidence that online corrective processes can also contribute to the earliest portions of the trajectory.

In contrast, many trajectory changes can be based on changes in the movement plan. Notably, Plamondon & Alimi (1997) demonstrated that many trajectory properties, such as discrete discontinuities, can be predicted without considering online feedback utilization. In such cases, the sensory information responsible for the aforementioned changes in performance was thought to come from information gathered as a consequence of previous actions (e.g., Knowledge of results; see Salmoni, Schmidt, & Waiter, 1984 for a review). Beyond the explicit
influences of knowledge of results, individuals can also place a greater emphasis on movement accuracy during movements. Unsurprisingly, such an emphasis leads to increases in movement accuracy (e.g., Adam, 1992). Notably, these increases in accuracy have been found for discrete skills such as soccer kicks whereby online feedback utilization is inherently limited (e.g., van den Tillaar & Fuglstad, 2016) and in reaching movements wherein online feedback utilization likely significantly contributed to performance (e.g., Elliott et al., 1991). Nevertheless, the increased focus on movement accuracy potentially influences both the offline and the online performance of individuals.

Ultimately, there are many distinct ways in which movements may be corrected online. These range from continuous or pseudocontinuous corrections, to graded adjustments to the initial impulse or primary submovement, and lastly, to several unique types of discrete secondary submovements in the later portions of the trajectory. Further, movements may also be amended on a trial-to-trial basis, making use of information gathered during previous attempts to optimize performance. Additionally, strategic intentions to be accurate may alter both the online and offline corrective processes employed. Importantly, such a diversity of corrective processes has highlighted the importance of the development of measurement techniques for the unique quantification of online feedback utilization during movements (cf., offline changes in performance).

2.4 Quantifying online control: Methods for measuring the use of sensory information during movement

The quantification of the utilization of sensory information during movements is an important step to understand the manner in which the accurate performance comes about. A number of methods have been proposed to measure the degree to which a movement has been modified between its onset and offset. The methods that have been typically utilized in the literature can be divided into two general categories: methods calculated within a single voluntary movement (i.e., within-trial measures) and methods which require calculation across a
number of movements (i.e., between-trial measures). The following two sections will describe some of the most influential methods from the literature.

2.4.1 Within-trial measures of online control

Beyond the work of Woodworth (1899), it can be argued that one of the most impactful contributions to the field of motor control was the formulation of a mathematical relationship between the spatial characteristics of the target of a goal-directed movement and the time required to complete such a movement (i.e., movement time [MT]). These spatial characteristics included the distance to be travelled between the start and target locations as well as the width of the target. This relationship was quantified by Paul Fitts (1954) and has subsequently been known as Fitts' Law (cf., Fitts' Theorem, see Heath, Weiler, Marriott, Elliott, & Binsted, 2011; Heath, Samani, Tremblay, & Elliott, 2016). Fitts' Law was derived from Information theory and Shannon's Theorem 17 (Shannon & Weaver, 1949). According to Fitts' Law, movement time increases in a logarithmic fashion to increases in a target's index of difficulty (ID), which was directly associated with increases in amplitude and/or decreases in target width (i.e., ID = \log_2[2*Amplitude/Width]). As Fitts defined it, the motor apparatus included sensory feedback loops that have a limited processing capacity. Increasing the needs to process information therefore has a lengthening effect of movement time. Consistent with this prediction is the finding that movements completed without concurrent visual feedback tend to have shorter movement times relative to those completed with the presence of concurrent visual feedback (e.g., Elliott & Madalena, 1987). Notably, Fitts' Law has been found to still describe performance when the availability of concurrent visual information about the hand and target locations is withdrawn (all R^2 >= .96; Wu, Yang, & Honda, 2010). Thus, the associated feedback loops may not be entirely visual in nature. However, endpoint accuracy was maximized in the presence of concurrent visual information. Also, full vision conditions (i.e., both hand and target visible) resulted in the steepest MT/ID slope (67 ms/bit), indicating greater movement time costs related to increases in target ID. That is, the presence of concurrent visual information resulted in comparably longer movement times, indicating that changes in visuomotor feedback utilization typically represent a relatively large contribution to the associated changes in movement times.
Longer movement times have been associated with the utilization of corrective mechanisms of an ongoing movement. A closer examination of the temporal aspects of specific kinematic markers within a movement have also provided important insights. Specifically, increases in movement times, which are associated with feedback based corrective processes, are potentially related to increases in the absolute time spent between peak limb velocity and the end of the movement (e.g., Elliott, Carson, Goodman & Chua, 1991). This time after peak velocity is roughly temporally coincident with the current-control phase of Woodworth (1899). Also, a greater proportion of time spent following peak velocity has also been implicated with feedback utilization (Elliott et al., 1991; Elliott & Hansen, 2010; Hansen, Tremblay, & Elliott, 2008; Jeannerod, 1988; cf., Heath et al., 2004). Thus, the evaluation of temporal measures based on movement time and time after peak velocity have supported the idea of increased reliance on feedback-related processes, resulting in prolonged time to complete a goal-directed action. In addition, intentions to complete accurate movements have also been associated with longer times after peak-limb velocity (e.g., Elliott et al., 1991). Further, the shortening of the time spent after peak limb velocity has also been associated with a greater contribution of online control when an unperceived target jump ultimately requires a shorter movement amplitude (e.g., Tremblay et al., 2016). And lastly, increases in the time spent after peak-limb velocity have also been proposed to come about via inefficiencies in feedback utilization (e.g., Kennedy, Bhattacharjee, Hansen, Reid, & Tremblay, 2015). Nevertheless, while an association between online feedback utilization and time spent after peak limb velocity has been reported, those associations could be strengthened by being corroborated by changes in the spatial domain.

Temporal variables such as movement time and time spent after peak velocity offer only circumstantial support for the utilization of feedback processes. That is, changes in these measures can be used only to infer an increased likelihood of the utilization of feedback processes. Also, they do not provide information about the changes in the spatial characteristics of movements which came about through the use of feedback. Therefore, before one can conclude that feedback has been utilized to alter a trajectory, one should expect to find direct evidence for adjustments in these trajectories. For example, when the target of a pointing
movement is suddenly shifted/perturbed spatially at movement onset, individuals implement trajectory corrections to the change in stimulus location, which results in a maintenance of movement accuracy (e.g., Komilis, Pélisson, & Prablanc, 1993). Consequently, adjustments of ongoing movements often require secondary accelerations to ensure movement accuracy (Meyer et al., 1988). Thus, the use of feedback may be quantifiable by measuring the number of discrete secondary accelerations in a reaching trajectory.

Alternatively, if one makes the assumption that discontinuities in kinematic profiles do primarily reflect feedback-related processes, a smooth trajectory would represent one utilizing limited feedback. Such a prediction has been indirectly asserted by a movement production model proposed by Flash and Hogan (1985), who proposed that reaching movements are planned in a manner that minimized jerk across the trajectory. A model based on the minimization of jerk can explain the spatial invariance often seen in movements of a range of durations and velocities. An extension of this notion is that a movement that must be completed with the involvement of feedback mechanisms would be expected to have an overall increase in the discontinuities of the profile, which would present themselves as an increase in the sum of the squared jerk of the trajectory. This method would be more sensitive to subtle adjustments due to feedback mechanisms because this jerk score would increase both in the presence of obvious discrete corrections and also more fine tuned smaller corrections. Such an approach fits well with the idea that feedback-based corrections are implemented in a pseudocontinuous fashion, and that discrete trajectory amendments may be undetectable (see Elliott et al., 1991). Unfortunately, as tempting as such an approach can be, caution must be taken before asserting feedback related processes by quantifying online control with a single value based on discontinuities or smoothness over an entire kinematic profile. This is the case for two reasons.

First, one must be careful not to attribute a measurement artifact as the implementation of feedback-based control mechanisms. This is particularly important when generating higher derivatives of position such as acceleration for further analysis because the differentiation process introduces noise into the signal (Hansen, Elliott, & Khan, 2007; Franks, Sanderson, & van Donkelaar, 1990; Kay, Munhall, Bateson, & Kelso, 1986). Franks et al. (1990) examined the
influence of filter cutoff frequency on the correspondence between accelerometer traces and double-derived position data. They reported that the cutoff frequency of the filter used to reduce such artifacts is important to consider. When researchers are interested in measuring the number of zero-crossings in the acceleration profile, a 12 Hz cutoff was deemed most appropriate. Alternatively, the assessment of significant deviations of accelerations not associated with zero-crossings was found to be optimized at 10 Hz. Also, the degree of correspondence between accelerometer traces and position-derived acceleration traces has been found to be influenced by the method of differentiation utilized (Hansen et al., 2007; Kay et al., 1986). As such, the distinction between trajectory amendment and data collection artifact is a challenging undertaking. Researchers have subsequently resorted to subjective criteria. For example, Elliott and Chua (1993) recommended that to be confident that an actual alteration to the trajectory has occurred, a peak in the acceleration trace of no less than 10 % of the absolute maximum acceleration had to be identified, and the duration between the peak and the next minimum in the profile needed to be at least 72 ms. Such values could theoretically improve one's confidence that a correction had been made and that such a peak was not simply an artifact of the data processing. Ultimately, the association of discontinuities in kinematic profiles with feedback-related processes is a difficult task. One must take care in their data processing and calculation of the derivatives of position to avoid overestimating trajectory amendment quantification. Alternatively, the reliance on directly measured acceleration data may provide a signal less biased by these potential confounds.

Second, in addition to the possibility of measurement artifact, not all discontinuities in kinematic profiles are necessarily associated with feedback processes (e.g., Dounskaia, Wisleder, & Johnson, 2005; Fradet, Lee, & Dounskaia, 2008; Wisleder & Dounskaia, 2007). Dounskaia et al. (2005) examined incidence rates of corrective submovements between discrete and reciprocal aiming movements. An increase in the number of submovements for the discrete compared to the reciprocal task was observed. The authors suggested that some submovements may come about as part of the natural process of stopping the limb on a target, irrespective of accuracy demands. That is, the increase in the number of submovements was attributed to the dissipation of forces
required to stop a moving limb on a target. Wisleder and Dounskaia (2007) followed this work and manipulated both the task (i.e., discrete vs. reciprocal) and the accuracy demands (i.e., different target sizes) in a similar experiment. In addition, they directly examined the incidence of specific submovement types based upon Meyer et al.'s (1988) descriptions. The authors defined larger submovements based upon velocity and acceleration traces as Type-1 and Type-2 submovements, respectively. These submovements represented movement reversals (i.e., Type-1) and reaccelerations (i.e., Type-2). Fine-tuned submovements caused by changes in deceleration evidenced by zero-crossings in the jerk profile were defined as Type-3 submovements. The authors found that the number of Type-3 submovements scaled with target size, but Type-1 and Type-2 submovements did not. That is, as the accuracy demands of the movement increased, the incidence of jerk profile zero-crossings increased. Additionally, the incidence of these Type-3 submovements did not vary as a function of movement task (i.e., discrete vs. reciprocal), whereas increases in the incidence of both Type-1 and Type-2 submovements were found for the discrete relative to the reciprocal aiming task. The authors therefore implicated the Type-3 submovements more directly with online feedback processes. Thus, although some submovements likely come about as a consequence of feedback-related processes, others may be generated irrespective of feedback utilization, through the termination processes at the end of a movement.

2.4.2 Between-trial measures of online control

The above-mentioned methodologies utilized for the quantification of the utilization of feedback-based mechanisms contributing to the accurate completion of movement could be quantified as within-trial measures. An alternative approach is to generate measures based on a number of trials, to compare conditions wherein feedback-based processes are hypothesized to take place (i.e., between-trial measures).

Messier and Kalaska (1999) examined the trial-to-trial spatial variability of goal-directed aiming movements at discrete temporal kinematic markers (i.e., peak acceleration, peak velocity, and movement end). One of the important findings of their work was the smaller correlation
coefficients between peak acceleration and movement end, as compared to those contrasting peak velocity and movement end. It was concluded that these changes likely came about via corrective mechanisms and could not be entirely attributed to pre-planned processes.

Other correlation-based methods were developed by Elliott, Binsted, and Heath (1999). They posited that to maintain accurate performance, the amplitude travelled after peak velocity would need to compensate for the overshooting or undershooting experienced at peak velocity. Consequently, they predicted and found negative correlations between the distances travelled before and after peak velocity. Heath and colleagues (Heath, 2005; Heath, Westwood & Binsted, 2004) fine tuned this methodology into what is typically known as an $R^2$ analysis. Under this type of analysis, the spatial position at earlier points in the movement are correlated with the spatial position at the end of the movement. Either kinematic markers (i.e., peak acceleration, peak velocity, and peak deceleration) or normalized proportions of movement time (e.g., 25, 50, and 75% movement time) have been utilized. In general, lower correlation coefficients are interpreted as evidence of more corrective processes and higher correlations are indicative of more pre-planned movements. That is, the more a position in the movement predicts the endpoint, the less alterations likely occurred between the two points. Such differences have been found to be robust for comparing conditions with and without concurrent visual feedback (Heath, 2005; Khan, Lawrence, Franks, & Buckolz, 2004; Tremblay, Hansen, Kennedy, & Cheng, 2013). Also, instead of squaring the correlation coefficients, as in the $R^2$ analyses, some researchers have chosen to transform the correlations to a Z-score using an r to Z transform (Williams, Grierson, & Carnahan, 2011) or from an r to a squared Z-score (i.e., $Z^2$; Bernier, Chua, Franks, & Khan, 2006).

Khan et al. (2003) also followed up on the work of Messier and Kalaska (1999), by directly assessing movement variability across trajectories, to elucidate online versus offline processing. It was argued that variability across kinematic markers can be informative regarding the utilization of corrective feedback because if a trajectory started off-course and continued uncorrected, the variability at later kinematic markers should increase. The presence of corrective mechanisms would be exemplified by a levelling-off or a decrease in the variability at
later kinematic markers. Importantly, however, Khan et al. (2003) proposed that differences in
the variability profiles between vision and no vision conditions could be associated with online
corrective mechanisms if the form of the variability profile was different across conditions. In
contrast, similarly shaped variability profiles could come about via offline influences. Khan et al.
(2003) tested this notion and tasked participants with aiming movement in with (i.e., FV) or
without (i.e., NV) concurrent visual feedback. Participants completed their movements using one
of four different target movement durations (i.e., 225, 300, 375, and 450 ms). When comparing
performance across vision conditions, it was determined that at the two shorter movement
durations (i.e., 225 & 300 ms), participants' variability profiles differed in magnitude but not in
form. This indicated that decreases in variability at these durations were due to offline
processing. Conversely, at the longer two movement durations (i.e., 375 & 450 ms), there was a
proportionally larger decrease in variability following peak limb deceleration in the presence of
concurrent visual feedback. Because the decreases in variability were proportionally different
across visual conditions, the authors inferred differential influence of online control. Overall,
between-trial measures of online control operate on a different set of assumptions relative to
within-trial measures. Thus, their utility has tended to be complementary to the analysis of
within-trial measures.

2.4.3 Within- vs. between-trial measures of online control

Overall, the methods typically utilized for the quantification of the utilization of feedback
processes during goal-directed movements can be divided into two general types: within-trial
methods, and between-trial methods. The within-trial methods described above include
movement time, time after peak velocity, the number of discrete discontinuities in the kinematic
profiles, and the squared integral of the movement jerk (i.e., jerk score). These methods
generally allow for an increase in confidence in one's assertion that feedback processes have
been utilized on a given trial. However, none of the aforementioned methods allow for
conclusive assertions regarding the causal influences on the changes in movement
characteristics.
The second type of online control quantification methods described above were those based on correlations or variability across a number of trials. Like the within-trial methodologies, these methods have also been moderately successful at increasing one's confidence of the presence or absence of online feedback utilization. The variability-based methods, though, make measurable predictions of the influence of offline processing on the measures themselves. Therefore, between-trial measures may be more sensitive to detecting the contributions of feedback-based corrective mechanisms than within-trial measures. Yet, the weakness of these multiple-trial measures lies in the simple fact that multiple trials are required. Naturally, these methods are unable to quantify or assess the contribution of individual trials in the manner the other measures do. Further, they may be inherently more susceptible to biased estimates of the contributions of online control via offline, trial-to-trial changes in planning.

Overall, while it appears that the current methodologies employed for the quantification of feedback-based processes during goal-directed action have been relatively successful as a group, none of them can adequately assess individual trial performance while remaining specifically sensitive to online control processes (cf., offline processes). One alternative method in which to quantify feedback utilization during goal-directed actions is to evaluate the time required by such processes.

2.5 The duration required for corrective sensorimotor feedback processes

In addition to the mere utility of the general presence/absence of sensory information to reaching performance, the minimum time required to make use of sensory information has been extensively studied as well. Two prominent classes of paradigms have been used for these investigations. An earlier methodology entails withdrawing or perturbing the quality of a source of sensory information and measuring the shortest possible movement time where the manipulation exerts a significant effect on performance (e.g., Woodworth, 1899). The underlying assumption of this sensory withdrawal paradigm is that the use of sensory feedback during action is a time-consuming process. If sufficient time has not elapsed to allow to the use of such sensory
information for the guidance of action, the withdrawal of the sensory information will have no
effects on performance. A more recent methodology entails the alteration of the environment,
often a change of actual or perceived position of either the moving limb or the target during
action, and measuring the latency of the first noticeable correction to the trajectory (i.e.,
compared to no perturbations; e.g., Saunders & Knill, 2003). Within this type of perturbation
paradigm, there have been a number of computational methods used to determine the time
required for online feedback to exert an influence. The following four sections of the current
dissertation reviewed these two overall paradigms, namely the sensory withdrawal and the
perturbation methods, as well as their contributions to the quantification of corrective processes
in the visual and proprioceptive modalities. Working under the assumption that online feedback
utilization is an iterative process, the processing times measured using these methodologies led
to predictions about what latency (ms) or rate (Hz) the examined feedback processes could
effectively function at. Table 2.5.1 reports a summary of the estimates of sensorimotor latencies
and their associated potential iterative rates described in the currently reviewed literature.

Table 2.5.1 Reported sensorimotor feedback loop times, and their estimated iterative rates
frequencies based on the targeted sensory modality and the methodological approach.

<table>
<thead>
<tr>
<th>Manuscript</th>
<th>Modality</th>
<th>Methodology Type</th>
<th>Corrective Latency</th>
<th>Corrective Frequency</th>
</tr>
</thead>
<tbody>
<tr>
<td>Woodworth (1899)</td>
<td>Vision</td>
<td>Withdrawal</td>
<td>428 ms</td>
<td>2.3 Hz</td>
</tr>
<tr>
<td>Keele &amp; Posner, (1968)</td>
<td>Vision</td>
<td>Withdrawal</td>
<td>190 to 260 ms</td>
<td>3.9 to 5.3 Hz</td>
</tr>
<tr>
<td>Carlton (1981)</td>
<td>Vision</td>
<td>Withdrawal</td>
<td>135 ms</td>
<td>7.4 Hz</td>
</tr>
<tr>
<td>Zelaznik et al., (1983)</td>
<td>Vision</td>
<td>Withdrawal</td>
<td>120 ms</td>
<td>8.3 Hz</td>
</tr>
<tr>
<td>Vince &amp; Welford (1967)</td>
<td>Vision</td>
<td>Perturbation</td>
<td>350 to 450 ms</td>
<td>2.2 to 2.9 Hz</td>
</tr>
<tr>
<td>Carlton &amp; Carlton (1987)</td>
<td>Vision</td>
<td>Perturbation</td>
<td>160 to 240 ms</td>
<td>4.2 to 6.3 Hz</td>
</tr>
<tr>
<td>Manuscript</td>
<td>Modality</td>
<td>Methodology Type</td>
<td>Corrective Latency</td>
<td>Corrective Frequency</td>
</tr>
<tr>
<td>-----------------------------</td>
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<td>----------------------</td>
</tr>
<tr>
<td>Saunders &amp; Knill (2003)</td>
<td>Vision</td>
<td>Perturbation</td>
<td>160 ms</td>
<td>6.3 Hz</td>
</tr>
<tr>
<td>Sarlegna et al. (2003)</td>
<td>Vision</td>
<td>Perturbation</td>
<td>320 to 470 ms</td>
<td>2.1 to 3.1 Hz</td>
</tr>
<tr>
<td>Franklin &amp; Wolpert (2008)</td>
<td>Vision</td>
<td>Perturbation</td>
<td>130 to 324 ms</td>
<td>3 to 7.7 Hz</td>
</tr>
<tr>
<td>Saunders &amp; Knill (2005)</td>
<td>Vision</td>
<td>Perturbation</td>
<td>117 to 200 ms</td>
<td>5 to 8.5 Hz</td>
</tr>
<tr>
<td>Day &amp; Lyon (2000)</td>
<td>Vision</td>
<td>Perturbation</td>
<td>125 to 160 ms</td>
<td>6.7 to 8 Hz</td>
</tr>
<tr>
<td>Franklin et al. (2008)</td>
<td>Vision</td>
<td>Perturbation</td>
<td>150 ms</td>
<td>6.7 Hz</td>
</tr>
<tr>
<td>Saijo et al. (2005)</td>
<td>Vision</td>
<td>Perturbation</td>
<td>122 to 127 ms</td>
<td>7.9 to 8.9 Hz</td>
</tr>
<tr>
<td>Smeets &amp; Brenner (1997)</td>
<td>Vision</td>
<td>Perturbation</td>
<td>110 ms</td>
<td>9.1 Hz</td>
</tr>
<tr>
<td>Oostwoud Wijdenes et al. (2013a)</td>
<td>Vision</td>
<td>Perturbation</td>
<td>100 to 150 ms</td>
<td>6.7 to 10 Hz</td>
</tr>
<tr>
<td>Higgins &amp; Angel (1970)</td>
<td>Vision</td>
<td>Perturbation</td>
<td>98 ms</td>
<td>10.2 Hz</td>
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<tr>
<td>Steyvers et al. (1972)</td>
<td>Proprioception</td>
<td>Degradation</td>
<td>78 to 106 ms</td>
<td>9.4 to 12.8 Hz</td>
</tr>
<tr>
<td>Chernikoff &amp; Taylor (1952)</td>
<td>Proprioception</td>
<td>Perturbation</td>
<td>119 ms</td>
<td>8.4 Hz</td>
</tr>
<tr>
<td>Higgins &amp; Angel (1970)</td>
<td>Proprioception</td>
<td>Perturbation</td>
<td>136 ms</td>
<td>7.4 Hz</td>
</tr>
<tr>
<td>Redon et al. (1991)</td>
<td>Proprioception</td>
<td>Perturbation</td>
<td>200 ms</td>
<td>5 Hz</td>
</tr>
<tr>
<td>Franklin et al. (2008)</td>
<td>Proprioception</td>
<td>Perturbation</td>
<td>50 to 150 ms</td>
<td>6.7 to 20 Hz</td>
</tr>
</tbody>
</table>
2.5.1 Visual processing time as assessed through the withdrawal of visual information

It seems inherently obvious that sensory information is important for the implementation of online corrective processes. What is not inherently obvious, however, is the amount of time taken to process and implement the corrective processes. An initial answer to this question was provided by Woodworth (1899), when he examined the relationship between movement duration and accuracy under the eyes-open and eyes-closed conditions. The convergence of movement accuracy when the movement cadence surpassed 140 movements per minute, leading Woodworth to suggest that approximately 428 ms of vision was required for the effects of visual feedback to become apparent in the movement outcomes. A more direct assessment of the duration of movement required to facilitate accuracy of performance was completed by Keele and Posner (1968). These authors investigated the influence of the presence or absence of concurrent vision across a range of movement durations. The availability of vision was manipulated by extinguishing the lights in the room upon the determination of movement onset on half of the trials. It was reported that movements needed to be between 190 and 260 ms for the processing of visual information to take place and facilitate improvements in accuracy. This estimate was close to half the estimate of Woodworth (1899) and this difference was attributed to the fact that Woodworth's participants performed reciprocal aiming movements while participants in Keele and Posner's study performed discrete movements, which did not require time-consuming movement reversals. At a latency of 190 to 260 ms, this early work approximated the maximal rate of visual feedback processing time at approximately 3.9 and 5.3 Hz.

Carlton (1981) furthered the understanding of the amount of time required to utilize visual feedback by withholding visual information until later portions of the movements. Acceleration profiles were investigated beyond the time at which vision was made available and the analysis resulted in two main conclusions: later vision appeared to be important for the maintenance of accuracy, and the time required with vision to utilize feedback mechanisms was substantially less that the earlier estimates of approximately 190-260 ms. Carlton estimated that
vision was only required for approximately 135 ms for the influence of feedback mechanisms to become apparent. This much shorter required time for the use of visual information during action was corroborated by Zelaznik, Hawkins and Kisselburgh (1983), who had participants complete rapid aiming movements to targets in the presence or absence of concurrent visual information. They found differences in endpoint bias and variability between vision present and vision absent conditions, even for movement durations as short as 120 ms. Zelaznik et al. (1983) attributed the differences between their results and those of Keele and Posner (1968) to the fact that Keele and Posner (1968) quantified movement accuracy based on a hit/miss criterion. Indeed, Zelaznik et al. (1983) examined endpoint variability, which proved to be more sensitive. The work of Carlton (1981) as well as Zelaznik et al. (1983) indicated that visual feedback utilization may occur at shorter latencies than previously reported (i.e., 120 to 135ms), and that the frequencies associated with their estimates ranged from 7.4 to 8.3 Hz.

2.5.2 Visual processing time as measured by perturbations of an ongoing action

A second paradigm used to measure the feedback mechanisms latencies is to actively alter the sensory environment in which an individual is acting. When new sensory information is provided during movement, such as when a visually-derived target stimulus is suddenly and unexpectedly moved at the onset or during the completion of an action, a visual perturbation is said to have taken place. By measuring the elapsed time between a visual perturbation and a measurable change in limb trajectory, one can estimate the time required by the central nervous system to make a correction (i.e., the corrective reaction time). Because using vision to complete a goal-directed movement requires the knowledge of the position of one's hand and the position of the target, a visual corrective reaction time could be theoretically estimated through a perturbation of either location. Typically, a visual perturbation of the position of the target of a movement is technically easier to accomplish. However, in virtual environments, where the position of the hand is represented by an LED or a cursor on a screen, the manipulation of hand position can also be accomplished in a relatively straightforward manner.
Early work on the latency for individuals to alter ongoing movements was reported by Vince and Welford (1967). Participants in that study were instructed to complete a line drawing movement in response to a coloured line stimulus. Upon an imperative stimulus, participants, were instructed to complete the task either at a comfortable speed or as rapidly as possible. On some trials, a secondary stimulus was displayed and participants were required to switch tasks, which was to either speed up or slow down the movements. It was reported that the time required to slow an ongoing movement was significantly longer than the time required to accelerate one. The authors identified the change in muscular activation as the likely cause for the discrepancy between switch costs (i.e., approximately 350 ms for slow to fast and 450 ms for fast to slow: see Figure 1 in Vince & Welford, 1967). In a similar vein, Carlton and Carlton (1987) investigated the time to alter an ongoing shoulder flexion movement to a new target that could be either farther or closer than the original target. The authors found that corrections occurred more rapidly when they coincided with compatible muscle activation related to the originally planned movement. That is, if a visual perturbation was triggered during the agonist firing early in an extension movement, the latency of the correction was reduced (~160 ms; see Carlton & Carlton, 1987, Figure 4), relative to the latency of amendments triggered following the planned agonist burst (~200 ms see Carlton & Carlton, 1987, Figure 4). Similar, albeit more subtle, results were found for reversal movements during the firing of the antagonist muscle (240 ms early, 200 ms late; see Carlton & Carlton, 1987, Figure 4). Thus, both the work of Vince and Welford (1967) and Carlton and Carlton (1987) indicated that the timing of a perturbation may influence the response latency of the correction and that this latency may be influenced by the current state of the muscles at the time of the perturbation.

Brenner and Smeets (1997) performed target perturbations by manipulating the actual or the perceived position of the target of a reaching movement, to assess the latency of the associated corrective processes. The perceived target position was manipulated through the implementation of a moving background. Latencies of corrective reaction times were calculated by comparing the velocity profiles of opposing perturbations. Working backward from 200 ms post perturbation, Mann-Whitney $U$ tests were computed for each sample and the first non-
significant comparison was used to determine the corrective latency. The results indicated that individuals who exhibited relatively long movement times (~400 ms for a 40 cm reaching movement) also showed consistent latencies of correction to both target perturbation types, at approximately 110 ms post perturbation (equivalent to 9.1 Hz).

Subsequently, Knill and Saunders (2003) also studied the corrective reaction times to perturbations of hand position, where the position of the hand, represented by a cursor on a screen, unexpectedly shifted during an ongoing action. In one experiment, the position of the cursor was varied in the axis orthogonal to the primary movement axis (i.e., direction) either early (i.e., 25% movement distance) or late (i.e., 50% movement distance) in the movement, and during either slow (i.e., 600 ms movement time) or fast (i.e., 400 movement time) movements. A regression analysis was used to estimate the latency of the correction to the perturbation. Specifically, the authors modelled the aiming trajectories with an autoregressive linear function. This allowed for the moment-to-moment prediction of the cursor position based upon previous time points. When the authors included an additional term representing the influence of the perturbation on finger position, they could isolate the time-point when this additional term explained a significant amount of additional variance in the trajectory.

Regardless of movement speed or position at perturbation, the correction latency was found to be approximately 160 ms (i.e., yielding a potential rate of 6.3 Hz). Saunders and Knill (2005) followed up these experiments and examined the influence of perturbations in both the orthogonal and parallel directions to the axis of movement on corrective visual reaction times (i.e., perturbations to the amplitude and direction of an ongoing movement). Regarding perturbations of movement direction, it was determined that the corrective reaction time could be as low as 117 ms (i.e., 8.5 Hz). Adjustments to changes in movement amplitude yielded a slightly different pattern of results. First, corrective latencies were longer for amplitude perturbations compared to direction perturbations (i.e., 130-200 ms). Second, amplitude perturbations yielded slightly faster corrective latencies for fast movements and for later perturbations. Overall, the shorter corrective latencies reported by Saunders and Knill (2005) as compared to their previous study (i.e., Saunders & Knill, 2003) were attained using an adapted
version of the aforementioned regression technique. In this adapted method, estimates of response latencies were generated from data averaged between participants. In contrast, the earlier study (i.e., Saunders & Knill, 2005) estimated latencies for each participant. Additionally, the latencies in the later experiment were generated using bootstrapping techniques and the modelling of the perturbation weight described above. The authors posited that the differences in corrective latencies they reported were due to an increased sensitivity in their modified regressive methods. Thus, regressive models was suggested to be a promising approach to assessing corrective reaction times.

Another regression-based technique was utilized by Oostwoud Wijdenes, Brenner, and Smeets (2013a), who sought to reevaluate the corrective reaction times to perturbations of targets in either amplitude or direction. Their technique to quantify the corrective reaction time employed regression and extrapolation, as previously proposed in Oostwoud Wijdenes, Brenner, and Smeets (2011). With their technique, the difference in acceleration values across trials was computed between perturbation and no perturbation trials. In the resulting difference plot, the first maximum between 100 and 290 ms post perturbation was identified. The magnitude of the maximum was deemed to determine the intensity of the corrective response. The latency of the response was determined by fitting a line between 20 % and 80 % of the rising portion of the maxima and extrapolating the line backwards to find the intersection with zero acceleration. That zero-crossing was thought to represent the latency of the correction. Using this method, it was determined that comparable corrective latencies between 100 and 150 ms (i.e., between 10.0 and 6.6 Hz) were observed for both amplitude and direction perturbations. In addition, Oostwoud Wijdenes, Brenner, and Smeets (2013b) evaluated this regressive methodology in comparison to two other methods often used in the determination of corrective latencies to perturbations: 1) those based on threshold values (e.g., Veyrat-Masson, Brière, & Proteau, 2010); and 2) those based on confidence intervals, or some measure of variability (e.g., Sarlegna et al., 2003). Typically, threshold methods were described as using discrete values, sometimes based on predefined absolute values including the timing, the proportion, or the magnitude of a specific movement parameter. When comparing trajectories based on confidence intervals, one assesses
two trajectories sample-by-sample and determines when the trajectories are significantly different from one another. These three methods were compared using a simulation of data with distance corrective latencies. Oostwoud Wijdenes et al. (2013b) generated simulated data and determined that the most accurate method was found to be the extrapolation intercept method, when applied to acceleration profiles. Thus, the estimates reported through the use of these specific regression-based methodologies have likely provided the most precise estimates of corrective reaction times to perturbations of movement amplitude and direction. That is, these perturbations are likely corrected at a common latency of approximately 100 to 150 ms.

Overall, recent methodological developments have yielded increasingly more sensitive measures for the quantification of a visual corrective reaction time specifically through the use of regressive and extrapolation techniques. However, in addition to the methodological difficulties in determining the corrective latencies, another factor may have influenced the values attained. The distinction between perturbations of the target compared to perturbations of the representation of the hand should not be overlooked. Specifically, Sarlegna et al. (2003) examined the corrective reaction times of participants to changes in target and hand position in the parallel axis to movement (i.e., amplitude manipulation). Corrective reaction times were calculated by examining the spatial position at every 10 ms of the movement and determining when a perturbation trial differed from a no perturbation trial. When the target position was perturbed, significant corrections were identified at a latency of approximately 320 ms (3.13 Hz). Corrective reaction times for hand location perturbations were found to occur only when the hand position was perturbed against the direction of movement, and at a slightly longer latency (~470 ms; 2.13 Hz). Thus, perturbations of movement amplitude through hand representation perturbations have resulted in longer and less stable estimates of corrective reaction times (e.g., Sarlegna et al., 2003; Saunders & Knill, 2005). One possible explanation for these discrepancies, in addition to the possibility of measurement error raised above, is the idea that the perceived location of one's hand can be represented in multiple sensory modalities. Specifically, in addition to the visual representation of the hand, participants also have a proprioceptive representation of their hand. Importantly, this proprioceptive representation was not targeted in the above-
mentioned studies. Thus, a closer look at the processing times associated with proprioceptive contributions to online control was deemed to be warranted.

2.5.3 Proprioceptive processing time as measured by the degradation of the proprioceptive information during action

The removal of concurrent visual information regarding performance of goal-directed movements has been found to reduce accuracy (e.g., Woodworth, 1899). It has therefore been noted that visual information is highly important to feedback-related processes during ongoing action. There is, however, evidence of feedback processes even in the absence of concurrent visual information (Elliott et al., 1991). That is, the largest number of discontinuities in the trajectories examined by Elliott et al. (1991) were found in the absence of concurrent visual information. Importantly, these discontinuities could theoretically still come about through feedback processes mediated by proprioception (i.e., a sense of the spatial position of their arm). Therefore, the ability of proprioception to contribute to feedback processes and the latencies at which it may act were examined in the following paragraph.

An evaluation of the possibility of proprioceptive feedback mechanisms was undertaken by Steyvers, Verschueren, Levin, Ouamer, and Swinnen (2001), wherein individuals performed bilateral elbow extensions in the presence or absence of tendon vibration. Tendon vibration has been found to elicit illusory motion in the joint associated with the vibrated tendon (see also Goodwin, McCloskey, & Matthews, 1972). In the Steyvers et al. study, individuals performed reciprocal bimanual elbow movements at different rates (i.e., cycle durations ranging from 394 to 1500 ms), and, on half of the trials, biceps tendon vibration was applied. The authors were interested in the effect of movement cadence on the influence of vibration during performance. The rationale was that as movement speeds increase, the control of the movements may shift from a closed-loop to an open-loop mechanism. That is, for the durations investigated, it was posited that the shortest durations, which yield the fastest movements, may be too short for proprioceptive feedback processes to exert their effects. Contrary to this hypothesis, movements of all durations were significantly influenced by the presence of vibration, indicating that
proprinoceptive feedback mechanisms were able to exert influence on performance. The timescale at which the feedback elicited its first effects were found in the first half cycle of even the fastest movement rate (i.e., 197 ms per half-cycle). Divergence between the vibration versus no-vibration trials was estimated to occur between 78 and 106 ms following the initiation of vibration, which provided evidence that the latency of these corrective processes may occur at rates between 9.4 and 12.8 Hz.

2.5.4 Proprioceptive processing time as measured by perturbations of proprioceptive information

Another method to directly assess the proprioceptive system's ability to respond to changes in limb position in a corrective manner is to measure the response of the system in terms of either forces produced by the limb or in the electromyographical (EMG) traces of the primary muscles involved in response to an external load applied to the arm. Chernikoff and Taylor (1952) measured reaction times of individuals in response to the release of their arm from a horizontal position by cutting power to an electromagnet. Reaction times were measured using an accelerometer and the first change in acceleration following the release of the arm was determined by the corrective reaction time. Chernikoff and Taylor (1952) reported that kinesthetic (i.e., proprioceptive) corrective reaction times could occur at intervals as short as 119 ms (8.4 Hz).

Because visual reaction times tend to be faster during than for the initiation of a goal-directed action (see Carlton, 1981), the measurement of corrective reaction times to proprioceptive perturbations during movements could also prove insightful. Redon, Hay, and Velay (1991) directly assessed this question by examining the performance of participants under conditions where tendon vibration was applied at different stages of ongoing movements. Specifically, participants completed fast and slow aiming movements (i.e., MTs ranged from 200 to 800 ms) in the dark, across three experiments. Across conditions, proprioceptive perturbations were implemented via vibration of the antagonist muscle. Vibration was applied at a range of time points across the experiments: 1) throughout the movements (i.e., Experiment 1); 2) for the
first 200, 400, or 600 ms of the movement (Experiment 2: 800 ms MT target); or 3) for only the first or last 200 ms of the movement (Experiment 3: 800 ms MT target). Importantly, vibration was found to exert an influence on performance both when the movement duration was 200 ms and when only the last 200 ms of an 800 ms movement was perturbed. Based on these findings, Redon et al. (1991) concluded that proprioceptive reaction times during action could iterate at latencies no longer than 200 ms (i.e., 5 Hz). Overall, proprioceptive information can be available at latencies which allow for its utilization in the modification of ongoing movements. The nature of this utilization, however, is a matter of contention because the information could be utilized in independently of, or in concert with, concurrently available visual information. The following sections will address these non-mutually exclusive possibilities.

2.6 Evidence for multiple feedback loops in the online control of action

While it may be simplest to talk conceptually about the use of sensory feedback in terms of a singular process, doing so may be an oversimplification. A first source of potential evidence for this assertion is the finding that individuals can make use of a range of distinct sensory information to correct an ongoing goal-directed action. Important contributions to this line of research have come from experiments wherein the manipulations of sensory modalities have been relatively isolated.

2.6.1 Corrective processes that may not require the use of proprioceptive information

Evidence for a unique feedback mechanism was first identified by Pélisson, Prablanc, Goodale, and Jeannerod (1986). They evaluated individuals' ability to correct movement trajectories to perturbations of target position employed during saccadic suppression, which is the period during an eye movement where visual perception is significantly reduced (e.g., Bridgeman, Hendry, & Stark, 1975) and when vision of the hand was unavailable. Notably, it
was found that although participants were unaware of the target perturbation, they were able to integrate the new target location smoothly into the trajectory. Participants were therefore making use of a seemingly automatic corrective process, which quickly made use of the change in the visual environment to attain movement accuracy. Prablanc and Martin (1992) followed this experiment with a similar paradigm and actively manipulated vision of the hand, and found similar performance regardless of the visibility of the hand. The sensory nature of the feedback process was further isolated by Bard et al. (1999), who assessed a deafferented participant within a comparable paradigm. This participant (i.e., patient GL) suffered from a severe loss of proprioception below the nose resulting in the abolition of touch, vibration, pressure, kinesthesia and reflexes in all four limbs (e.g., Forget & Lammarre, 1987). Notably, the patient was able to complete fast corrective processes, without concurrent vision of the hand or awareness of the target perturbation (Bard et al., 1999). Therefore, the feedback mechanisms associated with the fast corrective processes observed in these studies can function adequately without concurrent sensory information from the proprioceptive system of the moving limb. The mechanisms by which this feedback process operated were likely through the use of visual information (feedback mechanisms; e.g., Keele & Posner, 1968) and internal models (i.e., feedforward mechanisms; e.g., Miall, Weir, Wolpert & Stein, 1993).

It was further demonstrated that corrective processes can be completed in the absence of proprioceptive information regarding the position of the hand (Sarlegna, Gauthier, Bourdin, Vercher, & Blouin, 2006). In their study, a deafferented patient (i.e., GL) corrected ongoing trajectories to target position perturbations during reaching movements without online vision of the moving limb. Performance on the task was similar regardless of whether the perturbed target remained illuminated, briefly flashed on or off, or was implied via an auditory tone presented at movement onset. GL was able to correct the ongoing movements but was unaware of the form of the corrected trajectories, which differed from those of controls. Specifically, the abnormal form of GL's trajectories did not exhibit direct corrections to the new target locations as observed in control individuals; rather, the corrections unfolded in a staircase-like manner (i.e., first moving horizontally, then continuing forward). Therefore, the feedback or feedforward processes
underlying these corrections were likely at least in part under non-voluntary, automatic control. Also, because the trajectories differed in form between GL and control participants, it is likely that proprioceptive information contributes to the corrective mechanisms when available. Importantly, however, the feedback processes demonstrated by GL aided performance in the absence of afferent (i.e., proprioceptive) feedback from the moving limb.

2.6.2 Corrective processes that may primarily make use of proprioceptive information

In addition to evidence of feedback mechanisms which can function in the absence of proprioceptive input, there is also evidence of the existence of proprioceptive feedback mechanisms in goal-directed action. Gosselin-Kessiby, Kalaska and Messier (2009) reported that when completing a card-posting task without concurrent visual feedback, and only a proprioceptive reference, both blind-folded sighted and blind individuals performed online corrections to their trajectories (see also Gosselin-Kessiby, Messier & Kalaska, 2008 for another example of blindfolded participants). Evidence for corrections were present across both blind and blindfolded participants even when they attempted to align their reaching arm (orientation of the card to be posted) prior to initiating the movement. Additionally, no significant differences were observed between congenitally blind (n = 7) and postnatally blind participants (n = 5; age of onset of blindness range 6-27 years, M = 16.4 years). Therefore, there appears to be a functional mechanism through which feedback-based control can be implemented with the direct use of proprioceptive information alone.

2.6.3 Unique latencies of corrective processes between sensory modalities

Another source of potential evidence for the possibility of multiple feedback mechanisms is the finding that perturbations of visual and proprioceptive information tend not to result in equivalent corrective reaction times. Higgins and Angel (1970) had participants complete two tasks. There was a visual tracking task, whereby a participants followed a target line with a cursor line, controlled by a joystick. Also, there was a proprioceptive reaction time task, where an unexpected force was applied to the joystick in one of two directions and the participants were
required to counter the force on the joystick as quickly as possible. Corrective reaction times to erroneous movements with visual feedback were found to be consistently shorter (98 ms; 10.2 Hz) than proprioceptive reaction times while maintaining a posture (136 ms; 7.3 Hz).

To assess the nature of feedback processing in the central nervous system, Franklin, So, Osu, and Kawato (2008) pitted concurrent visual and proprioceptive perturbations against each other. This joint perturbation was employed by representing the hand position with a cursor while individuals made reaching movements by moving a robotic arm. The visually-determined position of the arm could be independently manipulated/perturbed from the proprioceptive information. The proprioceptive information was perturbed by applying forces on the moving hand through the robot arm. These two perturbations were simultaneously applied either in the same direction or in conflicting directions. Regardless of the presence or direction of the visual perturbation, consistent modifications (i.e., as measured by changes in force production) were present in response to the proprioceptive perturbation at latencies between 50 and 150 ms (i.e., potential rates of 6.7 to 20 Hz), while the responses to visual perturbations occurred after approximately 150 ms (6.7 Hz) in the opposite direction to the visual perturbation, regardless of the direction of the proprioceptive perturbation.

The possibility of multiple feedback processes through the examination of corrective reaction times to both visual and proprioceptive has garnered support. If these two modalities exerted their influence through a common feedback mechanism or loop, then the latency and/or the rate at which they exerted their influence would be expected to be comparable. Because the latency feedback utilization between the two sensory modalities tends to be different, a multiple processes account provides a logical explanation.

2.6.4 Evidence for multiple feedback mechanisms utilizing visual information: Fast and slow processes

In addition to the potential for differential feedback mechanisms across sensory modalities, there is evidence for the utilization of multiple feedback mechanisms within vision. As stated previously, corrective reaction times to perturbations of visual information are often
found to occur at latencies shorter than normal reaction times for simple movements (Carlton, 1981; Meyer et al., 1988; cf., Sarlegna et al., 2003). Because these fast acting corrective processes occur at latencies shorter than normal visual reaction times, visuomotor correction processes are likely different from visuomotor preparation processes. Also, visuomotor correction processes could be further segregated into separate sub-processes.

Evidence for a distinct, fast corrective process has been provided by Pisella et al. (2000), who examined the performance of an individual with optic ataxia (i.e., patient I.G.) and control participants with a visual perturbation paradigm. During reaching movements, the target was sometimes spatially shifted and the participants were instructed respond to the perturbation by either correcting the ongoing movement or stopping the ongoing movement. In addition, the perturbations were defined through a change in target location or by a colour switch of two isoluminant coloured stimuli. Control participants smoothly corrected ongoing movements to changes in the location perturbation. In the stop condition, control participants exhibited evidence for automatic corrective processes. Even though they were not instructed to correct the ongoing movement, their trajectories veered in the direction of the perturbation prior to stopping. Conversely, I.G. exhibited a reduced ability to correct ongoing movements in response to location perturbations (see also Rossetti et al., 2005), and showed no evidence for automatic responses in the location stop condition. When the perturbations were defined by colour shifts, control participants were able to correct their ongoing responses, but in a slower more deliberate manner (see also Cressman, Franks, Enns & Chua, 2006). When required to stop an ongoing response, control participants exhibited no evidence for automatic correction in the trajectories. In contrast to the location-based perturbations, I.G. exhibited comparable performance to controls in response to the colour shift perturbations. Additionally, similar deficits to location perturbations had been reported by Desmurget et al. (1999) in neurologically-intact individuals when applying transcranial magnetic stimulation that were deemed to target the area associated with optic ataxia (i.e., PPC). Therefore, the fast automatic corrective processes exhibited by the neurologically-intact individuals and the slow voluntary corrective processes exhibited by the neurologically-intact as well as the individual with optic ataxia may represent unique feedback
mechanisms governed by separate processes (see also Rossetti et al., 2005). Alternatively, however, the absence of fast corrective processes to colour-based stimuli has also been proposed to be due to a slower transduction of information in the colour-based parvocellular neural pathway as compared to the luminance driven magnocellular neural pathway (Kane, Wade, & Ma-Wyatt, 2011). Additional support for this notion was found by Veerman, Brenner and Smeets (2008), who found modulations/variations of visual corrective reaction times of approximately 50 ms, based on the properties that defined the visual feature (slower for colour and texture relative to luminance, size, shape or orientation). Importantly, however, these findings cannot discount the performance differences observed regarding the location-based perturbations.

Thus, there may be at least two ways in which ongoing visual information can be utilized during action: slow deliberate voluntary corrections, and fast automatic corrections. The presence of this automatic feedback mechanism during action has received further support from a number of studies. First, when perturbations are small enough that a correction would not be necessary to ensure the successful attainment of the target, automatic corrections have been shown to be generated anyway (Veyrat-Masson, et al., 2010). Also, corrections were implemented when a secondary perturbation cancelled the need for a correction (Brière & Proteau, 2011). Further, Day and Lyon (2000) found, with neurologically-intact participants, that responses to target jumps could occur at either a short (i.e., 125-160 ms) or long latency (i.e., > 160 ms). Importantly, the short latency responses were not under voluntary control, whereas the long latency responses were. This two tiered response has been replicated by Franklin and Wolpert (2008; Experiment 1; see also Cressman, Cameron, Lam, Franks, & Chua, 2010; Franklin, Reichenbach, Franklin, & Diedrichsen, 2016), who instructed individuals to voluntarily adjust an ongoing movement in the direction of a visual perturbation. These authors found consistent short latency responses acting at a latency between 130 and 230 ms (i.e., 4.3 to 7.7 Hz) in the direction compensatory to the perturbation, in advance of the voluntary response, which occurred in the instructed direction, at an average latency of 324 ms (i.e., 3.1 Hz). Therefore, visual feedback during goal-directed action appears to function with at least two distinct processes, a fast automatic process, and a slow voluntary process.
More recent work has challenged the idea of the automaticity of the fast corrected process described above. Therefore, the independence of the processes has been called into question. Cameron, Cressman, Franks and Chua (2009) proposed that the automaticity of the fast corrective processes are partially under voluntary control. They came to this conclusion through the inclusion of an additional condition to those used by Pisella et al. (2000), namely an ignore-the-perturbation condition. That is, when participants were instructed to ignore the perturbation and complete the pointing movement as planned, the influence of the target jump had a lesser effect on performance than in a location-stop condition. This suppression has been subsequently found to require cognitive resources because one's ability to suppress the automatic response was lessened when one had to concurrently monitor a stream of numbers for repeated digits (McIntosh, Mulroue, & Brockmole, 2010). In contrast to the inhibition of the short latency response, Cameron, Cheng, Chua, van Donkelaar, and Binsted (2013) explicitly tested the possibility of facilitation of corrective responses by manipulating the predictability of location perturbations. They found that foreknowledge about the likelihood of a perturbation had no influence on the latency of the corrective response. Therefore, it appears that the automatic corrective responses already function at a rate near their maximal effective physiological limit. That is, the rate of functioning of these processes could be hitting a ceiling effect such that corrective processes cannot be facilitated beyond this rate. Therefore, while there is evidence to suggest that the automatic corrective processes can be suppressed cognitively, there was little evidence that they could be facilitated. An important consideration from these experiments is that the latencies of the automatic corrective processes were relatively stable when they were not inhibited.

Nevertheless, there appears to be at least two ways in which ongoing visual information can be utilized during action. There are discrete voluntary alterations in the trajectory and such corrections and automatic corrections. Notably, the discrete corrective processes appear to function at a longer latency than the automatic corrective processes. Further, it is possible that such correction mechanisms can be explained by qualitatively different visuomotor processes.
2.6.5 Evidence for multiple feedback mechanisms utilizing visual information: Multiple automatic processes

Although one could come to the conclusion that there exist a voluntary and an automatic mode by which feedback is utilized in the control of ongoing movement, recent evidence points to an even more complex organization with the possibility of additional feedback processes. One such example was the finding that ongoing aiming movements can be perturbed by altering the background sensory information during action, without altering the specific hand or target location (Proteau & Masson, 1997). That is, when only the background (i.e., not the target) shifted in the opposite direction of the cursor displacement at movement onset, participants exhibited a significant target undershoot (see also Brenner & Smeets, 1997). This indicated that visual information about the absolute location of the target or the hand could not overcome the effect of the surrounding visual information. The authors proposed the relevant information was garnered from the relative motion between the background and the cursor, which was related to a limb velocity estimate. While velocity is by its nature, inextricably tied to displacement and time, velocity information by itself can be independent from absolute positions. Indeed, real-time limb velocity has been proposed to play an important role in the control of limb movements (e.g., Kennedy, et al., 2015; Tremblay & de Grosbois, 2015; Tremblay et al., 2017; Tremblay et al., 2013). Therefore, sources of sensory information other than the absolute position of the hand and/or target may be utilized to implement visuomotor processes, which has been directly tested.

Although feedback-based corrective processes have typically been associated with spatial regulation of the hand and target positions, the modulation of action based on additional factors could represent additional distinct feedback mechanisms. Grierson and Elliott (2008) sought evidence for multiple forms of online control during reaching by combining a target position perturbation with a physical perturbation of hand position through the use of an air compressor to apply forces to the moving hand. Notably, both perturbation types were delivered at the onset of the movements. They found that corrections to target perturbations became evident in the kinematic measure following peak velocity, while the corrections of the hand position perturbations were apparent earlier in the trajectory. When the perturbations were applied
together, their influences interacted, and the authors suggested that the corrective processes associated with the two types of perturbation were likely occurring in parallel during at least a portion of the trajectory (i.e., each process negating or amplifying the other).

Further evidence for feedback-based control in the early phases of movement was found by Caljouw, van der Kamp, Lijster and Savelsbergh (2011). They isolated early control processes by having participants perform goal-directed hitting motions of a ball to reach a visual target at a specified distance. The authors manipulated the configuration and distance of a Müller-Lyer illusion during the hitting motion. The wings-out and wings-in configurations only exerted an influence on performance when the location of the target stimulus was also spatially perturbed. The authors argued that the spatial perturbation was facilitating the involvement of a control process different to that of the stationary stimulus during the early stages of the movement. Likewise, Grierson and Elliott (2009) also sought to find evidence for early control as an additional feedback process to spatial hand-target feedback mechanisms using the Müller-Lyer illusion. They employed two perturbations. The first, based on the Müller-Lyer illusion, resulted in relatively late changes to ongoing trajectories. The second, a moving background perturbation, resulted in relatively early trajectory modifications based on perceived velocity of the moving limb. Thus, in accordance with the findings of Caljouw et al. (2011), early control processes appear to be relatively insensitive to the influences of the Müller-Lyer illusion. When Grierson and Elliott (2009) applied both the Müller-Lyer illusion and the moving background perturbations concurrently, the influence of each of the perturbations was additive and did not interact. This lack of an interaction indicated that the modification elicited by each of the perturbations came about through two unique mechanisms. Therefore, there is some evidence that unique visuomotor mechanisms may exert their influence on a trajectory at different portions of the movement.

The automaticity of this early corrective process to changes in background motion has also been investigated. Specifically Saijo, Murakami, Nishida, and Gomi (2005; Experiment 2) instructed individuals to complete reaching movements to a target across a textured background. On some trials, the background texture shifted to the right or the left. Participants were also
instructed to either correct in the same direction as the moving background, or to correct in the opposite direction as the moving background. Importantly, changes in acceleration were measured at a relatively short latency (i.e., between 122 and 127 ms) in the direction of the moving background, regardless of instruction set. Thus, similar to target location perturbation paradigms (Day & Lyon, 2000), moving background perturbations elicit automatic short latency responses, which exert an influence on performance even when participants are instructed to react in a direction opposite to the direction of the perturbation.

This multiple processes view was formally presented within the multiple processes model (Elliott et al., 2010). In this model of goal-directed action, movements are thought to be completed in a manner consistent with previous incarnations of two-component models of reaching (e.g., Meyer et al., 1988; Woodworth, 1899). That is, movements tend to start with a relatively ballistic early phase followed by a slower, homing-in phase. Contrary to the assertion laid out in classical two-component models, which predicted a singular, late acting feedback mechanism, the multiple processes model predicts a minimum of three independent and potentially concurrently acting feedback mechanisms. The first two already mentioned are the late control of the hand, based on the spatial relations between the hand and the target (i.e., hand-target regulation), and early control of the hand based on the perceived sensory consequences of the ongoing trajectory (i.e., impulse regulation). The third proposed control process was not as elaborately described as the others and could possibly take place throughout the trajectory. Such processes would come about through the monitoring and adjusting motor outflow based on a feedforward mechanism, using forward internal models (i.e., outflow-control processes; e.g., Desmurget & Grafton, 2000). Such a mechanism would not be tied to slow sensory-based feedback processes and could result in fast, fine-tuned trajectory profiles (e.g., Miall & Wolpert, 1993). Corrections based on forward models bypass the sensory delays and thus could theoretically function at a much higher rate. Ultimately, based on this model of goal-directed aiming, there are theoretically three different online control processes (outflow-control, impulse-regulation, and hand-target regulation processes). Central to the purpose of this dissertation, each process potentially contributes to the accuracy of ongoing movement at its own rate or frequency
of iteration. More importantly, these mechanisms most likely rely on more than just visual inputs.

2.7 Evidence for fewer, multisensory feedback mechanisms

Although there is evidence that the control of ongoing voluntary action is potentially mediated by several feedback loops, there are alternative, yet non mutually-exclusive, explanations. The information made available to the sensorimotor system during action may instead be combined and integrated to optimize the trajectory amendments. The manner in which multisensory information may be combined has been proposed to occur in a statistically optimal fashion (e.g., Ernst & Banks, 2002; Ernst & Bülthoff, 2004). That is, by combining sensory signals to generate the estimate of a sensory event and integrating different estimates, one can theoretically achieve a more precise overall estimate of the sensory event than any individual estimate alone.

2.7.1 Basic principles of multisensory integration

Ernst and Banks (2002) argued that the relative weighting of multiple sources of sensory information leading towards a singular outcome or judgment could come about through a maximum likelihood estimation process, whereby the weight of each information source is modulated by the inverse of its variance. This work expanded upon earlier work suggesting that the combination of sensory cues within a modality likely functions in this manner (e.g., Blake, Bülthoff, & Sheinberg, 1993; Ernst, Banks, Heinrich, & Bülthoff, 2000; Knill & Saunders, 2003; Landy, Maloney, Johnston, & Young, 1995). Essentially, the source of information with the lower variability will lead to a proportionally greater influence on the final judgment or outcome. Participants completed a size judgment visual-haptic task, whereby they were asked to report which of two stimuli were taller (i.e., visual height). The variability of the visual estimates was actively manipulated through the implementation of visual noise. As the visual noise level increased, the combined estimate became more similar to the haptic-alone estimates. Ernst and Bülthoff (2004) suggested that in order for sensory information to be integrated in a statistically
optimal fashion, both estimates must be redundant. That is, the estimates must be represented in the same units and coded in the same frame of reference.

More recently, however, it has been determined that receiving multiple estimates of information in a comparable frame of reference does not ensure a statistically optimal integration of the information. Notably, Gepshtein, Burge, Ernst and Banks (2005) examined visually- and haptically-derived estimates of a spatial extent (i.e., distance between two stimuli) when the information came from spatially-coincident and spatially-discrepant locations. When the sensory information from the two modalities was provided in a spatially coincident configuration, evidence for integration of signals was found. However, if the information was provided in a spatially discrepant configuration (i.e., spatially separated), the precision of the estimates was significantly reduced. Thus, it appears that, at least in terms of performance of perceptual tasks, multiple sources of sensory information can be integrated into singular estimates in a statistically optimal fashion although this is not always the case. Moreover, it is less clear how such multisensory combination and integration takes place during goal-directed action.

2.7.2 Multisensory integration during action

While it seems likely that sensory information can be integrated into singular estimates in a statistically optimal fashion for perceptual tasks, there is also evidence for integrative processes in the production of goal-directed action. It has been proposed that when sensory information is utilized to plan goal-directed arm movements, a series of transformations occur which convert hand and target location information into the same reference frame as the visual information (Blouin, Saradjian, Lebar, Guillaume, & Mouchnino, 2014; Crawford, Medendorp, & Marotta, 2004). Thus, the sensory information utilized in the production of goal-directed action is likely organized in a manner which could theoretically make use of process of multisensory integration as outlined by Ernst and colleagues (Ernst & Banks, 2002; Ernst & Bültthoff, 2004).

Additionally, there is evidence that altering the ambiguity of visual information directly influences feedback-based online control processes during reaching. Körding and Wolpert (2004) varied the spatial ambiguity of a cursor during a perturbation of visual information
regarding the spatial location of the hand during reaching. Ambiguity of the visual position of the
cursor was induced by representing the cursor with two dimensional Gaussian profiles of
increasing width. Increases in ambiguity should conceivably result in increases in the variability
of the spatial estimate. Accordingly, the authors reported that increases in ambiguity resulted in
decreases in the amount of correction to the perturbation. Because the perturbation was visual in
nature and the proprioceptive signal was maintained at normal levels, the observed changes in
trajectory corrections could conceivably come from a shift in the weighting from vision towards
proprioceptive inputs. Thus, these findings provide evidence for the existence of multisensory
integrative processes contributing to the control of ongoing movements.

In contrast, there is also evidence that the act of moving alters the ability of individuals to
perform multi-sensory integration. Tremblay and Nguyen (2010) revealed that audio and visual
signals were integrated to a lesser extent during the high-velocity portions of a limb trajectory.
More recently, Loria, de Grosbois, and Tremblay (2016) reported sub-optimal integration of an
audio-visual cue for the accurate completion of a high-velocity flinging movement. Thus,
although there is evidence that multisensory integration can occur during movement, the
optimality of this use has been called into question.

A final hurdle for an integrative approach to sensory processing during movement stems
from the reported discrepancies in the timings of sensory information coming from different
modalities. Specifically, receiving information at different latencies could pose a computational
problem for multisensory integration. This potential difficulty was addressed by Cameron, de la
Malla and Moliner (2014). They simulated data whereby visual and proprioceptive estimates of
hand location during goal-directed movement were received at different latencies. The presence
of any temporal lag, regardless of sensory modality logically resulted in an inherent
underestimate of distance travelled by the limb at any given instance of time. The difference in
latency between sensory modalities resulted in different spatial estimates of limb location, and
the perceived position of the hand was determined by a weighted statistical process. To correct
for the delayed sensory information, the authors suggested that a constant shift in perceived
position is applied, which allows for an accurate representation of position in real-time. When
vision is occluded during action, this shift induces an overestimation of limb amplitude along the trajectory. Notably, this bias was predicted to increase with increases in velocity and sensory delay. The model fitted reasonably well when compared to previously findings in the literature that described the overestimation of arm position during movement in the absence of vision. Thus, sensory processing from multiple modalities, received at different latencies, may still be incorporated into singular feedback mechanisms using statistical approaches to multisensory integration.

2.7.3 Possible reconciliation between multiple processes and multisensory integration during action

Even though the multiple processes model of Elliott et al. (2010) has intuitively focused on the notion of multiple feedback processes, some facets of the theory are also consistent with some evidence for multisensory integration as well. Specifically, Grierson and Elliott (2008; 2009) posited that the influence of the early form of control, more recently known as impulse regulation, could be elicited through vision (e.g., moving background) or proprioception (e.g., air compressor force perturbations). Grierson, Lyons, and Elliott (2011) combined these two perturbations of early control and did not find additive influences of the perturbations on control. The moving background perturbations resulted in compatible main effects on constant error (i.e., a reduction in amplitude with a backward moving background) but did not influence any other variables. Conversely, performance on all kinematic variables was significantly influenced by the air compressor perturbation. Importantly, there were no interactions found between the perturbation types. Thus, participants responded in a manner consistent with a multisensory approach and relied more upon the physical (i.e., visual and proprioceptive) perturbation for corrective processes than on the illusory, visual perturbation. Ultimately, this finding illuminates the possibility of multiple parallel processes and multisensory integration both exerting influences to the utilization of feedback for the online control of goal-directed movements. Although various methods have been employed to support the many theoretical contributions to online control processes, methodologies for the quantification of such individual contributions to reaching performance is warranted.
2.8 Measurement of iterative signals: Frequency domain analyses

Traditionally, kinematic analyses of goal-directed action have typically focused on two measurable aspects of the action, namely the spatial and temporal features (see Section 2.3). These approaches have provided a wealth of information regarding the utilization of sensory feedback and the control of voluntary action. However, certain issues, such as the quantification of said feedback utilization and the specific rates at which feedback is utilized have remained difficult questions to answer. The continued difficulty stemmed in part from the notion that the feedback-based corrective processes are not always distinguishable through traditional examinations of kinematic profiles. That is, because corrections may occur in an overlapping fashion (Elliott et al. 1991), one cannot simply look for discrete discontinuities in profiles to ascertain the extent of online control processes. Consequently, alternative methodologies are required to elucidate more directly the use of feedback-mechanisms in goal-directed action. A potentially useful tool which may shed new light on the matter comes from signal-processing in the form of frequency domain analyses.

2.8.1 Frequency domain analyses: Basic concepts and methodologies

Frequency domain analyses employ data collected as a function of time (i.e., how long the process takes) and represents it as a function of frequency (i.e., how often the process takes place in each unit of time). Any measure collected over time can be converted into a frequency representation, be it the volume of a loud-speaker, the changing pitch of the song of a vocalist, temperature changes throughout the day, or the trajectory of a goal-directed arm movement. The process of converting information collected with respect to time, to a frequency representation, is known as the Fourier Transform. The Fourier Transform decomposes a signal into a combination of sine and cosine waves of different oscillation rates. Note that sine and cosine of the same oscillation frequency are simply phase shifted copies of one another. The relative contribution of each frequency to the composition of the time-dependent data can be estimated by combining the contributions of all the sine and cosine waves at each specific frequency. When the frequency data is represented in this manner, it is known as a power spectrum. By examining a power
spectrum function (i.e., spectral analysis), one can determine which frequencies are contributing more to the waveform than others. Importantly, if multiple waveforms oscillating at different frequencies are added, the additive relationship extends to the frequency domain as well (e.g., Brigham, 1974).

The ease of computation of power spectrum was greatly improved with the development of the Fast-Fourier-Transform (Cooley & Tukey, 1965). This empowered researchers to employ this technique in a wide array of contexts (see: Bracewell, 1986; Brigham, 1974). The utility of Fourier Transforms is exemplified in its widespread use in a wide range of data types. It can be applied to individual streams of data as well as average traces of data.

Direct comparisons of multiple power spectrum functions can be made by calculating the proportional frequency make-up of a waveform. That is, the power spectra can be normalized such that informative comparisons between signals of different magnitudes can be made. In addition to the contributions of oscillations of different latencies, a coherence analysis can be used to assess the relationship between multiple time-locked signals at particular oscillation frequencies (e.g., Bloomfield, 1976; Warner, 1998). Coherence analyses can be used to determine the percent of variance of a particular oscillation frequency in one signal given its presence in another time-locked signal. That is, coherence analyses can estimate the strength of a relationship between two signals at a given frequency. Thus, Fourier Transform analyses, and the computation of power spectra, are useful tools in the analysis of signals for the purposes of isolating iterative contributions. Therefore, the analysis of iterative contributions to movements brought about by feedback utilization could therefore be a fruitful application of Fourier transforms and spectral analysis.

2.8.2 The application of frequency domain analyses to goal-directed actions: Manual tracking behaviours

Converting the kinematic trajectories from a time-based representation to a frequency-based representation could prove insightful. This is because the use of feedback may involve a specific consistent latency. The presence of a continuous or pseudocontinuous feedback loop
should result in an iterative or wavelike influence on a trajectory. If multiple iterative processes significantly contribute to the composition of a trajectory or waveform, their influence will be apparent in the power spectrum function of that waveform. Importantly, these differences will be apparent in the data because the rate limiting factor in the corrective processes is the duration of the feedback loops (Miall, Weir, & Stein, 1985; cf., Craik, 1947).

A direct application of frequency domain analyses in the quantification of feedback utilization during goal-directed movement was provided by van Galen, van Doorn, and Shomaker (1990). They computed power spectra for acceleration profiles of participants completing a line drawing task and argued that afferent feedback loops (i.e., those utilizing incoming sensory information) should be apparent in the power spectrum at frequencies less than 8 Hz (i.e., 8 oscillations per 1000 ms or 125 ms per oscillation). In their study, adduction movements exhibited less spectral power than abduction movements in the 1-4 Hz range. It was argued that in a drawing task adduction movements are better practised and require less feedback and/or feedforward processes to ensure accuracy. Therefore, greater power in abduction movements could represent the presence of, or an increase in, feedback and/or feedforward processes. Thus, this seminal experiment provided evidence that relative feedback utilization can be attained through frequency analyses.

This type of logic and analysis was expanded to reciprocal goal-directed reaching tasks by van Donkelaar and Franks (1991). Participants in their study performed reciprocal aiming movements to a remembered pattern of a cursor, by flexing and extending at the elbow joint. These movements were produced at a control pace (1.1 Hz), slowly (.45 Hz) or as fast as possible (i.e., participant dependent; 3.6 to 6.3 Hz). Power spectra were estimated across conditions from the acceleration profiles of the movements. For both the slow and control conditions, the greatest proportion of power was found to fall in the 0 to 12 Hz range, with negligible power at higher frequency ranges (i.e., 20 to 30 Hz). This range of 0 to 12 Hz coincided with the frequency range that van Galen et al. (1990) attributed to corrective processes. The as-fast-as-possible condition, however, expressed higher power at both the lower (i.e., 0 to 12 Hz) and higher (i.e., 21 to 30 Hz) frequency ranges. The increase in power at the lower
frequencies for the fast movements was not expected because there was likely not enough time for much feedback-based corrections to occur (i.e., segment movement time of approximately 100 ms). Thus, the relationship between movement speed and frequency power was not significantly informative regarding the quantification of the relative use of feedback in this case. However, if one acknowledges that some proprioceptive-based feedback processes may occur at shorter latencies than visual corrective processes, the fast condition may have benefit from feedback despite the short movement times. This hypothesis could explain the increased power in the fast movements in the 0 to 12 Hz range, which was unanticipated by the authors. In addition, an important methodological aspect of the van Donkelaar and Franks (1991) study was the fact that the movements were made in response to a remembered cursor sequence. That is, the target of the ongoing movement was never concurrently available to the participants. Thus, it is not clear if the extent to which online control mechanisms were reflected across the experimental conditions. The study did show, however, that changes in performance on reaching tasks are quantifiable using frequency analyses.

To directly assess the influence of feedback on frequency power spectra during action, careful consideration is needed in the experimental conditions to be compared. Sosnoff and Newell (2005) conducted a study directed at examining the influence of the intermittency of visual information and the magnitude of force applied on the power spectra of individual's ability to continuously control a cursor. Participants performed isometric contractions against a force transducer to manipulate the height of a cursor, corresponding to one of three normalized force levels. The cursor position was made available to the participants at a range of visual intervals (i.e., 0.2 to 25.6 Hz or once every 5000 ms to 39 ms). As visual information was provided at increasing rates, the frequency power spectra became increasingly broad (i.e., a greater contribution of a larger range of oscillation frequencies). This broadening stemmed primarily from decreases in the power spectra below 4 Hz. However, with increasing rates of visual feedback, there were also significant decreases in spectral power up to 12 Hz. Additionally, similar to the findings of van Donkelaar and Franks (1991), responses requiring more force tended to result in greater overall power across the measured spectrum. Sosnoff and Newell
(2005) concluded that the tendency to broadening frequency power spectra with increasing visual feedback rates was evidence for multiple continuous control processes, acting at different latencies. Such a notion is compatible with the contemporary multiple processes model of online control (Elliott et al., 2010).

Stitt and Newell (2010) followed-up on the above studies and generated a four-component model for the maintenance of isometric force in frequency power spectra. The four proposed components were: 1) a peak around 1 Hz representing task-related activation, 2) a peak around 12 Hz, representing physiological tremor caused by central activation, 3) between these peaks a 1/f noise-like process (e.g., see Slifkin & Eder, 2014 for an explanation) with a negatively sloped area, which could represent the multiple time-scales of feedback loops, and 4) a low level white-noise contribution (i.e., baseline and constant level across all frequency bands). This model of isometric force production in the frequency power spectrum was able to quantify performance changes in individuals as they age (i.e., flattening of the 1/f region with age). It also allowed for a more detailed description of the within-trial variability, which is not possible in the time domain. Thus, work employing frequency analyses appears as a useful alternative method to quantifying differences in behaviour and, in particular, feedback-related processes taking place during goal-directed actions.

This attribution of specific frequencies to the control of visuomotor feedback processes has been demonstrated by McAuley, Farmer, Rothwell, and Marsden (1999). The authors evaluated the ability of participants to simultaneously track a horizontally sinusoidally moving target with both their finger and their gaze. The angle between the index finger and the hand was measured with a goniometer and controlled the motion of a cursor on a screen (i.e., the metacarpophalangeal joint of the index finger). In some conditions, the participant was asked to track a moving target with the cursor. Also, the participant was either asked to track the target with their eyes or maintain their gaze on a fixation point. The target pattern to be tracked was made visible either continuously or intermittently (i.e., visible only at the extreme edges of the sinusoidal pattern). Likewise, the cursor representing the angle of the metacarpophalangeal joint was displayed continuously, intermittently, or not at all. Spectral analyses of the finger angular
velocity trajectories resulted in peaks at approximately 8 Hz, as well as increased power in the 3 Hz region. In the latter region, the low frequency power was deemed to be attributable to the sinusoidal target pattern's often diminished discernible peaks. Regarding the eye movements, analyses sometimes revealed peaks in the power spectra around 3 and 10 Hz. When examining the participants that exhibited peaks at approximately 3 Hz in both tasks with a coherence analysis, the authors found evidence for synchronicity between finger and eye only when concurrent vision of both the finger and target were available. The authors posited that this coherence in the presence of concurrent visual feedback of the finger angle was evidence for a oscillation relating to common visuomotor feedback loops. Because the coherence between tasks around 10 Hz was found to not be dependent upon the availability of visual feedback, it therefore likely represented a common central oscillation unrelated to visuomotor feedback mechanisms. The authors attributed the 3 Hz oscillation to visual feedback mechanisms, but unfortunately, some caveats must be taken into consideration when interpreting their findings.

The findings of McAuley et al. (1999) demonstrated the capability of frequency analyses to discern visuomotor feedback processes from the trajectories of goal-directed actions. Unfortunately, the authors did not detrend the target oscillation from their signal before computing power spectra. Consequently, the contamination of the target motion of the power spectra may have attenuated peaks at 3 Hz, which the authors later implicated in feedback-related processes. Still, the 3 Hz feedback related oscillation reported coincides with the slower voluntary feedback mechanisms described above (~300 ms; see Section 2.5.4). Although the coherence of the 10 Hz oscillation was not dependent on concurrent visual feedback, the oscillation time associated with this rate (i.e., ~100 ms) does approximately coincide with fast corrective mechanisms associated with goal-directed movement (see Section 2.5.4). The 10Hz oscillations could therefore also be associated with feedback-related processes, reliant upon non-visual sources of information or following integration with visual information.
2.8.3 The application of frequency domain analyses to goal-directed actions: The analysis of trial-to-trial variability

In addition to identifying feedback processes from the trajectories of movements, frequency analyses have also been used to evaluate feedback usage by examining trial-to-trial variability (i.e., in a similar vein to the correlational analyses described in Section 2.3). Specifically, Miyazaki, Kadota, Kudo, Masani, and Ohtsuki (2001) examined trial-to-trial variability and correlations in both time and position at kinematic landmarks using fractal analysis (i.e., a form of analysis that makes use of power spectra). They found evidence for trial-to-trial relationships for the early kinematic markers (i.e., peak acceleration and peak velocity), but not later (i.e., movement end), both for time and position variability. The power spectra of the trial-to-trial differences for the early markers approximated a $1/f$ noise-like form. The $1/f$ noise is also known as pink noise and it represents data which is moderately correlated with itself at both short and longer timescales (Gardner, 1978; cf., Diniz et al., 2011 for a review of alternative interpretations). The authors argued that the lack of correlations at the later kinematic markers indicated that the trial-to-trial differences in these variables were due to online feedback utilization and not trial-to-trial changes in planning.

The work above was followed up by Valdez and Amazeen (2008; 2009), who examined the presence of $1/f$ noise in the trial-to-trial temporal variability at kinematic markers. They found that when $1/f$ noise was present, it was maximized at peak velocity. This pattern of findings was only present when their movements were self-paced and was facilitated when the target width was decreased (i.e., perpendicular to the axis of movement). When the participants were instructed to move as fast as possible, the $1/f$ noise at peak velocity was no longer found. The authors argued that the $1/f$ pattern in the spectrum represented overlapping processes acting at different latencies, as described by Gardner (1978). The overlapping processes were hypothesized to be the planning and the online control of action, such as those described by Woodworth (1899) and Glover (2004; Glover & Dixon, 2002). The lack of $1/f$ noise in the faster movements was deemed to be caused by insufficient time for control processes to significantly alter the timing of the trajectories. Miyazaki et al. (2004) reported that when the movements
were completed in the presence of concurrent visual feedback, the variability of endpoints of goal-directed movements could be represented with a white-noise spectral structure. Alternatively, movements completed without concurrent visual feedback yielded a pink \(1/f\) noise structure, which led the authors to conclude that movement planning exerted a pink noise variability on movement endpoints while online control exerted a white noise effect.

Slifkin and Eder (2012) followed-up the above work by examining the influence of increasing movement amplitude (between 6.35 and 101.6 mm) in a reciprocal aiming task. They hypothesized that increased amplitudes would result in increased feedback utilization (e.g., Elliott, Helsen, & Chua, 2001). Such a hypothesis was warranted because greater movement amplitudes require greater force, and in general, greater force results in greater variability of force (Schmidt, Zelaznik, Hawkins, Frank, & Quinn, 1979), which in turn would result in a greater need for online feedback to maintain accuracy. As hypothesized, the authors found that longer amplitudes in the presence of concurrent visual information shifted the spectral structure of the trial-to-trial amplitude variability from pink to white. Therefore, the degree of \(1/f\) (or pink) noise in the structure of the trial-to-trial endpoint variability has shown promise in discerning feedback utilization in goal-directed actions.

Altogether, frequency domain analyses have proven informative in terms of quantifying reaching performance, identifying feedback utilization during isometric force tracking tasks, and determining if a large number of movements have tended to be influenced by online feedback or not. Ultimately, frequency domain analysis may prove informative for the quantification of online feedback utilization for discrete reaching movements as well.

### 2.9 Potential sources of upper-limb oscillatory behaviour

Although one of the main purposes of the current dissertation was to examine the utilization of sensory information for the online control of upper-limb reaching movements, such feedback loops represent only one of many potential sources of limb oscillations. That is, the impact of such feedback loops may exert their influence on limb trajectories not in isolation, but in addition to other processes and phenomena. Importantly, many of these other sources of limb
oscillations may occur at frequencies comparable to those deemed to be related to online feedback utilization. Thus, the influence of sensory feedback utilization may result in graded changes of already existing limb oscillation rates, rather than the appearance, or presence/absence of unique frequency domain peaks. The current section has briefly reviewed potential cortical and non-cortical contributions to limb oscillations.

2.9.1 Central mechanisms

Many brain regions have been associated with the generation and control of limb movements. However, the posterior parietal cortex (PPC) has been identified as a particularly important contributor. In fact, Milner and Goodale's (1992) dual-stream model of visual processing posited that visual information associated with the control of action traverses from primary visual areas along the dorsal stream to the PPC. Desmurget et al. (1999) demonstrated the importance of the PPC in movement control by using transcranial magnetic stimulation (TMS) to inhibit spatially defined, cortically mediated functioning while participants performed a reaching task. Importantly, when the PPC was inactivated by the TMS, participants were unable to make significant corrections to ongoing movements in response to changes in target locations. In a similar study utilizing grasping movements, Glover, Miall, and Rushworth (2005) argued that the PPC was most important for the initiation of movement corrections, rather than the execution of said corrections. That is, the application of TMS only disrupted potential corrections but not when the correction error signals had already been processed. The role of the PPC in the initiation of movement corrections was further supported by Archambault, Ferrari-Toniolo, and Battaglia-Mayer (2011). They found that correlations between neural activity and hand kinematics remained high for both perturbed and unperturbed movements, whereas these correlations dropped significantly for frontal, motor related areas (i.e., M1 and PMd). Furthermore, areas of the PPC have been implicated in cortico-cortical circuits with areas of the frontal cortex and it has been suggested that the premotor cortex serves as an intermediary between M1 and PPC (e.g., Rizzolatti & Matelli, 2003).
Although the aforementioned studies highlighted the importance of the PPC for the implementation of online corrections, the other two major components (i.e., M1 and PMd) also serve important purposes. For example, Lee and van Donkelaar (2006) demonstrated that the application of TMS over PMd also disrupts online corrective processes, particularly during a visuomotor adaptation task. Furthermore, the relative roles of M1 and PMd in such parieto-frontal networks have been proposed to be based on relative timing differences in the neural activation during movement. That is, in response to a visual perturbation, activation generally peaks first in the premotor cortex and only later in the primary motor cortex, followed by activity in the posterior parietal cortices (e.g., Archambault et al., 2011). This order was argued to support the idea that the premotor cortex mediated the influence of top-down intentions. The primary motor cortex mediated early and continuous control of kinematics and the posterior parietal cortex was associated with the estimates of limb kinematics required to achieve the desired goal (see also Archambault, Ferrari-Toniolo, Caminiti, & Battaglia-Mayer, 2015). These roles in online control are consistent with the work of Franklin et al. (2016), who argued that early corrections can be initiated by the system, prior to the integration of multiple frames of reference in the PPC. Furthermore and notably, Archambault et al. (2011) found that during perturbed movements, there was evidence for parallel processing of both the original target and the new target in all three areas (i.e., PMd, M1, and PPC; for M1, see also Georgopoulos, Kalaska, Caminiti, & Massey, 1983). That is, multiple movement plans (i.e., original and corrections) could be represented simultaneously, which could result in smooth transitions from one movement plan to the next. Ultimately, such overlapping of motor processes could provide a neural explanation as to how relatively smooth trajectories can be observed even in the presence of online corrective processes (i.e., pseudocontinuous control mechanisms; Elliott et al., 1991).

In addition to parietal-frontal circuits, evidence also exists for the contribution of the cerebellum in the control of action. For example, Desmurget et al. (2001) examined reaching performance without vision of the moving limb, whereby the visual target of the movement was perturbed on some trials during the orienting saccade (see also Pélisson et al., 1986). Using positron emission tomography, they found that an important circuit for the control of such
perturbed actions existed between the PPC, the cerebellum, and the primary motor cortex via the brainstem (i.e., the pontine nucleus). It was argued that the absence of online vision of the limb may have facilitated the relative contribution of this non-visual circuit. In this non-visual circuit, the PPC served an error-detection role, whereas the cerebellum generated the required correction. Such corrective processes governed by the cerebellum have been historically associated with internal models and feedforward control mechanisms (e.g., Miall, Weir, Wolpert & Stein, 1993). Thus, in the absence of online vision of the hand, the state estimates of the hand location were likely governed to a greater extent by the influences of these feedforward processes. Further, the potential importance of the cerebellum to movement control was highlighted by Atkin, Inessa, and Kozlovskaya (1976), who reported a modulation of a perturbation induced 5 to 8 Hz tremor during a goal-directed limb movement, through the reversible freezing of cerebellar nuclei in non-human primates. The authors argued that the elicited oscillations may have represented a diminished cortical control signal associated with returning the limb to the intended target. Nevertheless, the cerebellum may play an important role in movement control. However, the influence may be more associated with feedforward, rather than feedback-based control.

Lastly, transcortical circuits also exist and contribute to behaviour through the processing of proprioceptive information. Proprioceptive information influences ultimate motor cortex output via pathways at least traversing primary somatosensory areas (e.g., see Scott, 2015 for a review). The shortest latency responses that can be observed in pyramidal tracts descending from primary motor cortex in response to a force perturbation of the limb can be identified in as little as 20 ms (e.g., Evarts & Tanji, 1976). Only after at least 40 ms do voluntary intentions appear to exert an influence on the proprioceptively-driven responses (e.g., Evarts & Tanji, 1976; see also Scott et al., 2015). These voluntary influences are likely mediated by additional transcortical areas such as the PMd, the supplementary motor area (SMA), and subcortical regions such as the basal ganglia (e.g., Scott et al., 2015). Furthermore, experiments examining performance of individuals suffering from optic ataxia who have suffered damage to their PPC have demonstrated deficits in pointing accuracy to a contralateral hand, indicating that the area also mediates the processing of proprioceptive information during action (e.g., Blangero et al., 2007).
Ultimately, the commonality of the importance of these cortical areas (i.e., M1, PMd, SMA, & PPC) for both the visual and proprioceptive control of action permits the possibility of interactions between these systems for the multisensory control of ongoing actions. Overall, many neural circuits exist in the central nervous system that could contribute iterative oscillatory behaviours. Additionally, a number of potential peripheral contributions exist as well.

2.9.2 Additional sources of upper-limb oscillations not directly related to central feedback loops

One source of limb oscillations stems from the notion that the limb can be represented as a mechanical system (e.g., Morrison & Newell, 2000). That is, the natural oscillation frequency of a limb or limb segment can be estimated through a mathematical equation (e.g., Morrison & Newell, 2000):

\[ F_n = \frac{1}{2\pi} \sqrt{\frac{K}{M}} \]  

(1)

F represents the oscillation frequency, K represents the limb stiffness, and M represents the mass of the limb. As such, adding mass (e.g., Stiles, 1980; Stiles & Randall, 1967; Vaillancourt & Newell, 2000) has been found to decrease the rate at which a limb mechanically oscillates. Also, increasing limb stiffness with a spring (e.g., Joyce & Rack, 1974) or through co-contraction (e.g., Morrison & Newell, 2000) have both been found to increase the oscillation rate. Approximate rates of mechanical oscillations have been estimated for the elbow (e.g., 3 - 5 Hz; see Fox & Randall, 1970), wrist (e.g., 8 - 12 Hz; see Elble & Randall, 1978), and finger (e.g., 17 - 30 Hz; see Stiles & Randall, 1967). Importantly, because the rates associated with centrally-driven mechanisms are not directly tied to mechanical properties of the limb, these rates should be generally robust to changes in limb mass or stiffness (e.g., Elble & Koller, 1990).

Another mechanistically distinct, yet potentially related, avenue to limb oscillations is the contribution of spinal reflex pathways (e.g., Elble & Koller, 1990). Monosynaptic stretch reflexes can influence muscle activity and ultimately limb movements at latencies of
approximately 25 to 50 ms (e.g., the monosynaptic stretch reflex response; e.g., Latash, 2008). Importantly, this short latency reflex is traditionally understood to be not modifiable by voluntary intention (e.g., Rothwell, 1994, cf., task-specific modulation: Mutha, Boulinguez, & Sainburg, 2008). Conversely, a longer latency reflex (i.e., approximately 50 to 75 ms), known as the M2 reflex response, transcends the spinal cord and reaches brain centres. Notably, this response is modifiable by voluntary intention but is not entirely under voluntary control (e.g., Forgaard, Franks, Maslovat, Chin, & Chua, 2015; Rothwell, 1994). Theoretically, such reflex mechanisms could generate oscillatory behaviour at rates between 13.3 and 40 Hz. However, the ultimate influence of these reflex processes is often significantly mediated by the mechanical properties of the limb (e.g., Elble & Koller, 1990). Furthermore, centrally-driven presynaptic inhibition of the afferent signals associated with these reflex responses may increase or decrease the relative influence of these reflexes on limb position, depending on the time-course of the muscle activation (e.g., Meunier & Pierrott-Deseilligny, 1989). Ultimately, spinal reflex pathways could contribute to limb oscillations at a number of different timescales, depending on the particular active pathway. Notably, these spinal pathways may also play an important role in other physiological sources of limb-oscillations such as tremor.

One of the most common research areas relating to limb oscillations is the study of tremor, which can be broadly defined as any involuntary, rhythmic, sinusoidal movements of the limb (Elble & Koller, 1990). Many physiological and pathological forms of tremor have been described and studied (see Elble & Koller, 1990). Given that the current dissertation focused on neurologically-intact individuals, a thorough review of pathological forms of limb tremor was not deemed useful. Still, in neurologically-intact individuals, tremor during movement is often observed and is known as physiologic tremor (e.g., Elble & Koller, 1990). This tremor is typically contributed to by at least two major components: a mechanical component, and a non-mechanical component (Elble & Koller, 1990). The mechanical component is influenced by changes in inertia and loads, which therefore emerges at varying frequencies. In contrast, the non-mechanical component typically resides in the 8 to 12 Hz range (e.g., Elble & Koller, 1990). The latter component in physiologic tremor has been proposed to be exploitable by the motor
system for the purposes of both movement initiation (e.g., Goodman & Kelso, 1983) and online control (e.g., Bye & Neilson, 2010).

In addition to normal physiological tremor, essential tremor is a pathological tremor that represents the most common movement disorder among humans (e.g., Elble & Koller, 1990). Essential tremor is often most evident during movement and exhibits its influence in the 4 to 12 Hz range (e.g., Elble & Koller, 1990). Notably, essential tremor is not significantly influenced by the addition of mass loads (e.g., Elble, Higgins, Leffler, & Hughes, 1994). Also, it has been suggested that essential tremor likely originates from an abnormal physiologic tremor (e.g., Elble et al., 1994).

Ultimately, the oscillatory contributions of mechanical, physiologic, and essential tremor to behaviour overlap with the timescales associated with the contributions of control. Thus, changes in online control will likely only have a graded influence on the frequency composition of performance rather than on discrete and unique frequency contributions.

2.10 Interim summary and rationale

The accurate performance of goal-directed action is often completed with such ease that few appreciate the inherent complexities of the processes taking place. Accuracy is maintained in part through the utilization of sensory information available online for feedback-related processes. The accurate assessment of such feedback utilization during goal-directed action has proven difficult. Recent models of online control posit that there are multiple distinct processes acting across the movement (e.g., Elliott et al., 2010) and the ultimate corrections mediated by these processes may take many forms. Many methodologies developed for the quantification of online control may also be influenced by offline, trial-to-trial changes in performance. Fortunately, despite the variety of mechanisms and potential avenues from which online control can influence reaching behaviours, the corrective reaction times of the hitherto proposed feedback processes appear to be relatively stable (Brière & Proteau, 2011; Cressman et al., 2010; Oostwoud Wijdenes et al., 2013a; Saunders & Knill, 2003; Veyrat-Masson et al., 2010). This temporal stability affords a novel approach to the quantification and evaluation of online
control processes during reaching. Namely, analysis in the frequency domain may be particularly suited to quantify at least some forms of online feedback utilization. That is, distinct corrective mechanisms (i.e., iterative processes) acting at relatively fixed latencies should be dissociable from one another using frequency analyses. Consistent with this prediction, frequency domain analyses have shown promise in identifying the contributions of iterative feedback processes in visuomotor tracking and isometric force regulation (McAuley et al., 1999; Sosnoff & Newell, 2005). Unfortunately, to date, such an approach has not been utilized to examine online control processes during discrete goal-directed reaching movements. Because online control processes may function through mechanisms unique to these actions, the application of frequency analyses for the quantification and identification of iterative processes contributing to online control was deemed to be warranted.

2.11 Main hypotheses

The main assumption of the current body of work was that online control mechanisms iterate at relatively stable and distinct rates. It has been assumed that sensory feedback delays are the rate-limiting process in online feedback utilization and that the associated processes normally function near their maximal rates. Therefore, unique and separate iterative contributions to the control of goal-directed movement may be apparent in the frequency power spectra of reaching trajectories. As a result, it was first hypothesized that frequency domain analyses would be sensitive to the contributions of visually-mediated, iterative online control processes.

Second, because unique feedback mechanisms are likely to result from a unique set of computational processes and are governed by a unique physiological flow of information, the contributions of each iterative feedback mechanism was hypothesized to be measurable at distinct frequencies in the power spectra. For example, the utilization of proprioceptive information may benefit from shorter feedback loops to influence behaviour relative to visual information (e.g., Steyvers et al., 2001). As a consequence, proprioceptive feedback mechanisms may prove to be identifiable at a higher iterative frequency as compared to visually-based mechanisms. Third, because of the predicted stable iteration times of feedback processes, once
specific frequencies have been identified and associated with online feedback processes, their relative contributions to performance was predicted to be directly measurable, and relatively robust to the presence of offline, trial-to-trial influences on movement trajectories. And lastly, if and when specific frequencies have been associated with specific sensory feedback conditions, the association between the specific frequencies and online control was expected to be apparent when accuracy requiring task demands were manipulated. That is, under conditions wherein greater relative contributions of online control are expected, a greater relative contribution of the associated frequency was predicted.
3   Common Methodology

All experiments included herein were controlled using custom MATLAB (The Mathworks Inc., Natick, MA) scripts. Position data collected to quantify movement kinematics was collected using an Optotrak Certus motion tracking system (Northern Digital Inc., Waterloo, ON, Canada). Acceleration data was collected using differentiated position data and directly through the use of a triple-axis accelerometer (Model: MMA7631, Sparkfun Electronics, Niwot, CO, USA). Vision of the environment was controlled with PLATO liquid-crystal goggles (Milgram, 1987; Translucent Technologies Inc., Toronto, ON, Canada). In all experiments, right-handed participants were asked to completing goal-directed upper-limb movements with their right, dominant hand.

The five experiments contained in the four manuscripts of the current dissertation contrasted conditions in which differential use of feedback was expected to occur during goal-directed action. These contrasts were accomplished primarily through the manipulation of the available sensory information during reaching. Acceleration profiles were attained in each of these conditions for individual reaching movements and the contribution of the primary acceleration-deceleration (i.e., representative of the pre-planned components of the movement) was removed from the signal (i.e., detrended) by fitting a 5th order polynomial (i.e., 4 bends) to the data. That is, the MATLAB polyfit() function was utilized to determine the coefficients of the best-fitting 5th order polynomial. Then these coefficients were applied with the MATLAB polyval() function to generate the fitted polynomial. Then, the fitted polynomial was subtracted from the acceleration trace to yield the residuals. These residuals of these fits were assumed to be representative of adjustments made to the ongoing movements and were evaluated using a proportional power spectrum (see Appendix 1 for the associated MATLAB script). First, the Fourier coefficients were computed via the MATLAB FFT() function. Second, the power spectra were calculated by multiplying these coefficients by their complex conjugates (i.e., via the MATLAB conj() function) and dividing by the transform length. Lastly, the relative contributions of each frequency to the residual variability was estimated by normalizing the
power spectra, through dividing the power at individual frequencies by the total power observed up to the Nyquist frequency (i.e., sampling rate divided by two). Subsequently, these proportional power spectra (i.e., pPower) were then visually inspected and areas associated with observable peaks were statistically examined using repeated measures ANOVAs with respect to both their frequency (i.e., iterative latency of contribution) and their magnitude (i.e., relative contribution to the variance examined).

Across all four manuscripts, the error bars displayed in figures represent within-subjects 95 % confidence intervals as per the recommendation of Loftus and Masson (1994; see also Masson & Loftus, 2003).
4 Manuscripts

4.1 Manuscript 1: Proof of concept examining the sensitivity of frequency domain analyses to visuomotor online control

An earlier version of this manuscript has been published:

Quantifying online visuomotor feedback utilization in the frequency domain. *Behavior Research Methods*. doi10.3758/s13428-015-0682-0
Quantifying online visuomotor feedback utilization in the frequency domain
4.1.1 Abstract

The utilization of sensory information during activities of daily living is ubiquitous both prior to and during movements (i.e., planning and online control respectively). Because of the overlapping nature of online corrective processes, the quantification of feedback utilization has proven difficult. The current study primarily sought to evaluate the utility of a novel analysis in the frequency domain to identify visuomotor feedback utilization (i.e., online control). A second goal was to compare the sensitivity of the frequency analysis to that of currently utilized measures of online control. Participants completed reaching movements to targets located 27, 30, and 33 cm from a start position. During reaches, vision of the environment was either provided or withheld. Performance was assessed across contemporary measures of online control. For the novel frequency analysis forwarded in this study, acceleration profiles of reaching movements were detrended with a 5th order polynomial fit, and the proportional power spectra were computed from the residuals of these fits. The results indicated that the use of visual feedback during reaching movements increased the contribution of the 4.68 Hz frequency to the residuals of acceleration profiles. Comparisons across all measures of online control showed that the most sensitive measure was found to be the squared fisher transform of the correlation between position at 75 % vs. 100 % of movement time. However, because such correlational measures can be contaminated by offline control processes, the frequency domain analyses forwarded herein represents a viable and promising alternative to detect changes in online feedback utilization.

KEYWORDS: online control; discrete reaching; power spectra; visuomotor feedback
Quantifying online visuomotor feedback utilization in the frequency domain

The human sensorimotor system must be sensitive to the dynamic nature of the environment in which voluntary movements are completed. One source of sensory information that is obviously important for the maintenance of movement accuracy is visual information. This capacity is exemplified through the use of visual feedback during an ongoing movement (i.e., online control). For example, utilization of feedback-related processes is apparent through the changes in accuracy brought about by manipulations of visual information after movement onset (e.g., Elliott & Madalena, 1987; Heath, 2005; Keele & Posner, 1968; Woodworth, 1899; Zelaznik, Hawkins, & Kisselburgh, 1983). Although the influence of online feedback-based processes is evident in behavioural outcomes, the quantification of online feedback utilization, and the manner in which feedback is utilized has been the subject of much debate (e.g., Elliott & Hansen, 2010; Khan et al., 2006).

Models of online control have been proposed to explain sensory feedback utilization during action and many have worked from the general assumption that accuracy is maintained via a servo-mechanism (i.e., Craik, 1947). For example, to explain the use of online feedback during action, Crossman and Goodeve (1963/1983) proposed a model of visual control wherein visual corrective feedback processes occurred in an iterative fashion, whereby corrections were completed serially at a fixed latency. Likewise, Howarth, Beggs, and Bowden (1971) also argued that feedback processes required a fixed latency of time from which to act. This latency, however, would be the limiting factor regarding the number of corrections per movement. More recently, Meyer, Kornblum, Wright, and Smith (1988) argued that the timing of corrective submovements could instead be described by statistically optimal processes. That is, the corrections were completed at a point in the movement when they would optimally improve movement accuracy. Although differences existed between the above models, common threads between them have included the notions that online feedback utilization is likely an iterative process which requires time.
The models described above also relied primarily on the idea that discrete discontinuities in kinematic profiles could be interpreted as evidence for online feedback utilization. As such, methodologies developed for the measurement of online feedback utilization have often relied upon the presence of discrete trajectory discontinuities. For example, Khan, Franks, and Goodman (1998) developed an index of error correction efficiency based on the reduction in error associated with a secondary submovement (i.e., the error-correction phase). Such submovements are often identified through an analysis of trajectory discontinuities (see Walker, Philbin, Worden, & Smelcer, 1998). Subsequent findings, however, have provided evidence that the simple reliance on the identification of trajectory discontinuities may not always provide conclusive evidence regarding feedback utilization. For instance, Elliott, Carson, Goodman, and Chua (1991) argued that discrete discontinuities in kinematic profiles may not always be apparent. That is, online corrective processes may instead occur in an overlapping manner, such that individual corrective submovements may not be discernible at the kinematic level. One source of evidence for this assertion came from the finding that the number of discrete discontinuities in a trajectory does not systematically decrease with the withdrawal of vision of the environment (e.g., Elliott et al., 1991). In comparison, the time spent moving following peak limb velocity (i.e., the deceleration phase duration) was reported to be more tightly linked to the vision manipulations employed. Therefore, it was argued that online corrective processes likely occurred in a temporally overlapping fashion, which resulted in smooth trajectory profiles. This idea has become known as the pseudocontinuous control model. The existence of overlapping corrections poses a potential problem for the identification and quantification of online feedback utilization during movement, especially those relying upon discrete discontinuities in the movement trajectory.

Another finding incongruent with the quantification of online feedback utilization based on the number of discrete discontinuities in a trajectory was presented by Dounskaia, Wisleder, and Johnson (2005). They examined reciprocal and discrete reaching movements and evaluated the number of discontinuities in the profiles. In the presence of online visual information, more discontinuities were observed for the trajectories of the discrete as compared to the reciprocal
movements. Thus, it was argued that some discontinuities may come about simply through the process of slowing a limb to a stop rather than as a consequence of online feedback utilization. If it is often neither apparent that a correction has been made, nor if the presence of discontinuities can be associated with online feedback utilization, how can one accurately assess the relative use of corrective processes based on discontinuities alone?

To address the above issue, many kinematic measures have been proposed as proxies for the quantification of the involvement of feedback-related processes for the online control of voluntary movements. That is, in the absence of the ability to directly measure and quantify online feedback utilization at the neurophysiological level, many behavioural measures have been put forth to provide a best estimate regarding the influence of online visuomotor mechanisms. These include time after peak velocity (e.g., Elliott et al., 1991), trial-to-trial variability (e.g., Khan et al., 2003; Messier & Kalaska, 1999), measurements of higher derivatives of position with respect to time, such as jerk (e.g., Flash & Hogan, 1985), and correlations of position at different movement proportions (e.g., Fisher²: Bernier, Chua, Franks, & Khan, 2006; R²: Heath, Westwood, & Binsted 2004; Heath, 2005; r: Messier & Kalaska, 1999; Fisher Z of the correlation between the distance travelled to and after peak velocity: Elliott, Binsted, & Heath, 1999). Increases in time after peak velocity have been proposed to be associated with online feedback utilization in part because the early phases of movement were initially believed to be completed without the influence of feedback (e.g., Woodworth, 1899). Thus, greater reliance on feedback would extend to the later portion of the movement. Alternatively, the analysis of normalized jerk (i.e., the third derivative of position) across a movement (i.e., a 'jerk score'; e.g., Tresilian, Stelmach, & Adler, 1997) has been proposed as a proxy for online feedback utilization. Movements unaltered by feedback have been assumed to be planned in a manner that minimizes jerk (i.e., discontinuities) and thus, increases in the normalized jerk, indicated a greater contribution of feedback utilization to the performance (e.g., Flash & Hogan, 1985). More recent methodologies for the quantification of online feedback utilization during reaches have relied on between-trial variability and correlations (e.g., Messier & Kalaska, 1999). In general, movements unaltered by online feedback have been assumed to
result in relatively stereotyped trajectories across a number of trials. Therefore, the predictability of position between different proportions of a trajectory could be theoretically utilized to assess the influence of feedback-related processes. Lower correlations have therefore been taken as evidence for adjustments across trajectories, which has been attributed to online feedback utilization (e.g., Elliott et al., 1999; Heath, 2005). Although each of these measures can provide evidence supporting the possibility that feedback mechanisms have been utilized, all are potentially contaminated by offline (i.e., trial-to-trial) changes in behaviour. Indeed, trial-to-trial changes in the symmetry of the velocity profile (i.e., differences in how stereotyped the profiles were from one trial to the next) can also come about through changes in the planning process, resulting in characteristically different timing and forces of agonist and antagonist muscle contractions during reaches (e.g., Plamondon & Alimi, 1997). Evidence for this assertion has come from the finding that performance is maximized when the availability of visual feedback is scheduled in a blocked manner as compared to a randomized schedule (e.g., Elliott & Allard, 1985). In addition, both the relative certainty of the availability of feedback (e.g., Zelaznik et al., 1983) and the availability of vision on preceding trials (e.g., Cheng, Luis, & Tremblay, 2008) have been shown to influence endpoint accuracy across reaches. Thus, changes in reaching performance, which could otherwise be erroneously attributable to online feedback utilization, could theoretically come about through offline changes in performance.

Another potential solution to the problems associated with the measurement of online control resides in the frequency domain. The relative contribution of different oscillation frequencies to a signal can be represented by a normalized power spectral density function (e.g., Warner, 1998). These frequencies can also be represented as a duration/iteration rate (i.e., seconds per cycle rather than cycles per second). Because corrective reaction times to visual perturbations tend to be relatively stable throughout reaching movements (e.g., Cressman, Cameron, Lam, Franks, & Chua, 2010; Proteau, Roujoula, & Messier, 2009; Saunders & Knill, 2003), the influence of online corrective feedback processes based on visual information likely exerts its influence at a specific frequency (i.e., a rate). Thus, rather than simply estimating the number of discontinuities in a trajectory, the contributions of specific iterative influences,
presumably associated with specific feedback processes, can be quantified and evaluated. Additionally, representing the trajectory in the frequency domain circumvents the difficulty in identifying online feedback utilization caused by temporally overlapping corrective processes. These overlapping processes contribute to the same frequencies in the frequency domain (i.e., they are additive). This type of analysis has been previously applied to a line-drawing task (van Galen, van Doorn, & Schomaker, 1990), small goal-directed finger and wrist movements (van Galen, Lambert, & Schomaker, 1992), and reciprocal reaching trajectories (van Donkelaar & Franks, 1991). However, these studies needed be extended by including comparisons of performance across different sensory environments to more directly assess online control processes.

One goal of the current experiment was to directly test the prediction that differences in performance due to online feedback utilization would be measurable in the frequency domain (i.e., the proportional power spectra) of the limb trajectories of discrete reaching movements. Participants were tasked with completing goal-directed reaching movements to stationary targets in the presence or absence of online visual feedback. These two sensory environments were chosen to identify the frequencies accounting for the differences in performance mediated by visual feedback processes during reaching movements. Due to the wave-like form of the acceleration traces of discrete reaching movements (i.e., sine-wave shape), acceleration traces were chosen for the frequency analysis. Because the process of differentiation amplifies high frequency noise in signals (e.g., Bracewell, 1986), acceleration traces were gathered directly using a triple axis accelerometer rather than from double-differentiated position data. Kinematic profiles were converted to a frequency representation using a Fast Fourier Transform (FFT). The FFT output was then converted to a proportional power spectra (pPower; % spectral power), so that differences between the two visual conditions could be directly assessed (see Warner, 1998). It was hypothesized that increased feedback utilization in the presence of online visual information would result in an increase in the pPower as compared to performance in the absence of online visual feedback. The specific frequency at which this difference resided could potentially identify the iterative rate at which visual feedback has been utilized. This frequency
was hypothesized to be in the range of up to approximately 10 Hz (i.e., iterative rates of feedback utilization up to around 100 ms) (e.g., Carlton, 1992; Saunders & Knill, 2003; Zelaznik et al., 1983). Although separate online control processes have been proposed (i.e., impulse vs. limb-target regulation processes: see Elliott et al., 2010), the explicit quantification of these sub-processes was deemed to be beyond the scope of the current study.

A secondary goal of the current experiment was to compare the herein proposed frequency analysis to contemporary measures of online control in regards to their ability to identify differences in performance between conditions with/without online vision available (see also Elliott & Hansen, 2010; Khan et al., 2006). This was achieved by examining the magnitude of the effect sizes of significant effects involving visual availability manipulations. In addition to the effect sizes associated with these significant effects, the effect sizes associated with theoretically-driven individual comparisons were also undertaken. This would allow for the identification of the individual comparisons associated with particular measures of online control most sensitive to changes in the availability of visual information.

4.1.2 Methods

Ten participants (3 female 7 male, mean age = 25 yrs, \(SD = 5.8\)) were recruited for participation from the University of Toronto community. All participants were self-declared right-handed and had normal or corrected-to-normal vision at time of participation. All participants gave informed written consent prior to participation. Participants were reimbursed ($10 CAD) for their participation.

Participants were seated in front of a custom aiming console. A palpable home-position was located 30 cm to the right of the participant's midline. Participants wore an infrared light emitting diode (IRED) on their right index finger. Participants' index finger position was monitored at a sampling rate of 200 Hz by an Optotrak Certus motion tracking system (Northern Digital, Waterloo, ON, CA). In addition, participants wore an orthotic wrist-brace and held a flat, rigid custom plastic tool (2 cm \(\times\) 12 cm \(\times\) 0.4 cm) against the underside (i.e., the inferior surface)
of their right index finger (i.e., held the finger straight). This tool was held such that it extended from approximately the base of the participant's index finger to the base of the distal phalanx. Consequently, the pad of the index finger of the participant was not obstructed. A triple-axis accelerometer was affixed to this tool (model MMA7361L, Sparkfun Electronics, Niwot, CO, USA). The accelerometer was sampled concurrently with the Optotrak data at 200 Hz, using the analog-input ports on a multi-function data acquisition card (model PCI-6042E, National Instruments, Austin, TX, USA). Participants were instructed to complete a right-to-left (i.e., lateral-to-medial) goal-directed reaching movement from the home position to a target LED (i.e., upon the target's illumination) as quickly and accurately as possible, but with a greater emphasis on movement accuracy. Participants were also instructed to keep the accelerometer (i.e., the moving finger/tool) as close to perpendicular to the axis of movement as comfortably as possible during reaches. The direction of movement was chosen primarily for two reasons. First, ending the movements near the participant's midline minimized the potential for occlusion of the target by the reaching limb. Second, movements along the medial-lateral axis were chosen to minimize the cross-contamination of the axes of the accelerometer. Three target amplitudes were used (27, 30, and 33 cm), and the 30 cm target amplitude LED was positioned approximately at the participant's mid-line (i.e., mid-saggital plane). All target LEDs were situated beneath the surface of the aiming console and were not visible to the participant until they were illuminated. Three target amplitudes were employed in an attempt to reduce the predictability of the specifics of an upcoming trial and thus, in turn, reduce the degree to which movements could be influenced by offline processing. The task itself, namely a simple discrete reaching movement, was chosen to provide a straightforward context from which to infer changes in performance due to online feedback utilization, while being consistent with the literature that has investigated online control mechanisms (e.g., Elliott & Hansen, 2010; Plamondon & Alimi, 1997; Wallace & Newell, 1983).

Reaching movements were completed in two sensory environments: with online visual feedback (i.e., full-vision condition: FV) and without (i.e., no-vision condition: NV). The availability of online visual information was manipulated using liquid crystal goggles (Translucent Technologies, Toronto, ON, CA). In the NV condition, the goggles occluded visual
information at movement onset. Movement onset was determined by the first instance of a velocity above a threshold of 30 mm/s in the primary movement axis for two consecutive samples. Movement offset was determined by the first time after which the finger velocity in the primary movement axis fell below 30 mm/s for two consecutive samples. Participants completed 10 familiarization trials followed by a total of 30 FV trials and 30 NV trials to each of the three targets. A total of 180 experimental trials were completed by each participant (i.e., 30 trials × 2 Vision Condition × 3 Target Amplitudes) in approximately 30 minutes. The order of the trials of both vision conditions was randomized within the experiment. The experimental procedures and data acquisition were controlled via custom MATLAB scripts (The Mathworks Inc, Natick, MA, USA). All error bars depicted in figures represent within-subject 95% confidence intervals (see Loftus & Masson, 1994).

4.1.2.1 Design and analysis

Participants' performance was quantified and analyzed across five sets of dependent variables. The first four of these included a selection of currently utilized measures for the quantification of online control, and the fifth was the novel frequency-based approach forwarded in the current study. The currently utilized methodologies considered included both within-trial and between-trial measures of online control, whereas the frequency-based approach was a within-trial measure. The currently utilized methodologies were first evaluated to validate performance differences across the vision conditions, prior to the forthcoming analysis in the frequency domain.

The first set of conventional dependent variables was calculated with respect to movement end and were operationally defined as movement end kinematic measures. These included temporal dependent variables such as movement time (MT), time to peak velocity (TTPV), time after peak velocity (TAPV), and proportional time after peak velocity (i.e., pTAPV). MT was defined as the elapsed time between movement-onset and movement end. The magnitude and timing of peak velocity were determined by the maximal velocity achieved between movement-onset and movement end. Also, endpoint spatial measures were employed
and included constant error (i.e., endpoint bias: CE) and variable error (i.e., endpoint standard deviation: VE). Each of these variables was quantified in both the primary and secondary movement axes (e.g., CE<sub>Prim</sub> and CE<sub>Sec</sub> represent the constant error in the primary and secondary axes, respectively). The primary movement axis was defined as the axis of the coordinate system wherein the greatest displacement was achieved (i.e., movement amplitude). In contrast the secondary movement axis was oriented orthogonal to the primary movement axis and represented changes in movement direction rather than movement amplitude. The second set was spatio-temporal in nature, and included only peak velocity in the primary movement axis (i.e., PV). The third set of dependent variables was based on trajectory characteristics (i.e., trajectory-based kinematic measures), and included jerk score (i.e., JScore) as well as a spatial variability-analysis at 25, 50, 75, and 100 % of MT (e.g., Variability @ 75%<sub>MT</sub>). The JScore was calculated via equation (1).

\[
JScore = \sqrt{\frac{SS_{Jerk}}{2} \times \left[ \left( \frac{MT}{Seconds} \right)^{5} \times \left( \frac{Jerk_{VoltsRange}}{1000} \right)^{2} \right]}
\]  

Wherein SS<sub>Jerk</sub> represents the sum of the squared jerk across the trajectory, MT<sub>Seconds</sub> represents the movement time in seconds, and Jerk<sub>VoltsRange</sub> represents the difference between the maximum and the minimum jerk recorded from the differentiated accelerometer trace, across a trajectory. The variability-analysis was associated with the raw spatial variability (i.e., the between-trial within condition standard deviation) at different movement proportions, across all trials within a condition. Additionally, between-trial correlational analyses were completed at 25, 50, and 75 % of MT. These analyses included: r-squared analysis (i.e., R<sup>2</sup>), fisher-z analysis (i.e., Fisher), and fisher-z squared analysis (i.e., Fisher<sup>2</sup>). The R<sup>2</sup> was computed as the squared Pearson correlation between position at selected proportions of movement time and position at movement end (e.g., R<sup>2</sup> @ 75%<sub>MT</sub>). Likewise, the Fisher variable was calculated as the Fisher r to Z transformed versions of the same correlations. The Fisher<sup>2</sup> was the square of the Fisher variable. These trajectory-based measures were also assessed in both the primary and secondary movement axes.
(e.g., Fisher°m & Fisher°s). These variables were analyzed to help assess their own relative validity and to help validate the frequency analysis that followed.

The last and critical set of dependent variables assessed was evaluated in the frequency domain. Acceleration trajectories were recorded with the accelerometer in the primary and secondary movement axes. To isolate trajectory discontinuities, a 5th order polynomial was fit to each acceleration trajectory and the residuals were converted into proportional power spectra (pPower) with a frequency resolution of 1.56 Hz (see Figure 4.1.1). A 5th order polynomial was chosen for the fit because acceleration traces of discrete aiming movements exhibit four bends (i.e., one centred around movement initiation, one centred around peak acceleration, one centred around peak deceleration and one centred around movement end. The detrending of the acceleration trace allowed for the direct comparison of discontinuities across conditions irrespective of differences in MT. The polynomial fitting was completed using the polyfit() function in MATLAB. The weights associated with the fitted polynomial were utilized by the MATLAB polyval() function to generate the polynomial. This generated, smooth polynomial was detrended from the acceleration trace via point-by-point subtraction (see Appendix 1). The power spectra were calculated by first applying a Hanning truncation window to the residuals of the polynomial fit and the FFT was computed using the fft() function in MATLAB using a transform length of 128 samples (i.e., to capture a movement duration up to 640 ms). The multiplication of the Hanning window with the residuals ensured that the data substrate slowly tapered to zero at the ends, which reduces the presence of artifacts such as spectral leakage in the output of the FFT (see Randall, 2008; Warner, 1998). It also served the purpose of minimizing the influence of any accelerometer artifacts present at the start or end of the movement. The power spectra were computed from the FFT output by multiplying the Fourier coefficients by their complex conjugates (i.e., via the MATLAB conj () function) and dividing by the transform length. The proportional power (i.e., pPower) was computed for each frequency as a percentage of the sum of power of all describable frequencies up to the Nyquist frequency (i.e., up to 100 Hz). For the purposes of the analysis, pPower was assessed across the first seven frequencies ranging from 1.56 up to 10.94 Hz.
All dependent variables were statistically evaluated using repeated-measures ANOVAs. The analyses of the movement end based variables, along with the analysis of JScore and PV were all structured as 2 Vision Condition (FV, NV) × 3 Target Amplitude (27, 30, & 33 cm) repeated-measures ANOVAs. The analysis of the trajectory-based variables associated with multiple movement proportions (i.e., Variability, $R^2$, Fisher, & Fisher$^2$) were assessed with the same first two factors and an additional factor of Movement Proportion (25, 50, & 75 % of MT). In addition, the analysis of the Variability measure included a fourth level of Movement Proportion, namely 100% of movement time. The repeated-measures ANOVA completed on the frequency-based measure (i.e., pPower) was a 2 Vision Condition (FV, NV) × 3 Target Amplitude (27, 30, & 33 cm) × 7 Frequency (1.56, 3.12, 4.68, 6.25, 7.81, 9.37, & 10.93 Hz) design. This range of frequencies was chosen because the minimum time required to use visual information for online control, as evaluated via traditional methods, has been reported to be approximately 100 ms (i.e., 10 Hz; Carlton, 1992; Saunders & Knill, 2003; Zelaznik et al., 1983). Across all analyses, when the assumption of sphericity was violated, Greenhouse-Geisser corrected degrees of freedom were used to assess significance. All corrected degrees of freedom were reported to the first decimal place. Significant main effects and interactions involving Vision Condition were further assessed using a simple main effects approach and Bonferroni corrected multiple comparisons. Because Vision Condition was the most theoretically relevant factor, the decomposition of significant interactions were completed to examine differences across rather than within levels of Vision Condition. For these comparisons, the Bonferroni correction was applied based on the number of comparisons made rather than the total number of possible comparisons. When significant main effects of Target were observed, post-hoc analyses were completed via single degree of freedom polynomial contrasts (e.g., Pedhazur, 1982). Statistical analysis was completed using R (R Foundation, Vienna, Austria) and the ANOVAs were computed with the EZ package (Lawrence, 2013). Effect sizes reported represent the generalized eta squared (i.e., $\eta_G^2$; see Bakeman, 2005; Olejnik & Algina, 2003). In the case of analyses yielding significant main effects and significant interactions, only the interactions were further analyzed and interpreted.
4.1.3 Results

4.1.3.1 movement end dependent variables

The MT analyses resulted in main effects of Vision Condition ($F[1,9] = 6.10, p = .036, \eta^2_G = .009$) and Target Amplitude ($F[2,18] = 33.4, p < .001, \eta^2_G = .117$; see Figure 4.1.2, panel a). Movements completed in the presence of vision (i.e., FV) resulted in significantly longer MTs (405 ms, SD = 46) relative to movements completed without vision (i.e., NV: 396 ms, SD = 50). Post-hoc analyses of the main effect of Target Amplitude indicated a significant positive linear trend ($F[1,9] = 39.69, p < .001$). Movements to farther targets resulted in longer movement times (i.e., 27 cm: 378 ms, SD = 49; 30 cm: 401 ms, SD = 48; & 33 cm: 421 ms, SD = 51).

The TPV analyses yielded only a significant main effect of Target Amplitude ($F[1,7,15.6] = 12.56, p = .003, \eta^2_G = .056$). Post-hoc analyses of the main effect of Target Amplitude indicated a significant positive linear trend ($F[1,9] = 13.77, p = .005$). Farther Target Amplitudes resulted in longer TPV values (i.e., 27 cm: 151 ms, SD = 21; 30 cm: 157 ms, SD = 25; & 33 cm: 161 ms SD = 33).

The TAPV analyses resulted in only a significant main effect of Target Amplitude ($F[1.5,13.7] = 21.50, p < .001, \eta^2_G = .120$). Post-hoc analyses of the main effect of Target Amplitude indicated a significant positive linear trend ($F[1,9] = 27.19, p = .001$). Longer Target Amplitudes resulted in longer TAPV values (i.e., 27 cm: 232 ms, SD = 34; 30 cm: 249 ms, SD = 31; & 33 cm: 259 ms, SD = 26). Converse to the TAPV findings, pTAPV resulted in no significant main effects or interactions ($Fs < 1.3, ps > .280, \eta^2_G s < .007$) (Grand Mean = 62 %, SD = 4).

The assessment of CE$_{Prim}$ (i.e., constant error in the primary movement axis) resulted in a main effect of Vision Condition ($F[1,9] = 64.64, p < .001, \eta^2_G = .246$; see Figure 4.1.2, panel b). Positive and negative values indicated target overshoots and undershoots, respectively. Movements completed without vision (i.e., NV) resulted in significantly shortened movement amplitudes (i.e., -0.4 mm, SD = 2.7) compared to movements completed with vision (i.e., 3.4
mm, SD = 1.7). The analysis of CE_{sec} (i.e., constant error in the secondary movement axis) yielded main effects of both Vision Condition ($F[1,9] = 32.95, p < .001, \eta_G^2 = .104$) and Target Amplitude ($F[1.2,10.4] = 6.81, p = .014, \eta_G^2 = .177$; see Figure 4.1.2, panel c). Note that positive and negative values for CE_{sec} indicated movement endpoints that were further or closer to the body, relative to the target, respectively. Movements completed without vision (i.e., NV) resulted in endpoints that were further from the target away from the body (i.e., 6.2 mm, SD = 3.6) compared to movements completed with vision (i.e., FV: 3.9 mm, SD = 2.5). Post-hoc analyses of the main effect of Target Amplitude indicated a significant positive linear trend ($F[1,9] = 71.59, p = .018$). As the Target Amplitude increased, movement endpoints shifted closer to the body (i.e., 27 cm: 6.6 mm, SD = 3.9; 30 cm: 5.7 mm, SD = 2.9; & 33 cm: 2.8 mm, SD = 3.6).

The VE_{prim} analyses resulted in a significant main effect of Vision Condition ($F[1,9] = 7.05, p = .026, \eta_G^2 = .097$; see Figure 4.1.2, panel d). Movements completed without vision resulted in larger endpoint distributions (i.e., 8.1 mm, SD = 0.8) as compared to movements completed with vision (i.e., 7.1 mm, SD = 1.3). Conversely, the analysis of VE_{sec} did not result in any main effects or interactions ($F$s < 1.09, $p$s > .358, $\eta_G^2$s = .152) (Grand Mean = 5.2 mm, SD = 0.6).

### 4.1.3.2 Spatio-temporal dependent variable

The PV analyses yielded a significant main effect of Target Amplitude ($F[1.1,10.2] = 70.84, p < .001, \eta_G^2 = .082$). Post-hoc analyses of the main effect of Target Amplitude indicated a significant positive linear trend ($F[1,18] = 135.98, p < .001$) and a significant negative quadratic trend ($F[1,18] = 5.71, p = .028$). Larger Target Amplitudes led to larger PV values (i.e., 27 cm: 1.43 m/s, SD = 0.28; 30 cm: 1.57, SD = 0.31; & 33 cm: 1.64 m/s, SD = 0.34).

### 4.1.3.3 Trajectory-based dependent variables

Because effects of MT proportion (i.e., 25, 50, & 75 %_{MT}) in the trajectory-based dependent variables that included it were expected, and theoretically trivial, significant main
effects and interactions involving MT proportion were not subjected to post-hoc comparisons across levels of MT proportion.

The jerk score analyses in the primary movement axis (i.e., JScore_{Prim}) resulted in a main effect of Target Amplitude ($F[1.3,11.4] = 27.25, p < .001, \eta^2_p = .152$). Post-hoc analyses of the main effect of Target Amplitude indicated a significant positive linear trend ($F[1,9] = 34.76, p < .001$). JScore_{Prim} increased with increases in Target Amplitude (i.e., 27 cm: 1466, SD = 148; 30 cm: 1551, SD = 122; & 33 cm: 1601, SD = 112). The analyses of JScore_{Sec} yielded a significant main effect of Target Amplitude ($F[2,18] = 17.34, p < .001, \eta^2_p = .161$). Post-hoc analyses of the main effect of Target Amplitude indicated a significant positive linear trend ($F[1,9] = 28.92, p < .001$). JScore_{Sec} increased with increases in Target Amplitude (i.e., 27 cm: 1535, SD = 255; 1692, SD = 272; & 33 cm: 1819, SD = 278).

The analyses of the spatial variability across movement proportions in the primary movement axis (i.e., Variability_{Prim}) resulted in a main effect for Movement Proportion ($F[1.1,14.3] = 42.33, p < .001, \eta^2_p = .044$). Variability_{Prim} changed across the movement proportions (i.e., 25 %_{MT}: 16.12 mm, SD = 4.99 mm; 50 %_{MT}: 23.54 mm, SD = 5.97; & 75 %_{MT}: 12.41 mm, SD = 2.41; 100 %: 7.61 mm, SD = 0.93). The main effect of Target Amplitude neared conventional levels of statistical significance ($F[2,18] = 3.11, p = .069, \eta^2_p = .044$). The Target Amplitude × Movement Proportion ($F[2.7,24.5] = 2.82, p = .065, \eta^2_p = .029$) and the Vision Condition × Movement Proportion interactions ($F[1.3,12.1] = 3.55, p = .075, \eta^2_p = .024$) also neared conventional levels of statistical significance. The Variability_{Sec} analyses yielded significant main effects of Target Amplitude ($F[2,18] = 7.51, p = .004, \eta^2_p = .048$) and Movement Proportion ($F[1.3,11.4] = 18.71, p < .001, \eta^2_p = .273$). Post-hoc analyses of the main effect of Target Amplitude indicated a significant positive linear trend ($F[1,9] = 9.73, p = .012$). Variability_{Sec} increased with increasing Target Amplitude (i.e., 27 cm: 4.8 mm, SD = 1.1; 30 cm: 5.4 mm, SD = 1.3; & 33 cm: 5.6 mm, SD = 1.2). Across Movement Proportions, Variability_{Sec} increased then decreased (i.e., 25 %_{MT}: 3.8, SD = 1.5; 50 %_{MT}: 6.4, SD = 1.9; 75 %_{MT}: 5.7, SD = 0.8; & 100 %: 5.2, SD = 0.6).
Analysis of the $R^2_{\text{Prim}}$ data resulted in main effects of Vision Condition ($F[1,9] = 10.24, p = .011, \eta_G^2 = .067$) and Movement Proportion ($F[1.1,9.5] = 64.45, p < .001, \eta_G^2 = .408$). Trials completed in the presence of visual feedback resulted in significantly lower $R^2$ values (i.e., 0.16, $SD = 0.05$) as compared to trials completed in the absence of vision (i.e., 0.25, $SD = 0.09$; see Figure 4.1.3, panel a). $R^2_{\text{Prim}}$ increased with increases in Movement Proportion (i.e., 25 $\%_{\text{MT}}$: 0.11, $SD = 0.03$; 50 $\%_{\text{MT}}$: 0.13, $SD = 0.05$; & 75 $\%_{\text{MT}}$: 0.40, $SD = 0.12$). $R^2_{\text{Sec}}$ analyses resulted only in a main effect of Movement Proportion ($F[2,18] = 120.43, p < .001, \eta_G^2 = .605$). $R^2_{\text{Sec}}$ increased with increasing movement proportion (i.e., 25 $\%_{\text{MT}}$: 0.13, $SD = 0.07$; 50 $\%_{\text{MT}}$: 0.35, $SD = 0.13$; & 75 $\%_{\text{MT}}$: 0.67, $SD = 0.14$).

The assessment of the Fisher Z transformed correlations in the primary movement axis (i.e., Fisher$_{\text{Prim}}$) resulted in a main effect of Movement Proportion ($F[1.2,10.6] = 123.38, p < .001, \eta_G^2 = .418$) and an interaction between Vision Condition, Target Amplitude, and Movement Proportion ($F[4,36] = 3.71, p < .013, \eta_G^2 = .010$). This 3-way interaction was further analyzed by running separate 2 Vision Condition × 3 Movement Proportion repeated-measures ANOVAs for each of the three Target Amplitudes. Although all three analyses yielded significant main effects of Movement Proportion (all $F[2,18]s > 38, ps < .001, \eta_G^2 > .350$), only the 33 cm Target Amplitude resulted in a significant Vision Condition × Movement Proportion interaction ($F[1.3,11.5] = 4.53, p = .049, \eta_G^2 = .028$). Post-hoc analyses of this interaction, however, indicated that no significant differences existed between Vision Conditions across proportion for the 33 cm Target Amplitude (all $ps > .191$). The analysis of Fisher$_{\text{Sec}}$ resulted only in a main effect of Movement Proportion ($F[2,18] = 125.79, p < .001, \eta_G^2 = .583$). Fisher$_{\text{Sec}}$ increased with increasing Movement Proportion (i.e., 25 $\%_{\text{MT}}$: 0.26, $SD = 0.20$; 50 $\%_{\text{MT}}$: 0.67, $SD = 0.21$; & 75$\%_{\text{MT}}$: 1.24, $SD = 0.26$).

Squared Fisher Z values in the primary movement axis (i.e., Fisher$^2_{\text{Prim}}$) resulted in significant main effects of Vision Condition ($F[1,9] = 14.16, p = .004, \eta_G^2 = .047$) and Movement Proportion ($F[1.0,9.2] = 33.55, p < .001, \eta_G^2 = .309$). Also, the interaction between Vision Condition and Movement Proportion neared conventional levels of statistical significance ($F[1.1,9.9] = 3.91, p = .074, \eta_G^2 = .016$). Trials completed in the presence of visual feedback
resulted in significantly lower Fisher$^2_{\text{Prim}}$ values (i.e., 0.25, $SD = 0.13$) as compared to trials completed in the absence of vision (i.e., 0.44, $SD = 0.19$; see Figure 4.1.3, panel b). Fisher$^2_{\text{Sec}}$ analysis resulted in a main effect of Movement Proportion ($F[1.1,10.3] = 58.36, p < .001, \eta^2_G = .540$). Fisher$^2_{\text{Sec}}$ increased with increasing level of Movement Proportion (i.e., 25 $\%_{\text{MT}}$: 0.15, $SD = 0.10$; 50 $\%_{\text{MT}}$: 0.56, $SD = 0.26$; & 75 $\%_{\text{MT}}$: 1.68, $SD = 0.64$).

### 4.1.3.4 Frequency-based dependent variables

Because significant main effects of Frequency were expected and theoretically trivial, significant main effects were not subjected to post-hoc comparisons. The evaluation of the proportional power spectra of the acceleration traces in the primary movement axis (i.e., $p\text{Power}_{\text{Prim}}$) resulted in significant main effects for Target Amplitude ($F[2,18] = 5.84, p = .011, \eta^2_G = .009$), and Frequency ($F[1.4,12.9] = 20.84, p < .001, \eta^2_G = .630$). Also, a significant Vision Condition $\times$ Frequency interaction was found ($F[2.0,17.7] = 5.54, p < .014, \eta^2_G = .014$). Overall, proportional power increased with increasing Target Amplitude (i.e., 27 cm: 8.8 $\%$, $SD = 1.2$; 30 cm: 9.3 $\%$, $SD = 1.1$; & 33 cm: 9.7 $\%$, $SD = 1.1$). Post-hoc analyses of the main effect of Target Amplitude indicated a significant positive linear trend ($F[1,9] = 3.99, p = .013$). $p\text{Power}$ increased with increases in Target Amplitude (i.e., 27 cm: 8.8 $\%$, $SD = 1.2$; 30 cm: 9.3 $\%$ $SD = 1.1$; & 33 cm: 9.7 $\%$, $SD = 1.1$). The Vision Condition $\times$ Frequency interaction was further evaluated through post-hoc comparisons between Vision Conditions across the range of Frequencies. This analysis resulted in a significant difference in proportional power between FV and NV at the 4.68 Hz frequency level only ($p < .001$) (see Figure 4.1.4). That is, in the presence of online visual information, the proportional power in the 4.68 Hz level (i.e., $M = 12.7$ $\%$, $SD = 5.8$) was significantly greater than the proportional power attained when vision was unavailable during action (i.e., $M = 10.9$ $\%$, $SD = 5.8$).

The assessment of proportional power in the secondary movement axis (i.e., $p\text{Power}_{\text{Sec}}$) yielded significant main effects of Vision Condition ($F[1,9] = 7.99, p = .020, \eta^2_G = .007$) and Frequency ($F[1.6,14.3] = 23.76, p < .001, \eta^2_G = .606$). Additionally, there was a significant 3-way interaction between Vision Condition, Target Amplitude, and Frequency ($F[3.9,34.7] = $
3.70, \( p = .014, \eta_G^2 = .018 \)). This 3-way interaction was first assessed by completing a series of 2 Vision Condition \( \times \) 7 Frequency repeated-measures ANOVAs, that is, one for each of the three Target Amplitudes.

First, regarding the 27 cm Target Amplitude, significant main effects were found for Vision Condition (\( F[1,9] = 6.50, p < .031, \eta_G^2 = .111 \)) and Frequency (\( F[1.5,13.2] = 18.99, p < .001, \eta_G^2 = .612 \)). In the presence of vision, the proportional power across the range of frequencies examined was significantly greater (i.e., \( M = 7.6 \%, SD = 1.3 \)) than when vision was unavailable during action (i.e., \( M = 6.9 \%, SD = 1.4 \)). Second, regarding the 30 cm Target Amplitude, significant effects were found for the main effect of Frequency (\( F[1.8,16.1] = 23.14, p < .001, \eta_G^2 = .620 \)) and the interaction between Vision Condition and Frequency (\( F[2.0,18.4] = 8.07, p = .003, \eta_G^2 = .050 \)). Post-hoc comparisons between Vision Conditions across levels of Frequency indicated non-significant differences, although the comparisons made at 4.68 Hz (FV: 10.6 \%, \( SD = 4.7 \); NV: 8.1 \%, \( SD = 3.9 \)) and 6.25 Hz (FV: 14.5 \%, \( SD = 4.6 \); NV: 11.8 \%, \( SD = 3.3 \)) neared statistical significance (i.e., \( ps \) of .07 & .056, respectively). Lastly, regarding the 33 cm Target Amplitude, a main effect of Frequency was found (\( F[2.0,18.1] = 20.61, p < .001, \eta_G^2 = .591 \)). The main effect of Vision Condition also neared statistical significance (\( F[1,9] = 4.90, p = .054, \eta_G^2 = .008 \)).

4.1.4 Discussion

One goal of the current study was to evaluate the ability of frequency analyses to identify changes in performance attributable to online visual feedback utilization during discrete reaching movements. This goal was achieved by comparing participants' reaching performance under conditions wherein online visual information was either available or not. Differences between vision conditions were observed in both the primary and the secondary movement axes. In the primary movement axis, increases in pPower were observed at the 4.68 Hz frequency. In the secondary axis, no specific frequency was identified; however pPower increased in general in the FV condition relative to the NV condition. Such effects in the pPower potentially represented
differences in online visual feedback utilization. These differences were corroborated by FV vs. NV differences with conventional measures of online control.

The secondary goal of the current study was to compare existing measures of online control in terms of their sensitivities to changes in feedback-utilization brought about by manipulations of vision (i.e., FV vs. NV condition.). To this end, an analysis of effect sizes involving the Vision Condition factor was undertaken. Additionally, the effect sizes associated with theoretically-driven individual comparisons were also examined to identify the most sensitive individual measures. Ultimately, correlation-based measures such as $R^2$ and Fisher$^2$ yielded the highest individual effect sizes. The pPower analyses resulted in the highest within-trial effect sizes and represented a viable alternative.

4.1.4.1 Conventional measures of online feedback utilization

Overall, the analysis of conventional measures of online control resulted in significant FV vs. NV differences. These findings therefore helped to corroborate any differences found in the frequency analyses. First, considering the movement end temporal variables, a significant main effect of Vision Condition was found for MT. Longer MTs were observed for movements with compared to movements without online visual feedback (e.g., Carson, Chua, Elliott, & Goodman, 1990). Such an effect can theoretically be attributed in part to temporal costs associated with the utilization of feedback (see Fitts, 1954). Indeed, when utilizing targets with relatively high indices of difficulty (i.e., indices of difficulty above 3.58 bits; see Wallace & Newell, 1983), FV vs. NV performance differences may be more confidently associated with visual feedback utilization. As such, the current study employed targets of approximately 1 cm in width at distances ranging from 27 to 33 cm, yielding indices of difficulties of 5.75 to 6.04 bits. As a result, there is a reasonable level of confidence that the presence of vision during the movement (i.e., online feedback utilization) explains the observed differences in the investigated measures of online control. Unlike previous research however, no significant differences were found for TAPV or pTAPV (cf., Elliott et al., 1991), although the mean difference between Vision Conditions was in the expected direction for TAPV (i.e., FV = 251 ms; NV = 243 ms).
Notably, other studies have also failed to detect TAPV differences between FV and NV conditions (e.g., Heath et al., 2004).

Secondly, considering the movement end spatial variables, significant effects involving Vision Condition were found for $CE_{Prim}$, $CE_{Sec}$, and $VE_{Prim}$. The analysis of $CE_{Prim}$ resulted in significant relative undershooting in the NV condition relative to the FV condition. Although the relative undershooting in the NV condition was anticipated (e.g., Heath, 2005), an evaluation of the constant error values yielded a surprising result. That is, in the FV conditions, participants overshot the target amplitudes, whereas, in the NV conditions, participants tended to complete their movements significantly closer to the centre of the targets. That is, although participants appeared to generate more accurate movements in the NV condition, they were significantly less precise. One possible explanation for this pattern of results is that in the FV conditions the finger occluded view of the target during the latest portions of the reaching movement, leading to small, but significant overshooting. In contrast, in the NV conditions, no such occlusion was possible, and participants completed their movements to a shorter distance. Consistent with this explanation is the finding that reaching movements were significantly more accurate in secondary movement axis (i.e., $CE_{Sec}$) in the FV compared to the NV condition. All of these relative patterns of means have been reported previously for comparable reaching conditions (e.g., Heath, 2005).

Thirdly, the analysis of the trajectory-based measures resulted in significant effects involving vision condition for the $R^2_{Prim}$, $Fisher^2_{Prim}$, and the Variability$_{Prim}$ variables. Overall, performance in the presence of online visual feedback (i.e., the FV condition) resulted in lower $R^2_{Prim}$ and $Fisher^2_{Prim}$ values than when online visual feedback was not available (i.e., in the NV condition). These main effects were in line with previous findings differentiating FV from NV conditions (e.g., Heath, 2005; Khan, Lawrence, Franks, & Buckolz, 2004; Tremblay, Hansen, Kennedy, & Cheng, 2013; cf., Bernier et al., 2006). As such, these analyses of $R^2_{Prim}$ and $Fisher^2_{Prim}$ have provided evidence of greater alterations of the ongoing trajectories in the presence of online visual feedback as compared to performance in the absence of online visual feedback.
Ultimately, the analyses of conventional measures of feedback related processes (i.e., online control) in the current study have provided converging evidence that participants utilized the visual information available for feedback-related processes during reaches. Therefore, significant FV vs. NV differences in the conventional measures of online control could be confidently associated with differential use of feedback processes.

4.1.4.2 Frequency-based measurement of online feedback utilization

Through the analysis of contemporary measures of online feedback utilization, it appeared that participants were indeed making use of online visual information in the FV condition relative to the NV condition. Thus, a closer look at the differences in the pPower spectra from the frequency analysis was warranted. Vision Condition significantly influenced the pPower spectra for both the primary and secondary movement axes. In the primary axis, significantly greater pPower was observed at the 4.68 Hz frequency in the presence of online visual feedback (i.e., the FV condition) as compared to performance without feedback available (i.e., the NV condition). Likewise the secondary movement axis yielded a similar FV vs. NV difference although a specific Frequency of influence could not be identified. Because the FV vs. NV differences in performance were associated with specific changes in the pPower spectra in the primary movement axis, it is possible that these changes could be associated with differential online visual feedback utilization. Thus, analysis in the frequency domain appears to be sensitive to changes in performance brought about by differences in online feedback utilization in discrete aiming movements.

The critical frequency of 4.68 Hz can be associated as first glance with a feedback iteration time of 214 ms. That is, because the changes in performance brought about through changes in online feedback utilization were found to be related through with a specific/common frequency (i.e., 4.68 Hz), the use of feedback may exert its influence at the associated time-based rate. This frequency of 4.68 Hz and its associated iteration rate (i.e., 214 ms per cycle) is actually congruent with the hypothesized influence of feedback at 10 Hz (i.e., 100 ms per cycle; e.g., Knill & Saunders, 2003). The apparent discrepancy can be alleviated if one acknowledges the
possibility that in the absence of discrete secondary accelerations, corrective processes may be characterized by graded accelerations or decelerations rather than discrete acceleration-deceleration pairs (see Wisleder & Dounskaia, 2007). Also, because pPower represents trajectories in terms of sine and cosine waveforms, the 4.68 Hz frequency represents the rate of acceleration-deceleration pairs. However, this difference in pPower at 4.68 Hz could also theoretically be taken as evidence for the presence of graded adjustments of acceleration or deceleration (i.e., adjustments in the jerk rather than in the acceleration profile) that could be occurring at twice this rate (i.e., 9.36 Hz). This higher frequency estimate of the latency of online feedback utilization results in an iteration time of approximately 107 ms. Such a value is consistent with currently accepted corrective reaction times to visual perturbations (i.e., 100 ms; see Carlton, 1992; Brenner & Smeets, 1997; Saunders & Knill, 2005; Zelaznik, Hawkins, & Kisselburgh, 1983). Therefore, the level of frequency that was associated with performance differences was consistent with online visual feedback utilization latencies.

Although it may have also appeared that pPower had scaled proportionally with movement amplitude, a strict association between movement amplitude and pPower was not universally found. That is, despite the fact that the NV condition undershot the FV condition in the primary movement axis and overshot the FV condition in the secondary movement axis, both axes revealed a greater pPower in the FV as compared to the NV condition. Albeit, the specificity of the frequencies differentiating between the conditions was more clearly defined for the primary movement axis.

Although pPower was found to be a sensitive measure for dissociating performance across full-vision and NV conditions, it was theoretically possible that changes in MT were driving the observed effects. To test this possibility, a supplementary analysis was completed wherein between Vision Condition t-tests for MT and pPower\textsubscript{Prim} @4.68Hz were completed for each Target. If the MT differences were indeed driving the pPower effects, then a comparable pattern of differences between Vision Conditions was expected. Regarding the MT data, a significant FV vs. NV difference was observed for the 30 cm Target only (i.e., $p = .009$). Conversely, significant FV vs. NV differences in pPower\textsubscript{Prim} @ 4.68 Hz were observed for both the 27 and the 30 cm Targets (i.e., $ps < .015$). Thus, although MT and pPower may be related measures, they are distinct indicators of online control.
Whereas the current study manipulated Target Amplitude, the target width remained constant across targets. The absence of significant interactions between Target Amplitude and Vision Condition, at least for the primary movement axis, indicated a relatively robust pattern across the range of Target Amplitudes examined. Thus, further work explicitly manipulating precision demands (i.e., target widths) could prove useful before this association between pPower and feedback utilization can be made with greater confidence. Additionally, because the frequencies evaluated in the analysis of pPower were dependent on the collection rate and the movement times (i.e., 200 Hz/128 samples = 1.56 Hz increments), the preciseness of the estimates of iteration times should be taken with a certain degree of caution (see Warner, 1998). Ultimately, this frequency-based analysis remains subject to the same criticism as conventional measures of online control because they are indirect or implied measure of online control. It must be recognized that a direct evaluation of the underlying nature of online feedback utilization would require additional neurophysiological measurements, which is beyond the scope of the current study. Nevertheless, frequency-based analyses were found to be sensitive to changes in performance associated with online feedback utilization (i.e., performance differences across FV vs. NV) in a manner that may also identify the latency at which online visual feedback has been utilized.

4.1.4.3 A comparison of methods: Effect sizes

The secondary goal of the current study was undertaken through an analysis of the effect sizes associated with significant effects across all measures differentiating the FV from the NV condition. Although it is generally good practice to run power analyses to set appropriate sample sizes for investigations, the exploratory nature of the current study did not afford a predicted relevant effect size on which to base such an analysis. Instead, a post-hoc review of the achieved effect sizes across all variables was undertaken. Specifically, a comparison across measures' effect sizes was used to evaluate their relative sensitivities to changes in online feedback utilization. Regarding all significant effects able to differentiate between the levels of the Vision Condition factor (i.e., FV, NV), VE_{Prim} and R^2_{Prim} yielded the highest $\eta_p^2$ values (i.e., .097 & .067 respectively; see Table 4.1.1 & Table 4.1.2). The significant effects in the pPower analysis
resulted in $\eta_{G}^{2}$ values that were in the same range (i.e., .014 & .018 respectively; see Table 4.1.3) as those of the Fisher$^{2}$ prim (i.e., .010) and greater than that of MT (i.e., .009). Although the effects sizes associated with pPower were not the largest effect sizes attained, they were certainly in the range of currently utilized measures.

The observed pattern of greater effect sizes for CE and VE relative to pTAPV and trajectory-based variability measures (see Tables 4.1.1 and 4.1.2) has been previously reported by Elliott and Hansen (2010). Elliott and Hansen (2010) did not, however, report equivalently high effect sizes for the R$^{2}$ analysis. Indeed, they did not report a significant effect involving vision condition for the analysis of R$^{2}$. The key difference between the work of Elliott and Hansen (2010) and the current study could have stemmed from differences in offline (i.e., trial-to-trial) changes in performance. That is, the combination of only one target (cf., 3 target amplitudes in the current study) and the 'blocking' their vision conditions (cf., randomized vision conditions in the current study), resulted in highly predictable upcoming sensory consequences, and likely influenced the planning of their movements across conditions (e.g., Elliott et al., 2017). Additionally, Elliott and Hansen computed their R$^{2}$ type analyses from fewer trials per condition (i.e., 20) and through correlations at the occurrences of kinematic markers in the primary movement axis (i.e., peak acceleration, peak velocity, & peak deceleration; see also Heath, 2005). In contrast, the current study utilized a greater number of trials (i.e., 30), and normalized movement time proportions (i.e., 25, 50, & 75% MT, see also Tremblay et al., 2013). Thus, it may be that such analyses are more sensitive regarding assessments of percentage of MT (cf., Heath, 2005) or that a greater number of trials should be utilized (i.e., 30; see also Heath, 2005).

In addition to the general comparison of the effect sizes of the significant effects involving Vision Condition, the effect sizes associated with the most theoretically driven specific comparisons were separately assessed (see Table 4.1.4). This analysis was completed for two reasons: 1) to determine the measure that was most sensitive to vision manipulations; and 2) to determine which specific comparison could be most informative regarding evidence for the presence of online control. The comparisons considered included VE$^{2}$ Prim, MT, pTAPV, R$^{2}$ Prim.
Fisher$^2_{\text{Prim}}$, $R^2_{\text{Prim}} \ @ 75\%_{\text{MT}}$, Fisher$^2_{\text{Prim}} \ @ 75\%_{\text{MT}}$, and pPower @ 4.68 Hz for both the primary and secondary movement axes. Based on a direct comparison of the effect sizes associated with these variables, the largest effect size was associated with Fisher$^2_{\text{Prim}} \ @ 75\%_{\text{MT}}$, followed by $R^2_{\text{Prim}} \ @ 75\%_{\text{MT}}$, and VE$_{\text{Prim}}$. The effect sizes associated pPower in the primary and secondary movement axes resulted in intermediate effect sizes that were, however, larger than the effect sizes associated with the other within-trial measures, namely MT, TAPV, and pTAPV. Ultimately, these findings indicate that, the most sensitive current measure of online visuomotor control, as evidenced by the current assessment of effects sizes is the Fisher$^2_{\text{Prim}} \ @ 75\%_{\text{MT}}$. However, the trial-by-trial nature of Fisher$^2_{\text{Prim}}$ is also theoretically sensitive to offline changes in performance, which are not necessarily attributable to changes in online feedback utilization. For example, an individual may choose to change their prioritization of speed vs. accuracy based on their own performance on a trial-to-trial basis (e.g., de Grosbois, Heath, & Tremblay, 2016). That is, individuals may move their finger into the vicinity of the target at different rates across trials. As such, the form of the movement trajectory could significantly vary from trial-to-trial, irrespective to changes in online feedback utilization. Such changes in performance could come about as a function of practice. That is, the relative symmetry of reaching movements to a target can change over a series of trials with concurrent visual information available (e.g., Khan, Franks, & Goodman, 1998). Overall, this type of between-trial variability could theoretically induce false positives in the $R^2$ and Fisher$^2$ measures by lowering the predictability across trials between distance travelled at earlier movement proportions and the distance travelled at movement end. The within-trial nature of the removal of the unique 5th order polynomial trend from each of the acceleration profiles, followed by the frequency analyses forwarded in the current study, could theoretically circumvent the above-mentioned potential biases in estimates of online control potentially induced by offline processing. That is, the specificity of the differences in the frequency domain could theoretically identify changes in feedback utilization irrespective of offline, trial-by-trial changes in performance.
4.1.5 Conclusion

Overall, the evaluation of the Fisher$^2_{\text{rim}}$ at 75% of movement time has been found to be the best measure for dissociating performance between conditions wherein online visual feedback was available or withheld. However, the between-trial nature of the measure could have increased the susceptibility of the measure to offline changes in performance. In contrast, analyses in the frequency domain at 4.68 Hz for acceleration trajectories could be a more sensitive within-trial measure of online control and may be more robust to trial-to-trial changes in performance. Nevertheless, further research will be required to determine the relative sensitivities of within and between trial measures explicitly to systematic offline changes in reaching performance.

Although the use of sensory feedback during goal-directed actions is ubiquitous, the measurement of online feedback utilization has proven challenging. The current study applied analyses in the frequency domain, through proportional power spectra, to identify the presence of, and the latency at which feedback processes were taking place during discrete reaching movements. These analyses were successful in differentiating performance in the presence vs. absence of online visual feedback, while also confirming a potential minimum iterative rate of approximately 107 ms. Ultimately, the application of this frequency-based analysis to reaching trajectories provides an additional avenue to identify and quantify online feedback utilization.
4.1.6 References


doi:10.1080/00222895.1983.10735298
Table 4.1.1: Effect sizes associated with significant effects for measures not including the Movement Proportion Factor.

<table>
<thead>
<tr>
<th>Effect</th>
<th>MT</th>
<th>TTPV</th>
<th>TAPV</th>
<th>pTAPV</th>
<th>CEPrim</th>
<th>CESSec</th>
<th>VEPrim</th>
<th>VESSec</th>
<th>JScorePrim</th>
<th>JScoreSSec</th>
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<td>-</td>
<td>-</td>
<td>.246</td>
<td>.104</td>
<td>.097</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Target Amplitude</td>
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<td>.056</td>
<td>.120</td>
<td>-</td>
<td>-</td>
<td>.177</td>
<td>-</td>
<td>-</td>
<td>.152</td>
<td>.161</td>
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<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<td>-</td>
<td>-</td>
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<td>-</td>
</tr>
</tbody>
</table>

Note. Effect size reported = generalized eta squared (i.e., $\eta^2$); “$-$” = $p$ >= .05; * = $p$ < .05; ** = $p$ < .01; *** = $p$ < .001
Table 4.1.2. Effect sizes for the significant effects associated with the measures including the Movement Proportion Factor.

<table>
<thead>
<tr>
<th>Effect</th>
<th>$R^2_{\text{Prim}}$</th>
<th>$R^2_{\text{Sec}}$</th>
<th>Fisher Prim</th>
<th>Fisher Sec</th>
<th>Fisher$^2$ Prim</th>
<th>Fisher$^2$ Sec</th>
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<th>Variability Sec</th>
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<td></td>
<td>*</td>
<td>-</td>
<td>-</td>
<td>-.047</td>
<td>-.047</td>
<td>-</td>
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<tr>
<td>Target Amplitude</td>
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<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>.044</td>
<td>.048</td>
<td>**</td>
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<tr>
<td>Movement Proportion</td>
<td>.408</td>
<td>.605</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td>Vision Condition × Target Amplitude</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<tr>
<td>Vision Condition × Movement Proportion</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Target Amplitude × Movement Proportion</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<tr>
<td>Vision Condition × Target Amplitude × Movement Proportion</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

Note. Effect size reported = generalized eta squared (i.e., $\eta_G^2$); “*” = $p >= .05$; “*” = $p < .05$; ** = $p < .01$; *** = $p < .001$
Table 4.1.3. Effect sizes for the significant effects associated with the frequency-based dependent variables.

<table>
<thead>
<tr>
<th>Effect</th>
<th>pPower_{\text{Prim}}</th>
<th>pPower_{\text{Sec}}</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vision Condition</td>
<td></td>
<td>.007*</td>
</tr>
<tr>
<td>Target Amplitude</td>
<td>.009*</td>
<td>-</td>
</tr>
<tr>
<td>Frequency</td>
<td>.630***</td>
<td>.606***</td>
</tr>
<tr>
<td>Vision Condition × Target Amplitude</td>
<td></td>
<td>-</td>
</tr>
<tr>
<td>Vision Condition × Frequency</td>
<td>.014*</td>
<td>-</td>
</tr>
<tr>
<td>Target Amplitude × Frequency</td>
<td></td>
<td>-</td>
</tr>
<tr>
<td>Vision Condition × Target Amplitude × Frequency</td>
<td></td>
<td>.018*</td>
</tr>
</tbody>
</table>

Note. Effect size reported = generalized eta squared (i.e., $\eta^2$); “-” = $p \geq .05$; * = $p < .05$; ** = $p < .01$; *** = $p < .001$
Table 4.1.4. Effect sizes of individual comparisons between Vision Conditions for dependent variables exhibiting significant effects involving Vision Condition.

<table>
<thead>
<tr>
<th>Dependent Variable</th>
<th>Effect Size</th>
<th>MT</th>
<th>TAPV</th>
<th>VE_{Prim}</th>
<th>R^{2}<em>{Prim} @75%</em>{MT}</th>
<th>Fisher^{2}<em>{Prim} @75%</em>{MT}</th>
<th>pPower_{Prim} @ 4.68 Hz</th>
<th>pPowerSec @ 4.68 Hz</th>
</tr>
</thead>
<tbody>
<tr>
<td>Effect Size</td>
<td>.009</td>
<td>.017</td>
<td>.097</td>
<td>.131</td>
<td>.166</td>
<td>.025</td>
<td>.032</td>
<td></td>
</tr>
<tr>
<td>Rank</td>
<td>7</td>
<td>6</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>5</td>
<td>4</td>
<td></td>
</tr>
</tbody>
</table>

Note. Effect size reported = generalized eta squared (i.e., $\eta_G^2$)
Figure 4.1.1. An example of the data reduction process: a) The raw acceleration profile for the primary axis of movement; b) The best fitting 5th order polynomial of this profile; c) The substrate for the frequency analysis. (note: The residuals of the polynomial fit were multiplied by a Hanning truncation window); and d) The proportional power spectra of these preprocessed residuals.
Figure 4.1.2. A summary of the movement end dependent variables that yielded significant FV vs. NV performance differences: a) Movement time; b) $\text{CE}_{\text{Prim}}$; c) $\text{CE}_{\text{Sec}}$; and d) $\text{VE}_{\text{Prim}}$. Error bars represent within-subject 95% confidence intervals. * indicate the presence of a significant main effect of Vision Condition.
Figure 4.1.3. A summary of the trajectory-based dependent variables that yielded significant FV vs. NV performance differences: a) $R^2_{Prim}$; and b) $Fisher^2_{Prim}$. Error bars represent within-subject 95% confidence intervals. * indicate the presence of a significant FV vs. NV main effect.
Figure 4.1.4. Proportional power across Frequency for the two Vision Conditions in the primary movement axis. The FV condition yielded significantly greater proportional power in the 4.68 Hz Frequency. Error bars represent within-subjects 95% confidence intervals.
4.2 Manuscript 2: The search for unique processes contributing to performance

An earlier/edited version of this manuscript has been accepted for publication:

Distinct and flexible rates of online control
4.2.1 Abstract

Elliott, Carson, Goodman and Chua (1991) proposed a pseudocontinuous model of online control, whereby overlapping corrections lead to the appearance of smooth kinematic profiles in the presence of online feedback. More recently, it was also proposed that online control is not a singular process (see Elliott et al., 2010). However, support for contemporary models of online control were based on methodologies that were not designed to be sensitive to different online control sub-processes. The current study sought to evaluate the possibility of multiple distinct (i.e., visual and non-visual) mechanisms contributing to the control of reaching movements completed in a full-vision, a no-vision, or a no-vision memory-guided condition. Frequency domain analyses were applied to the acceleration traces of reaching movements. In an attempt to elicit a modulation in the online control mechanisms, these movements were completed at two levels of spatio-temporal constraint, namely with 10 and 30 cm target distances. One finding was that performance in the full-vision relative to both no-vision conditions could be distinguished via two distinct frequency peaks. Increases at the lower frequencies were associated with visuomotor mechanisms and increases at the higher frequencies were associated with non-visual mechanisms. Also, performance to the 30-cm target led to a lower peak at a lower frequency relative to the 10 cm target, indicating that the iterative rates of visuomotor control mechanisms are flexible and sensitive to the spatio-temporal constraints of the associated movement.
Distinct and flexible rates of online control

The notion that movements completed in the presence of vision exhibit greater accuracy than movements completed in the absence of vision is rather unsurprising. Common sense can posit that visual feedback mechanisms are utilized during movement execution to facilitate this increase in accuracy (cf., Plamondon & Alimi, 1997). As such, the adjustments in the trajectories should presumably be readily apparent in the kinematics of said movements. Yet, it has proven difficult to quantify these online feedback-based alterations to limb trajectories.

Early theoretical models have attempted to explain how accuracy could be attained through discrete changes to an ongoing limb trajectory (e.g., Crossman & Goodeve, 1983; Howarth, Beggs, & Bowden, 1972; Meyer, Abrams, Kornblum, Wright, & Smith, 1986; Woodworth 1899). Additional refinements for the identification of discontinuities during voluntary movements were subsequently developed and tested (e.g., Chua & Elliott, 1993; van Donkelaar & Franks, 1991; Walker, Philbin, Worden, & Smelcer, 1997). Furthermore, techniques quantifying the potential importance of discontinuities for online control have also been developed (e.g., Khan, Franks, & Goodman, 1998). Subsequently, however, the simple reliance on the presence or absence of trajectory discontinuities for the determination of feedback utilization has proven problematic for at least two major reasons.

First, the presence of discrete discontinuities has not been always associated with evidence of a greater contribution of online feedback (e.g., Jeannerod, 1986; cf., Flash & Hogan 1985) or higher levels of movement accuracy (e.g., Poston et al., 2013). For example, some discontinuities have been proposed to come about through the process of bringing a limb to a stop, irrespective of online feedback utilization. That is, under comparable viewing conditions, greater numbers of discontinuities have been reported for discrete reaching movements compared to reciprocal reaching movements (e.g., Wisleder & Dounskaia, 2007). Second, the absence of discontinuities has not necessarily been associated with a lack of feedback utilization. For example, Pélisson, Prablanc, Goodale, and Jeannerod (1986) reported that participants could
accurately complete reaching movements to targets that changed position around the time of movement onset (i.e., during the initial orienting saccade), without reporting evidence of any discrete corrections to the trajectory. Such problems with the identification of discrete trajectory amendments and their utility for the quantification of online control processes led to alternative models of online control.

The notion of online control without observable discrete discontinuities in trajectories has been formalized into the pseudocontinuous model (Elliott, Carson, Goodman & Chua, 1991). In this model, multiple corrections are thought to exert their influence on trajectories in a sequential/iterative, yet overlapping manner (i.e., successive corrections initiated prior to the full completion of previous corrections). This overlap between corrections was argued to be an explanation for the occurrence of relatively smooth trajectories even when one could be confident that feedback-based corrections had taken place. Importantly, the overlapping of movement corrections with ongoing movement plans has also been supported by both modelling (e.g., Flash & Henis, 1991) and neurophysiological studies (e.g., Archambault, Ferrari-Toniolo, Caminiti, & Battaglia-Mayer, 2015; Georgopoulos, Kalaska, Caminiti, & Massey, 1983). In the Elliott et al. (1991) study, participants completed reaching movements to targets with instructions to be either fast or accurate. Additionally, participants performed their movements in environments with (i.e., full vision) and without vision (i.e., no-vision & memory-guided no-vision). Elliott et al. (1991) identified discontinuities as zero-crossings in the acceleration traces of movements separated by at least 10 ms and achieving a magnitude of at least 0.01 m/s². In both experiments, Elliott et al. (1991) reported that the condition with the greatest number of discontinuities was found to be the accurate-instruction, memory-guided condition. Thus, these discontinuities were not solely mediated by online visual feedback utilization and instead, it was argued that some non-visual mechanism may also contribute to discrete trajectory amendments (e.g., proprioception: see Elliott et al., 1991). The presence/absence of visual feedback utilization (i.e., vision available vs. vision unavailable during action) was more strongly associated with a greater time spent following peak limb velocity than the incidence of discontinuities. Such results were in line with previous work, such as Soechting (1984), who reported similar increases
in time spent following peak limb velocity under full-vision conditions with decreases in target width, which presumably required a relatively greater reliance upon online visual feedback mechanisms. However, Elliott et al. (1991) also reported longer times following peak velocity in the memory-guided condition relative to the no-vision condition, indicating again that some non-visual mechanism may have contributed to performance in the memory-guided condition. Nevertheless, the development of the pseudocontinuous model led to the development of new measures of online trajectory amendments.

In light of Elliott et al.'s (1991) pseudocontinuous model of online control, methodologies for the quantification of feedback utilization have shifted towards multiple-trial measures based on movement-to-movement correlations (i.e., Bernier, Chua, Franks, & Khan, 2006; Elliott, Binsted, & Heath, 1999; Heath, 2005; Heath, Westwood, & Binsted, 2004; Messier & Kalaska, 1999). The general assumption of these approaches is that if modifications are not made to trajectories online, then the predictability of the variability early in the trajectory relative to the variability later in the trajectory should be relatively high across trials. That is, if all the movements are planned in a similar manner and online feedback processes do not significantly intervene, a relatively high degree of similarity across many repeated movements should be observed. Conversely, as relatively more online feedback processes are implemented, the aforementioned predictability between early and later trajectory variability across a number of trials should decrease because the required corrections likely differ from trial-to-trial. Although these approaches have been fruitful in dissociating performance between scenarios wherein differences in online feedback utilization are expected, their utility is inherently limited through their multiple-trial nature. Indeed, to the same extent that some discrete amendments could be tied to pre-planned limb stopping characteristics (e.g., Wisleder & Dounskaia, 2007), the scaling of separate limb trajectory profiles and the associated between-trial correlational measures may also be contaminated by pre-planned mechanisms. Altogether, the development of within-trial measures of online control likely represents a better strategy than multiple-trial measures to assess online sensorimotor control mechanisms, irrespective of offline changes in performance. That is, although performance may change from one trial to the next, based on differences in
movement planning (e.g., Roberts et al., 2013), within-trial measures cannot be influenced to the same extent to such trial-to-trial changes in performance because each estimate is based on a single trial. Furthermore, the vast majority of measures of online control are scalar estimates of control (e.g., variable error; time after peak limb velocity), which are inherently insensitive to the relative influences of distinct processes on movement performance, such as those proposed by Elliott et al. (1991; 2010).

One methodological approach that has the potential to be more sensitive to online trajectory amendments associated with multiple distinct processes such as those described by Elliott et al. (1991; 2010) is based on frequency domain analyses. Recently, de Grosbois and Tremblay (2015) forwarded such an analysis (i.e., proportional power or pPower analysis) for the quantification of online feedback utilization. These analyses made use of the frequency domain to identify the relative contributions of specific latencies of oscillation, which could be theoretically attributed to specific feedback processes. The development of this method was based on the notion that distinct feedback processes must rely on unique computations and neural pathways. Therefore distinct processes can influence performance at the specific latencies required by their individual set of computations (see de Grosbois & Tremblay, 2016). Ultimately, if such processes were to exert their influence on reaching performance in an iterative fashion, then their influence would be apparent in a frequency domain representation of reaching performance. For example, if a particular feedback mechanism exerted its influence on reaching performance every 100 ms, then an increase in the frequency domain representation would be apparent at the associated frequency of 10 Hz. Participants completed reaching movements to targets either with online vision (i.e., vision available throughout) or without (i.e., vision removed at movement onset). Trajectory data were recorded via an accelerometer and corrective contributions to these trajectories were isolated via a 5th order polynomial fitting procedure and evaluated in the frequency domain (see Figure 4.2.1). The pPower analysis successfully identified a greater contribution (i.e., a larger proportion of the power) at iteration rates of approximately 5 Hz, when online visual information was available (i.e., a full-vision) compared to when it was unavailable (i.e., a no-vision condition). That is, the contribution of
visuomotor online control mechanisms increased the relative magnitude of a particular portion of the frequency domain representation. Notably, this scaling did not result from the explicit presence/absence of a frequency domain peak. Thus, although the frequency of the visuomotor influence may be informative, the magnitude of the contribution allowed for differentiation of performance across conditions. Ultimately, frequency domain analyses have the unique potential to identify the contribution of distinct iterative sensorimotor mechanisms contributing to online trajectory amendments.

The main purpose of the current experiment was to detect, through the application of frequency domain analyses (de Grosbois & Tremblay, 2016), the possible presence of separate online control sensory feedback mechanisms, which have given rise to performance differences in the vision conditions utilized in Elliott et al. (1991). The importance of such an investigation is evident when one considers the fact that the Elliott et al. (1991) study represented a paradigm shift, as it proposed a model of control that is not necessarily dependent on identifiable discrete discontinuities (i.e., the pseudocontinuous model). Although the key finding of Elliott et al. (1991) was arguably a greater association between the time spent after peak velocity and online visual feedback utilization, a secondary finding of particular interest to the current study was an increase in the time following peak velocity in the memory-guided condition relative to the no-vision condition. It was suggested that this performance difference may have come about via a non-visual mechanism such as proprioceptive control (see Elliott et al., 1991). Frequency domain analyses (e.g., de Grosbois and Tremblay, 2015) have afforded a unique opportunity to detect distinct online control mechanisms (i.e., visual or otherwise) that can be associated with shifts in control strategies across sensory environments and instruction sets. That is, because unique sensorimotor mechanisms likely require unique timescales, it was hypothesized that frequency domain analyses could be utilized to identify specific iterative contributions to trajectories under different sensory environments. For example, proprioceptive responses can be elicited through a short latency (i.e., 25 to 50 ms), via spinally-mediated mechanisms (e.g., Scott, Cluff, Lowrey, & Takei, 2015). Such proprioceptive mechanisms could theoretically exert their influence at rates between 20 and 40 Hz. Conversely, visually-mediated responses inherently require longer
cortical contributions, and the fastest visually-mediated responses reported at the electromyographic level have been significantly slower (e.g., 85 ms; see Fautrelle, Prablanc, Berret, Ballay, & Bonnetblanc, 2010).

Another purpose of the current study was to evaluate the influence of changes in movement amplitude upon the influence of sensory-mediated online control mechanisms. Changes in movement amplitudes alter the spatio-temporal constraints of the reaching task, which may modulate sensory feedback mechanisms (e.g., Fitts, 1954). By acknowledging the likelihood that such mechanisms are time-consuming, slower feedback mechanisms may contribute to a lesser extent during shorter movements relative to longer movements. For example, Khan et al. (2003) reported that characteristically different visually driven feedback mechanisms likely require between 300 and 375 ms to exert a measurable difference in trajectory variability profiles. Therefore, changes in movement amplitudes may have a differential influence on distinct sensory feedback mechanisms operating at unique latencies. However, the rate of feedback utilization could be argued to be relatively stable, given the consistency of corrective reaction times to visual perturbations across a variety of movement characteristics (e.g., Cressman, Cameron, Lam, Franks, & Chua, 2010; Saunders & Knill, 2003; Veyrat-Masson, Brière, & Proteau, 2010). Such a view is based on the concept of a minimum visuomotor corrective latency.

Participants in the current study completed reaching movements under one of three vision conditions (i.e., full-vision: FV; no-vision: NV; and no-vision memory-guided: NV-MG) to targets located 10 and 30 cm away from the start position, with an instruction to focus on movement accuracy. Particular interest was given to the NV-MG condition considering that it has been proposed that performance under this condition may rely on a distinct, non-visual control mechanism (e.g., Elliott et al., 1991). Four main hypotheses were posited. First, it was predicted that conventional measures of movement planning and online control (i.e., reaction time & peak limb velocity; time after peak limb velocity & Fisher²) would distinguish performance across the FV, NV, and NV-MG conditions. Second, based on the findings of de Grosbois and Tremblay (2015), it was hypothesized that the influence of visuomotor online
control mechanisms would be apparent in frequency domain analyses and would yield greater contributions to the proportional power spectra in the FV compared to the NV condition at approximately 5 Hz. Third, it was hypothesized that if the performance in the memory-guided conditions is also mediated by a comparable feedback mechanism to the NV condition, then the proportional power at 5 Hz will also differentiate the memory-guided responses from the FV condition. Alternatively, if distinct, non-visual mechanisms (e.g., Elliott et al., 1991) contribute to performance in the NV-MG condition, then that condition should yield increased proportional power at one or more additional frequencies\(^2\). If the online control processes utilized in this condition were to be mediated by proprioceptive mechanisms, their influence could be expected to impact frequencies of approximately 20 Hz, or higher (e.g., latencies of 50 ms or lower; see Scott et al., 2015). Fourth, the use of two target amplitudes, was expected to influence spatio-temporal constraints of the movement and alter the opportunity and the requirement for the online control processes. As a result, it was hypothesized to increases in target amplitude would lead to greater increases in the pPower at approximately 5 Hz in the FV condition relative to the NV condition to a greater extent for the 30-cm compared to the 10-cm target. That is, when reaching to a 30-cm target, more time is available to implement online corrective processes, resulting in a greater relative contribution of such processes (e.g., Khan et al., 2003).

Additionally, given the relative stability of corrective reaction times to visual perturbations (e.g., Saunders & Knill 2003; Cressman, et al., 2010), it was hypothesized that visuomotor feedback mechanisms would operate at a constant rate (e.g., Crossman & Goodeve, 1983) and therefore exert their influence on the pPower spectra at a comparable frequencies for both target amplitudes. Alternatively, if moving to closer targets prompts more closely initiated trajectory amendments, then participants may resort to control strategies which could increase the rate at which online control processes operate.

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2 It has been previously proposed that online control may not necessarily act at regular intervals (e.g., Cruse, Dean, Heuer, & Schmidt, 1990; Navas & Stark, 1968: see discussion).
4.2.2 Methods

4.2.2.1 Participants

Eighteen individuals participated in the current experiment (i.e., 7 males; 11 females; age range 19 to 47; mean age = 24). All participants were right-handed as determined by a modified version of the Oldfield handedness questionnaire (1971). Participants provided written informed consent prior to commencement of the experiment and were compensated $10 CAD following participation.

4.2.2.2 Materials and apparatus

The experimental procedures were completed in a dimly lit room (i.e., lux = 1; see Figure 4.2.2 for a depiction). Participants sat in a kneeling chair in front of a desk upon which a custom aiming console was placed (51 cm long by 28 cm wide by 9 cm high). A home position (i.e., a 1 by 1 cm Velcro™ square) was affixed to the surface of the aiming console. This home position was aligned with the participant's mid-line. Inlaid under the surface of the aiming console were two green light emitting diodes (i.e., LEDs; appeared circular with a 0.5 cm diameter). These LEDs were positioned 10 and 30 cm to the right of the home position and were visible to the participant only when illuminated. These two target distances were chosen because movements of longer duration likely result in a greater contribution of sensory feedback mechanisms (e.g., Khan et al., 2003). Participants wore liquid-crystal goggles (PLATO; Translucent Technologies Inc., Toronto, ON, Canada; see Milgram, 1987), which manipulated the availability of vision of the environment. Also, based on the sampling frequency (see below), the computation time, the analog-to-digital transduction time and the time for the goggles to change state, the time between a kinematic criterion and change in vision condition was estimated at less than 7 ms. As such, the study was deemed to employ real-time manipulations. A wrist-brace was worn on the participant's right wrist, and it was fitted with a triple axis accelerometer (MMA7361L; NXP Semiconductors, Eindhoven, Netherlands). The accelerometer was connected to a multi-function data acquisition card (model PCI-6042E, National Instruments Inc., Austin, TX, USA). Participants also wore an infrared light emitting diode (i.e., an IRED) on the dorsal surface of the
distal phalanx of their right index finger. The position of this IRED was monitored by an Optotrak Certus motion tracking system (Northern Digital Inc., Waterloo, ON, Canada). The Optotrak and the accelerometer were sampled concurrently in real-time (i.e., on a sample-by-sample basis) at a common rate of 250 Hz. This sample rate was chosen based on the available hardware, and was the fastest rate at which both the IRED and the accelerometer could be concurrently sampled. The control of the experimental procedures were mediated by custom MATLAB (The Mathworks Inc., Natick, MA, USA; VERSION: R2010a) scripts.

4.2.2.3 Design and procedures

The primary task of participants was to complete rightward reaching movements from the home position aligned with their mid-saggital axis, to an illuminated target, following an auditory go-signal (see Figure 4.2.2). Participants were instructed to move quickly but to focus on maintaining a high level of accuracy. Performance was assessed in one of three visual conditions (i.e., full-vision: [FV]; no-vision: [NV]; and no-vision memory guided: [NV-MG]; see Figure 4.2.3 for exemplar trial progressions). Regardless of vision condition, each trial began with the participant's finger on the home position and the goggles closed (i.e., translucent). The goggles were then opened (i.e., made transparent) and the target for a given trial was illuminated (i.e., randomly selected on a trial-by-trial basis). Following a 3 to 3.5-s variable foreperiod, a piezoelectric buzzer (Mallory Sonalert Products Inc., Indianapolis, IN, USA) emitted a 50-ms sound to instruct the participant to begin a reaching movement. Movement start was defined as the first sample after which the instantaneous velocity of the finger—via a two-point differentiation—in the primary direction of movement rose above 30 mm/s for at least three consecutive samples (i.e., 12 ms). Movement end was determined when the instantaneous velocity of the finger fell below 30 mm/s and remained there for at least five consecutive samples (i.e., 20 ms). Regardless of vision condition, to minimize terminal feedback and therefore, the influence of offline control processes, the liquid-crystal goggles were closed when the movement end criterion was met (e.g., Roberts et al., 2013; Salmoni, Schmidt, & Walter, 1984). The three vision conditions differed in terms of the timing of the opening and closing of the liquid-crystal goggles prior-to and during the movement (see Figure 4.2.3). In the FV
condition, the goggles remained open from the time of the target illumination until the end of the
reaching movement. In the NV condition the goggles remained open from the target illumination
until the start of the movement. In the NV-MG condition the goggles were open for one second
following the target illumination. That is, in the NV-MG condition the goggles were closed 2 to
2.5 s prior to the go-signal and remain closed throughout the remainder of the trial (see Figure
4.2.3). These three vision conditions were arranged in three blocks of 100 trials (i.e., 50 trial per
target per vision condition). Importantly, the target amplitude was randomized from trial-to-trial,
thus minimizing the advantage of pre-programming a response prior to the go-signal. Each block
was preceded by 6 familiarization trials of the upcoming condition. Thus, a total of 318 total
trials were completed by each participant in approximately 60 minutes. Based on the blocked
arrangement of trials, there were six possible block orders. Block ordering across participants
was pseudorandomized wherein three participants completed each order.

4.2.2.4 Data processing and analysis

Although the primary analyses contrasted changes in online control mechanisms during
reaching, it is possible that trial-to-trial changes in performance also influenced performance
(e.g., planning differences arising from offline feedback; see Plamondon & Alimi, 1997),
especially when initiating movements under different sensory environments (e.g., Rossetti,
Stelmach, Desmurget, Prablanc, & Jeannerod, 1994). Thus, this alternate possibility was
evaluated through the additional analyses of reaction time (RT) and peak limb velocity (PV).

The main analysis was completed using three measures of online feedback utilization.
These included two conventional measures of online control, namely: the time spent after peak
limb velocity up until the end of the movement (i.e., time-after-peak-velocity: TAPV; e.g., Elliott
et al., 1991); and the square of the Fisher transform of the correlation of position at 75 %
movement time to the position at movement end (i.e., correlational analysis: Fisher\(^2\) analysis;
e.g., Bernier et al., 2006; de Grosbois & Tremblay, 2015). The 75 % movement proportion was
evaluated in the Fisher\(^2\) analysis (cf., Heath, 2005) because differences in feedback utilization
tend to be most apparent in the later stages of movements (e.g., Khan et al., 2006). The third and
novel measure of online feedback utilization was the frequency domain analyses (pPower analysis: see de Grosbois & Tremblay, 2016).

The frequency analyses were completed on the accelerations profiles of the movement trajectories in the primary movement axis. Acceleration profiles were chosen in part due to the similarity of their form to sine waves, which along with cosine waves, are key components of frequency domain analyses. The variability associated with discontinuities in the acceleration traces was isolated by fitting a 5th order polynomial to each of the acceleration traces and the residuals of these fits were forwarded to the frequency analyses. The fitted polynomials were computed via the MATLAB polyfit() and polyval() functions (see Appendix 1). That is, the polynomial weights were computed with the polyfit() function and the associated function values were calculated from those weights using the polyval() function. The choice in polynomial fit order (i.e., 5th) was determined by working from the assumption that through the minimization of jerk (e.g., Flash & Hogan, 1985), which stipulates that optimal movements are planned as smooth acceleration-deceleration profiles. That is, an unaltered acceleration trajectory should be characterized by four bends. Also, the variability of interest was expected to be more likely contained in the “corrective jitter” about this overall form (e.g., Noy, Alon, & Freidman, 2015). These residuals were pre-processed by multiplying a Hanning truncation window with the data (i.e., generated via the MATLAB hanning() function to be the same length as the data; e.g., Randall, 2008; Warner, 1998) before being converted into a frequency domain representation via a Fast Fourier Transform (FFT; via the MATLAB fft() function). The power spectra were computed by multiplying the Fourier coefficients by their complex conjugates (i.e., via the MATLAB conj () function) and dividing by the transform length. The spectra were normalized by the total power up to the Nyquist frequency (i.e., 125 Hz), which resulted in estimates of the proportional contribution of particular iterative rates/frequencies to the overall signal (i.e., the proportional power: pPower). The normalized spectra were computed and utilized instead of raw spectra because individual differences were anticipated, which would also contain both signal-dependent and signal-independent sources of noise (e.g., van Beers, Haggard, & Wolpert, 2004). As such, a relative metric was deemed to better represent the relative contributions of the online
control processes. An FFT transform length of 256 samples was chosen because movements to the 30-cm targets often exceeded 128 samples (i.e., 512 ms) resulting in a potential frequency resolution of 0.976 Hz (i.e., 250 Hz/256 samples). However, because many movements to the 10-cm target yielded movement times less than 128 samples, data from these movements would not afford a frequency resolution below 1.95 Hz. Thus, to evaluate all conditions comparably, all FFTs were first computed using a 256 sample transform length. Then, the pPower at each ascending pair of non-zero frequencies were binned to achieve a set of non-interpolated (i.e., the true frequency resolution of the 10-cm movements) estimates of pPower for both target amplitudes (e.g., frequency bin value associated with 1.95 Hz was computed as the sum of the pPower at 0.97 Hz and the pPower at 1.95 Hz). Importantly, this analysis provided an overall estimate of the frequency content across the entire trajectory, which was judged as being particularly sensitive to iterative corrective processes. Furthermore, given that sensorimotor feedback processes were expected to influence reaching trajectories at rates possibly exceeding 20 Hz (e.g., proprioceptive spinal feedback circuits; e.g., Scott et al., 2015), the associated spectra were evaluated up to 30 Hz.

Omnibus analyses were completed as 3 Vision Condition (i.e., FV, NV, NV-MG) x 2 Target (i.e., 10 cm, 30 cm) repeated-measures ANOVAs. Prior to the analysis of the pPower, the spectra were first qualitatively evaluated for the presence of observable peaks. Then, the frequency and magnitude of such peaks were further analyzed to evaluate the presence of differences between conditions. Effect sizes were reported as the generalized eta squared ($\eta_g^2$; see Bakeman, 2005; Olejnik & Algina, 2003). When the assumption of sphericity was violated, Greenhouse-Geisser corrected degrees of freedom were used to assess significance. Significant effects were further evaluated, when necessary, using a simple main effects approach with a focus on comparisons between vision conditions. Furthermore, when main effects and interactions were observed for the same experimental factor, only the highest-order interaction

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3 Some temporal information could be theoretical ascertained with more advanced frequency domain techniques. However, such temporal information would be inherently limited by the short duration of the movements employed in the current study.
was subjected to post-hoc analysis. In situations where post-hoc analysis required more than one statistical test, a Bonferroni correction was applied to the \( p \)-values of the tests, based on the number of tests completed (i.e., reported as \( p_{bs} \) where 'b' indicates that the \( p \)-value has been subjected to a Bonferroni correction, and 'x' indicates the number of tests corrected for). Lastly, all error bars depicted in figures represent within-subject 95% confidence intervals (see Loftus & Masson, 1994).

4.2.3 Results

A summary of all omnibus ANOVA effects and associated inferential statistic values can be found in Table 4.2.1. A summary of all dependent variables' means and standard deviations across conditions can be found in Table 4.2.2.

Although not directly associated with the main hypotheses, differences between end point accuracy and precision, as well as movement time could be expected based on the chosen manipulations (e.g., Elliott et al., 1991). As such, a supplementary analysis of these variables has also been completed (see section 4.2.6.1).

4.2.3.1 Evidence for planning differences

The analyses of RT resulted in a significant main effect of only Target (see Figure 4.2.4, panel a). RTs to the 10-cm Target (\( M = 291 \) ms, \( SD = 51 \)) were significantly shorter than RTs to the 30-cm Target (\( M = 299 \) ms, \( SD = 48 \)).

The analysis of PV resulted in significant main effects of Vision Condition and Target as well as a significant interaction between Vision Condition and Target (see Figure 4.2.4, panel b). Post-hoc analyses of the interaction were conducted through repeated-measures ANOVAs within each level of Target across the levels of Vision Condition. Ultimately, the pattern of PV results across the vision conditions at each target amplitude was comparable. That is, the ANOVAs for both the 10-cm and 30-cm targets yielded significant effects of Vision Condition, \( F_s(2,34) > 7.20, p_{bs} < .005, \eta^2_p > .073 \). Post-hoc pairwise comparisons were completed across vision
conditions within each target and revealed that the NV-MG condition yielded significantly slower PVs in comparison to the other two conditions for both targets (i.e., \( p_{0.03} < .042 \); see Table 4.2.2). Conversely, no significant differences in PV values were observed between the FV and NV conditions for either target (i.e., \( p_{0.03} > .621 \); see Table 4.2.2).

4.2.3.2 Evidence for online control

The analyses of TAPV yielded a significant main effect of only Target (see Figure 4.2.5, panel a). TAPVs to the 10-cm target (\( M = 185 \) ms, \( SD = 30 \)) were significantly shorter than TAPVs to the 30-cm target (\( M = 266 \) ms, \( SD = 40 \)).

Analysis of the square of the Fisher transform of the correlation between finger position at 75\% movement time and finger position at movement end (i.e., Fisher\(^2\)) yielded significant main effects of both Vision Condition and Target (see Figure 4.2.5, panel b). Post-hoc analysis of the main effect of Vision Condition resulted in significant differences between each of the three Vision Conditions (i.e., FV: \( M = 1.22 \), \( SD = 0.41 \); NV: \( M = 2.60 \), \( SD = 0.90 \); NV-MG: \( M = 4.33 \), \( SD = 0.93 \); all \( p < .001 \)). That is, Fisher\(^2\) values were lowest in the FV condition, intermediate in the NV condition, and highest in the NV-MG condition. The main effect of Target was driven by larger Fisher\(^2\) values for movements to the 10-cm target distance (i.e., \( M = 3.40 \), \( SD = 0.73 \)) as compared to movements completed to the 30-cm target distance (i.e., \( M = 2.03 \), \( SD = 0.52 \)).

Initial qualitative examination of the proportional power spectra (i.e., pPower) indicated that two general peaks could be observed in the range of frequencies examined (see Figures 4.2.6, panels a and b). One peak at the lower end of the spectra (i.e., between approximately 4 and 12 Hz), and another peak at a higher range of frequencies (i.e., between 18 and 24 Hz). Considering that individual differences in corrective reaction times have also been observed previously (e.g., with aging; see Sarlegna, 2006), both the frequency and the peak pPower were identified across these two ranges for each participant. Notably, these ranges were determined through the visual examination of the mean participant data (see Figure 4.2.6). For simplicity,
the lower peak was operationally defined as the \( \alpha \) (alpha) peak\(^4\) and explicitly identified as the maximum pPower between 3.90 and 13.65 Hz. The higher frequency peak was defined as the \( \beta \) (beta) peak and identified as the maximum pPower between 17.55 and 23.40 Hz. Analyses were completed for both the frequency and the magnitude of both the \( \alpha_{\text{peak}} \) and the \( \beta_{\text{peak}} \). Such analyses were completed via the identification of the magnitude and the frequency of the \( \alpha \) and \( \beta \) peaks, within each participant's condition-specific mean spectra. Then, these magnitudes and frequencies were subjected to analyses of variance with the same factorial arrangement as the other dependent measures.

Considering first the \( \alpha_{\text{peak}} \), the analysis of the frequency of this peak yielded a main effect of only Target. The \( \alpha_{\text{peak}} \) occurred at a significantly higher frequency for the 10-cm Target (i.e., \( M = 9.50 \text{ Hz}, SD = 1.81 \)) than the 30-cm Target (i.e., \( M = 6.79 \text{ Hz}, SD = 1.27 \)).

Analysis of the magnitude of the \( \alpha_{\text{peak}} \) yielded significant effects of Vision Condition and Target. Post-hoc analyses of the main effect of Vision Condition revealed a significantly greater pPower magnitude associated with the FV condition (i.e., \( M = 15.63 \% \), \( SD = 3.96 \)) relative to either the NV (i.e., \( M = 13.20 \% \), \( SD = 2.83 \)) or NV-MG (i.e., \( M = 12.55 \% \), \( SD = 4.04 \)) conditions (i.e., \( p_{\text{sh}} < .004 \)), which were not significantly different from one another (i.e., \( p_{\text{sh}} > .999 \)). The main effect of Target resulted from significantly greater pPower for the 30-cm Target (i.e., \( M = 16.99 \% \), \( SD = 4.20 \)) relative to the 10-cm Target (i.e., \( M = 10.61 \% \), \( SD = 3.08 \)).

Considering that no \( \beta_{\text{peak}} \) was observable for the FV condition (see Figure 4.2.6), only the other two vision conditions were first included in the analysis to identify the frequency at which this peak occurred (i.e., a 2 Vision Condition x 2 Target repeated-measures ANOVA). This analysis resulted in no significant effects or interactions. However, the mean frequency of the \( \beta_{\text{peak}} \) across the NV and NV-MG conditions was 19.26 Hz (\( SD = 0.71 \)). Therefore, regarding the

\(^4\) In addition to the alpha range of frequencies (i.e., 8 to 12 Hz), the theta (4 to 7.5 Hz) range of frequencies common to neurophysiological research (e.g., Michel, Lehmann, Henggeler, & Brandeis, 1992) was also included in our \( \alpha_{\text{peak}} \) range. However, alpha was chosen as a parsimonious label for this peak because the peak was observed at frequencies into this higher range (i.e., 9.5 Hz).
magnitude of the $\beta_{\text{peak}}$ for the FV condition in the primary movement axis, the nearest frequency that could be resolved (i.e., 19.50 Hz) was chosen.$^5$

The subsequent analysis of the magnitude of the $\beta_{\text{peak}}$ across all Vision Conditions in the primary movement axis yielded significant main effects of Target and Vision Condition. The effect of Target was driven by larger pPower associated with the 10-cm Target (i.e., $M = 5.16\%$, $SD = 1.65$) relative to the 30-cm Target (i.e., $M = 3.82\%$, $SD = 1.26$). Post-hoc analysis of the effect of Vision Condition indicated that the FV condition yielded significantly lower pPower (i.e., $M = 3.13\%$, $SD = 1.45$) relative to both the NV (i.e., $M = 5.11\%$, $SD = 1.35$) and-MG conditions (i.e., $M = 5.24\%$, $SD = 1.44$; $p_{sb3} < .001$), which were not significantly different from one another (i.e., $p_{b3} > .999$).

4.2.4 Discussion

The main purpose of the current study was to investigate if distinct (i.e., visual and non-visual) online control mechanisms underlie performance differences observed between FV, NV, and NV-MG conditions. Four hypotheses were forwarded. First, it was hypothesized that across vision conditions, conventional measures of movement planning and online control would indicate changes in the reliance on planning and online feedback utilization. Second, it was hypothesized that visuomotor online control feedback mechanisms would differentiate FV from the NV condition at approximately 5 Hz. Third, it was hypothesized that in the NV-MG condition, the reliance on a different feedback mechanism would result in changes in the frequency domain representation of performance based upon the timescale (i.e., frequencies) of the respective mechanism involved. Fourth and last, it was hypothesized that the distance to the target (i.e., 10 or 30 cm) would influence the relative reliance on feedback mechanisms. That is, longer movements would afford a greater relative contribution of comparable feedback

$^5$ Importantly, given the absence of an apparent $\beta_{\text{peak}}$ in the FV condition, the comparison between the FV condition and the two NV conditions could be considered as rather artificial. However, it was deemed important to statistically evaluate the relative power at a comparable frequency to ensure that the presence of the peak lead to a statistically significant increase in pPower.
mechanisms (i.e., comparable frequencies across targets). Each of these hypotheses has been contrasted with the results, as follows.

4.2.4.1 Performance differences between conditions

Prior to the evaluation of changes in the planning and control of the movements completed across vision conditions, supplementary analyses were performed on end point constant error and variable error. These analyses were completed to ensure that performance differences were present between the vision conditions conditions that could ultimately be attributable to changes in either planning or online control.

The supplementary analyses indicated that constant error in the primary movement axis reflected the tendency of participants to undershoot the 30-cm target in the NV-MG condition, relative to both the FV and the NV conditions. Second, lesser occlusion of vision led participants to exhibit smaller end point variability (i.e., FV < NV < NV-MG). Thus, given the different patterns of results across constant and variable error, the three vision conditions may have differed significantly in both their planning and their online control. For example, the observed target undershooting at the 30-cm target in the NV-MG condition may have resulted from strategic planning differences to minimize the possibility of energetically costly target overshoots in the presence of target-location uncertainty (e.g., Elliott, Hansen, Mendoza, & Tremblay, 2004). In contrast, the observed variable error differences could indicate that performance in the NV condition exhibited greater online feedback utilization than the NV-MG condition. That is, the NV condition may have benefit from the ability of the visual system to make use of the recently available visual information to perform online trajectory amendments (e.g., Elliott and Madalena, 1987).

4.2.4.2 Evidence for changes in movement planning across conditions

Two measures yielded significant differences pertaining to the planning of the voluntary reaches. First, the analysis of reaction time revealed only a significant effect of target distance. Movements to targets of significantly larger amplitudes are typically associated with longer
movement durations, which have been associated with planning differences measured via reaction times (e.g., Klapp & Erwin, 1976). It has also been reported that reaction times of movements completed under FV conditions are shorter than reaction times for movements in NV (e.g., Carson, Chua, Elliott, & Goodman, 1990; Khan, Elliott, Coull, Chua, & Lyons, 2002), however, such differences were not observed in the current experiment (see also Heath, 2005). Nevertheless, the pattern of reaction time results for the three vision conditions in the current study was consistent with the previous findings (i.e., FV < NV; e.g., Carson et al., 1990). Thus, based upon the analysis of reaction time, it is possible that participants made changes to their movement plans in response to changes in the experimental conditions. Such potential changes in planning from movement to movement may have biased the estimates of multiple-trial measures of online control towards false positives relative to within-trial measures.

Second, the PV results were interpreted as evidence of differences in planning mechanisms. Although recent models of online control posit that the influence of online control can take place before PV (e.g., Elliott et al., 2010), neurophysiological data associated with premotor cortex activity has been shown to parallel the velocity of an upcoming movement (e.g., Churchland, Santhanam, & Shenoy, 2006). As such, the analysis of the PV data can be used to support the idea that there were differences in movement planning between conditions. Participants reached higher peak velocities in the two conditions wherein vision was available during moment preparation and planning (i.e., the FV and NV conditions) as compared to the NV-MG condition. Notably, this was the case at both target amplitudes. Thus, there was evidence supporting the notion of differences in movement planning between the NV-MG condition and the other two vision conditions (i.e., the FV and NV conditions). Such an idea also is consistent with the real-time programming of action hypothesis (see Westwood & Goodale, 2003). That is, participants may have planned their movement based on the sensory information available to them at the time of movement initiation, resulting in more similar movement planning in the FV and NV conditions relative to the NV-MG condition. Altogether, performance differences in both RT and PV across the vision conditions were likely influenced by changes in movement planning. Ultimately, the forthcoming evaluation of online control must
be interpreted acknowledging the possibility of biases in multiple-trial measures considering that planning influences would predominantly exert their influence on a trial-to-trial basis.

4.2.4.3 Evidence for changes in online control: Conventional measures

Regardless of the potential for planning differences across the conditions in the current study, changes in online control were also anticipated between the FV and the NV conditions, especially at the 30-cm Target. First, considering the time spent following peak velocity in the primary movement axis, participants spent significantly more time after peak velocity when moving to the 30-cm compared to the 10-cm target. Because online feedback utilization is a time-consuming process, longer movements inherently afford a greater contribution of online feedback mechanisms (e.g., Howarth et al., 1972). Conversely, TAPV did not differentiate performance between any Vision Condition (i.e., FV, NV, & NV-MG). Although differences in the time following peak velocity has been associated with online visual feedback utilization (e.g., Elliott et al., 1991), the expected increases in TAPV in FV relative to NV conditions have not consistently been replicated (e.g., de Grosbois & Tremblay, 2015; Heath, Westwood, & Binsted, 2004). Also, the relative symmetry of a velocity profile may not necessarily be representative of modulations of visuomotor mechanisms alone (e.g., proprioceptive control; see Manson et al., 2014). Furthermore, in the Elliott et al. (1991) work, the TAPV was also longer when the instructions to be accurate were given. Ultimately, although TAPV may be positively correlated with online visual feedback utilization under some conditions, it may not be a valid measure of online visual feedback utilization under all situations.

The analysis of Fisher$^2$ indicated differential feedback utilization across vision conditions. The FV condition yielded greater evidence for the contribution of online control relative to both of the NV conditions. Also, the NV condition yielded evidence for a greater contribution of online control processes relative to the NV-MG condition. The FV vs. NV differences observed were consistent with previous findings and indicated that the trajectories of movements completed with online vision available were significantly less stereotyped across trials, relative to those without online vision (e.g., Bernier, Chua, Franks, & Khan, 2006; de Grosbois &
Tremblay, 2015; Heath, 2005; Tremblay, Hansen, Kennedy, & Cheng, 2013). Although, the difference observed between the NV and NV-MG conditions for the Fisher\textsuperscript{2} values has not been previously observed (e.g., Krigolson, Clark, Heath, & Binsted, 2007), online control differences have been proposed between NV and NV-MG conditions (e.g., Elliott & Madalena, 1987). That is, the performance in the NV condition, where vision of the environment was available during movement planning, may have benefited from a control mechanism more similar to the FV than NV-MG condition (cf., Franz, Hesse, & Kollath, 2009). Consistent with this notion was the proposition made by Elliott et al. (1991) that under NV conditions, there may be a persistence of visual information from which to control actions (see also Elliott & Madalena, 1987).

Alternatively, given its multiple-trial nature, the Fisher\textsuperscript{2} variable may also be sensitive to changes in movement planning from one trial to the next. Consistent with the possibility of planning differences between the NV and the NV-MG conditions, Rossetti et al. (1994) reported a negative relationship between endpoint variability and reaction time, only if the hand was concurrently visible at the time of the go-signal. Thus, the removal of the visibility of the hand in the NV-MG condition prior to the go-signal may have also altered planning processes in addition to online control. Such an assertion is consistent with the PV data examined above. Altogether, despite some expected differences in the measures typically associated with online control mechanisms, it is also possible that planning differences also contributed to the performance across the three vision conditions.

4.2.4.4 Evidence for changes in online control: Frequency domain analysis and the differential contributions of distinct visual and non-visual processes

Analysis in the frequency domain yielded three main findings. First, the current study replicated de Grosbois and Tremblay (2015) through greater pPower at the $\alpha_{\text{peak}}$ for the FV condition relative to both the NV conditions, indicating a greater contribution of visuomotor control processes at the $\alpha_{\text{peak}}$. The range of mean frequencies of the $\alpha_{\text{peak}}$ across targets amplitudes (i.e., 6.79 & 9.50 Hz: see above) could be associated with visuomotor iteration times of 105 to 147 ms, which is consistent with estimates of corrective reaction times to visual perturbations (e.g., Brenner & Smeets, 1997; Proteau, Roujoula, & Messier, 2009; Saunders & Knill, 2003;
Saunders & Knill, 2005) and the estimated processing time for visual information to stable targets (e.g., Zelaznik, Hawkins, & Kisselburgh, 1983). This range of frequencies was higher than those reported by de Grosbois and Tremblay (2015; i.e., 4.68 Hz), with a caveat. Although the 4.68 Hz frequency was the only reported significant difference in de Grosbois and Tremblay (2015), the adjacent peak frequency (i.e., 6.25 Hz) yielded a similar pattern of results and can be directly associated with the $\alpha_{\text{peak}}$ of the current study. That is, the peak frequency observed in de Grosbois and Tremblay (2015) was 6.25 Hz, which is arguably comparable to the mean $\alpha_{\text{peak}}$ frequency value observed for the 30-cm Target in the current study (i.e., 6.79 Hz). The difference observed in the current study may have reflected an increased statistical power due to a relatively large increase in both trials-per-condition (i.e., 50 vs. 30) and participants (i.e., 18 vs. 10). Overall, the pattern of results of the current study is consistent with the findings of de Grosbois and Tremblay (2015). As well, given the inherent sensitivity of frequency domain analyses to iterative processes, the current study reaffirmed the concept of an iterative online control process that yields overlapping adjustments implemented at regular intervals.

The second frequency domain analysis finding was that, in the absence of online visual information, a secondary, higher frequency peak was also observed (i.e., the $\beta_{\text{peak}}$, around 19.5 Hz). Differences were observed in the pPower spectra at the $\beta_{\text{peak}}$ between the FV condition and both the NV and NV-MG conditions. Admittedly, only the NV conditions yielded a clear $\beta_{\text{peak}}$. This was the case for both target amplitudes. Further, these differences could not logically represent the contribution of an online visuomotor feedback mechanism because of the higher pPower for the condition without vision compared to the FV condition. As such, this increase in pPower at the $\beta_{\text{peak}}$ likely reflected the contribution of some non-visually-mediated process. The proposed contribution of proprioceptive control processes, as suggested by Elliott et al. (1991), could possibly explain the increase in the pPower for the $\beta_{\text{peak}}$ analysis. Such high iteration rates are unlikely for cortically-mediated proprioceptive mechanisms (i.e., approximately 50 ms). However, adjustments to changes in force applied to an arm have been reported to occur at latencies consistent with this frequency peak (e.g., Franklin, So, Osu, & Kawato, 2008; Scott et al., 2015). The absence of the $\beta_{\text{peak}}$ in the full-vision condition is consistent with this explanation,
given that the presence of online visual feedback typically improves the accuracy and precision of reaching performance (e.g., Elliott & Madalena, 1987) and that the reliance on proprioceptive mechanisms may become more apparent in no-vision conditions (e.g., Elliott et al., 1991). In addition, there is evidence that central mechanisms can alter the excitability of spinal reflex pathways in a task-relevant manner (e.g., Meunier & Pierrot-Deseilligny, 1989). Thus, it is possible that in the presence of online vision, the contributions of the proposed proprioceptive process was suppressed to facilitate performance. Admittedly, another possible explanation for the $\beta_{\text{peak}}$ resides in changes in feedforward rather than feedback-based control. Such a control process would theoretically not be inherently limited by sensory-based feedback loops and could ultimately iterate at relatively faster rates (e.g., Desmurget & Grafton, 2000). Yet, it is not possible to prove this point either and further investigations are required to investigate this process.

Lastly, a third and non-mutually exclusive explanation to the ones above is a change in movement strategy. That is, given the foreknowledge of the upcoming visual conditions, participants may have opted to plan/control their movements in a strategically different manner. Such a proposition would lead to the prediction that under a trial order with randomized vision conditions, no $\beta_{\text{peak}}$ would be expected because participants would likely plan each movement in a similar manner prior to the knowledge of the upcoming vision condition (i.e., plan for the worst-case scenario; e.g., Elliott et al., 2004; Hansen, Glazebrook, Anson, Weeks, & Elliott, 2006; Zelaznik, et al., 1983). Given this prediction, it is unsurprising that randomized vision conditions of de Grosbois and Tremblay (2015) did lead to evidence for a $\beta_{\text{peak}}$. Thus, differences in pPower across vision conditions in the current study for the $\beta_{\text{peak}}$ could be mediated by changes in strategic planning and/or control mechanisms. Although further research is required to confidently identify the specific underlying mechanism of the observed changes in the $\beta_{\text{peak}}$, it remains that the high frequency peaks in the pPower analysis are necessarily associated with non-visual movement control processes. Critically, when randomizing vision conditions de Grosbois and Tremblay (2015) still observed significant differences between full vision and no-
vision conditions around the $\alpha_{\text{peak}}$, indicating that this lower peak very likely represents the contribution of a visuomotor online control process.

The third and most important finding was that the frequency at which the $\alpha_{\text{peak}}$ was observed was dependent upon the amplitude of the movement. That is, the peak was observed at a higher frequency when less time was available during the movement. By including a large difference in target amplitudes, the current study expanded upon the previous work of de Grosbois and Tremblay (2015). Consistent with their results, the contribution of visuomotor online control mechanisms increased the relative magnitude of the frequency content at the $\alpha_{\text{peak}}$. When the movements were made to the 30-cm target, the influence of visual feedback mechanisms was observed at a significantly slower rate (i.e., 140 ms) relative to performance associated with the 10-cm target (i.e., 105 ms). The corrective frequency associated with the 10-cm target represented a shift to a rate consistent with the lower limit of the range of correction latencies previously reported for hand movements (e.g., Carlton, 1992; Veerman, Brenner, & Smeets, 2008). Thus, it appears that when time is limited, participants may maximize the rate at which corrections are made. That is, the rate at which online corrections are made within a feedback mechanism may be flexible.

The idea of flexible control of action is not new per se. Visual and mechanical perturbation studies have yielded evidence for flexible control mechanisms (e.g., Cruse et al., 1990; Dimitriou, Wolpert, & Franklin, 2013; Knill, Bondada, & Chhabra, 2011; Liu & Todorov, 2007). More relevant to the present study, evidence for flexibility in the rates of feedback utilization and the association of distinct rates with distinct feedback mechanisms have been reported for both isometric force (e.g., Sosnoff & Newell, 2005) and manual tracking tasks (e.g., Navas & Stark, 1968; Miall, 1996; Miall & Jackson, 2006). However, the shortest correction intervals/delays in these studies were much longer (i.e., 250 ms or more) than the shortest periodicity detected with the frequency analyses in the current study (i.e., 9.5 Hz or approx. 105 ms). A theoretical explanation for a shift in the rate of fast corrections for reaching movements in the current study is grounded in the possibility that participants may not have been continuously correcting their ongoing trajectories (cf., Elliott et al., 1991). Rather, participants may have
instead adopted a strategy of continuous monitoring visual information accompanied with intermittent corrections (e.g., Proteau et al., 2009). Proteau et al. (2009) found evidence for this assertion in that removing vision of a cursor approximately 57-85 ms following a cursor jump had no significant influence on the accuracy of the corrected movements, relative to movements completed wherein the cursor remained visible following the cursor jump. This proposed monitoring strategy could come about logically through an optimization of energy expenditure (e.g., Elliott, Hansen, Mendoza, & Tremblay, 2004; Tremblay et al., 2017). That is, when making longer movements, fewer and more sparsely separated corrections may provide a more economical approach compared to a greater number of potentially inefficient corrections. Critically, the interval between trajectory amendments can significantly change as with amplitude-driven changes in spatio-temporal constraints.

Ultimately one significant caveat must also be acknowledged. That is, the frequency of the $\alpha_{\text{peak}}$ shifted for movements to the 10-cm target amplitude irrespective of vision condition. Thus, it is clear that some other factor influenced the frequency of this peak. One possibility is that mechanical factors due to changes in the relative involvement of the elbow and shoulder joints in the movement. That is, the shorter movement amplitude may have been mediated to a greater extent by elbow extension. As such mechanical oscillations associated movement at the elbow would result in a higher frequency relative to those attributable to the shoulder (e.g., Elble & Koller, 1990). This potential explanation requires further research, as does the definitive cause of the observed shift in frequency. Nevertheless, the amplitude of the $\alpha_{\text{peak}}$ reliably scaled with online visual feedback availability. Altogether, the current study does provide initial evidence in favour of the flexibility of the rates of online feedback utilization.

4.2.5 Conclusions

The purpose of the current study was to gain insights into the underlying online control sensory feedback mechanisms that differentiate performance across FV, NV, and NV-MG conditions. Overall, when assessing a measure of online control (i.e., Fisher$^2$), all three vision conditions differed from one another. Thus, using the traditional measures of online control, the
evidence for online feedback utilization was greatest in the FV, lowest in the NV-MG and intermediate in the NV conditions. However, this measure may have been contaminated by planning differences on a trial-to-trial basis.

The frequency domain analyses, however, yielded a different pattern of results across vision conditions. The presence of concurrent vision increased the contribution of visual control mechanism(s), potentially iterative in nature, at rates between approximately 7 to 10 Hz. Second, evidence for a distinct, non-visual mechanism acting at a faster iteration rate of approximately 20 Hz was found, although further research will be required to determine which non-visual process was utilized and if it is indeed an online control process. Last but not least, the frequency at which online visuomotor mechanisms exerted their influence decreased when reaching amplitudes increased from 10 cm to 30 cm, providing evidence of flexible rates at which online visual feedback is utilized during reaching movements. Altogether, reaching performance under different visual conditions is mediated by separate mechanisms and the iterative rate associated with visuomotor feedback utilization is flexible for the control of reaching movements.

4.2.6 Supplementary Analyses

4.2.6.1 End point accuracy, precision, and movement time analyses

End point accuracy was defined as the constant error of the average of the primary axis movement end points within each condition. End point precision was calculated as the variable error associated with the same movement end points. Movement time was defined as the time elapsed between movement onset and movement end.

Analysis of constant error in the primary movement axis yielded a significant Vision Condition by Target interaction, $F(2,34) = 6.21, p = .005, \eta^2_G = .022$. Significant differences were observed only at the 30-cm Target, whereby the NV-MG condition yielded significantly greater undershooting (i.e., $M = -22.5$ mm, $SD = 34.2$) relative to both the NV condition (i.e., $M = -4.9$ mm, $SD = 27.6$) and the FV condition (i.e., $M = 2.4$ mm, $SD = 3.2$; $p_{bs} < .018$), which did not differ significantly ($p = .826$). Conversely at the 10-cm Target, no significant differences
were observed between Vision Conditions (i.e., NV-MG: $M = -9.6$ mm, $SD = 18.3$; NV: $M = -3.2$ mm, $SD = 14.5$; FV: $M = 1.4$ mm, $SD = 2.9$; $p_{\text{FSS}} > .052$).

Likewise, analysis of end point variability in the primary movement axis yielded a significant Vision Condition by Target interaction, $F(2,34) = 6.15, p < .001, \eta^2_G = .184$. This interaction was sub-served by systematic increases in variable error from the NV-MG to NV to the FV condition for both the 10-cm (i.e., NV-MG: $M = 11.3$ mm, $SD = 3.3$; NV: $M = 7.5$ mm, $SD = 1.9$; FV: $M = 4.9$ mm, $SD = 1.2$; $p_{\text{FSS}} < .001$) and the 30-cm Target amplitudes (i.e., NV-MG: $M = 19.0$ mm, $SD = 5.8$; NV: $M = 11.8$ mm, $SD = 3.5$; FV: $M = 5.5$ mm, $SD = 1.3$; $p_{\text{FSS}} < .001$).

Lastly, a pattern of findings comparable to those observed for TAPV were observed for the analysis of movement time. That is, only a significant main effect of Target was observed, $F(1,17) = 656.16, p < .001, \eta^2_G = .574$. Movement times were significantly shorter when reaches were completed to the 10-cm Target (i.e., $M = 342$ ms, $SD = 47$) vs. the 30-cm Target (i.e., $M = 474$ ms, $SD = 57$).
4.2.7 References


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Table 4.2.1. A summary of the omnibus ANOVA analyses.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Main Effect of Vision</th>
<th>Main Effect of Target</th>
<th>Vision x Target Interaction</th>
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<tbody>
<tr>
<td></td>
<td>$F(2,34) = 3.07, p = .059, \eta_g^2 = .027$</td>
<td>$F(1,17) = 5.75, p = .028, \eta_g^2 = .005^*$</td>
<td>$F(2,34) = 0.66, p = .522, \eta_g^2 = .001$</td>
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</tr>
<tr>
<td>PV</td>
<td>$F(2,34) = 7.98, p = .001, \eta_g^2 = .078^{**}$</td>
<td>$F(1,17) = 666.86, p &lt; .001, \eta_g^2 = .771^{***}$</td>
<td>$F(2,34) = 6.44, p &lt; .004, \eta_g^2 = .012^{**}$</td>
</tr>
<tr>
<td>TAPV</td>
<td>$F(2,34) = 2.15, p = .132, \eta_g^2 = .026$</td>
<td>$F(1,17) = 344.71, p &lt; .001, \eta_g^2 = .517^{***}$</td>
<td>$F(2,34) = 0.93, p = .404, \eta_g^2 = .002$</td>
</tr>
<tr>
<td>Fisher$^2$</td>
<td>$F(2,34) = 86.29, p &lt; .001, \eta_g^2 = .662^{***}$</td>
<td>$F(1,17) = 71.28, p &lt; .001, \eta_g^2 = .362^{***}$</td>
<td>$F(2,34) = 0.10, p = .909, \eta_g^2 = .001$</td>
</tr>
<tr>
<td>αpeak pPower</td>
<td>$F(2,34) = 9.91, p &lt; .001, \eta_g^2 = .089^{***}$</td>
<td>$F(1,17) = 53.50, p &lt; .001, \eta_g^2 = .361^{***}$</td>
<td>$F(2,34) = 0.42, p = .661, \eta_g^2 = .003$</td>
</tr>
<tr>
<td>Frequency</td>
<td>$F(2,34) = 1.12, p = .337, \eta_g^2 = .024$</td>
<td>$F(1,17) = 58.70, p &lt; .001, \eta_g^2 = .296^{***}$</td>
<td>$F(2,34) = 0.51, p = .605, \eta_g^2 = .003$</td>
</tr>
<tr>
<td>βpeak pPower</td>
<td>$F(1,17) = 21.42, p &lt; .001, \eta_g^2 = .238^{***}$</td>
<td>$F(1,17) = 8.69, p = .009, \eta_g^2 = .131^{**}$</td>
<td>$F(2,34) = 0.28, p = .757, \eta_g^2 = .001$</td>
</tr>
<tr>
<td>αpeak Frequency</td>
<td>$F(1,17) = 0.95, p = .343, \eta_g^2 = .028$</td>
<td>$F(1,17) = 3.73, p = .070, \eta_g^2 = .028$</td>
<td>$F(1,17) = 2.53, p = .130, \eta_g^2 = .017$</td>
</tr>
</tbody>
</table>

Note. (*) $p < .05$; (**) $p < .01$; (***) $p < .001$; (^) analysis not including the FV condition
Table 4.2.2. Means and (standard deviations) of the dependent measures across all conditions.

<table>
<thead>
<tr>
<th>Measure</th>
<th>FV 10 cm</th>
<th>30 cm</th>
<th>NV 10 cm</th>
<th>30 cm</th>
<th>NV-MG 10 cm</th>
<th>30 cm</th>
</tr>
</thead>
<tbody>
<tr>
<td>RT</td>
<td>279 ms (58)</td>
<td>288 ms (54)</td>
<td>300 ms (53)</td>
<td>310 ms (47)</td>
<td>295 ms (59)</td>
<td>298 ms (55)</td>
</tr>
<tr>
<td>PV</td>
<td>0.56 m/s (0.09)</td>
<td>1.26 m/s (0.16)</td>
<td>0.53 m/s (0.13)</td>
<td>1.20 m/s (0.26)</td>
<td>0.48 m/s (0.14)</td>
<td>1.09 m/s (0.27)</td>
</tr>
<tr>
<td>TAPV</td>
<td>180 ms (26)</td>
<td>256 ms (35)</td>
<td>183 ms (37)</td>
<td>266 ms (50)</td>
<td>192 ms (39)</td>
<td>275 ms (49)</td>
</tr>
<tr>
<td>Fisher^2</td>
<td>1.87 (0.68)</td>
<td>0.57 (0.26)</td>
<td>3.28 (1.33)</td>
<td>1.91 (0.82)</td>
<td>5.05 (1.01)</td>
<td>3.61 (1.13)</td>
</tr>
<tr>
<td>αpeak pPower</td>
<td>12.13 % (4.13)</td>
<td>19.14 % (5.16)</td>
<td>10.25 % (3.00)</td>
<td>16.16 % (4.25)</td>
<td>9.45 % (3.46)</td>
<td>15.66 % (5.63)</td>
</tr>
<tr>
<td>αpeak Frequency</td>
<td>9.64 Hz (2.06)</td>
<td>7.26 Hz (2.49)</td>
<td>9.75 Hz (2.84)</td>
<td>6.83 Hz (1.53)</td>
<td>9.10 Hz (2.32)</td>
<td>6.28 Hz (1.26)</td>
</tr>
<tr>
<td>βpeak pPower</td>
<td>3.81 % (2.02)</td>
<td>2.44 % (1.60)</td>
<td>5.84 % (2.14)</td>
<td>4.37 % (1.32)</td>
<td>5.83 % (1.65)</td>
<td>4.65 % (1.80)</td>
</tr>
<tr>
<td>^βpeak Frequency</td>
<td>19.50 Hz (-)</td>
<td>19.50 Hz (-)</td>
<td>19.07 Hz (1.43)</td>
<td>19.93 Hz (1.71)</td>
<td>18.96 Hz (1.47)</td>
<td>19.07 Hz (1.26)</td>
</tr>
</tbody>
</table>

Note. (^) The 19.50 Hz frequency was used for the FV condition βpeak peak location. (-) Indicates that no variability was estimated for the associated condition.
Figure 4.2.1. Example of the pPower analysis technique across the three vision conditions: a) A raw acceleration trace (grey) and the best fitting 5th order polynomial (black); b) The residuals from the polynomial fit after applying a Hanning truncation window; and c) The pPower spectrum of the residuals.
Figure 4.2.2. A depiction of the experimental setup (Note. Not to scale).
Figure 4.2.3. An illustration of the trial progression in the three conditions. In the FV condition, the goggles were open from target onset to movement end. In the NV condition the goggles were open from target onset until movement start. In the NV-MG conditions, the goggles were open for one second following target onset. The vertical dashed gray line represents the temporal location of the go-signal. The shaded area represents the duration of the movement.
Figure 4.2.4. The results regarding the two main measures of movement planning across the three vision conditions: a) Reaction time; and b) Peak limb velocity. Error bars represent within-subject 95% confidence intervals.
Figure 4.2.5. The results regarding the two conventional measures of online control: a) The Fisher transformed squared correlation between position achieved at 75 % movement time vs. The position achieved at movement end; and b) Time elapsed after peak limb velocity until movement end. Error bars represent within-subject 95 % confidence intervals.
Figure 4.2.6. The pPower data across the experimental conditions measured via acceleration in the primary movement axis: a) The 10-cm target; and b) The 30-cm target. Error bars represent 95% within-subjects confidence intervals. The alpha and beta peaks have been labelled $\alpha_{\text{peak}}$ and $\beta_{\text{peak}}$, respectively. The FV condition yielded significantly larger pPower at the $\alpha_{\text{peak}}$ for both targets and significantly less pPower at the $\beta_{\text{peak}}$ for both targets. * indicates significant difference in peak magnitude (i.e., $p < .05$).
4.3 Manuscript 3: Evaluating the sensitivity of measures of online control to offline processes

An earlier version of this manuscript has been submitted to the journal *Motor Control*
Is online control immune to offline control processes in reaching?
4.3.1 Abstract

Voluntary movement can theoretically be influenced by both offline and online control mechanisms, which intuitively led to a challenge for the accurate quantification of the contributions of online control to performance. The current study sought to examine the relative sensitivity of four measures of online control to experimentally-induced, trial-to-trial changes in reaching performance (i.e., offline mechanisms). The measures evaluated included two multiple-trial measures (i.e., variable error [VE], and squared correlations of position at 75% movement time vs. movement end [$Z^2$]) and two within-trial measures (i.e., time-after-peak-limb velocity [TAPV] and a frequency domain analysis [pPower]). Participants completed reaching movements to a target located 30 cm away, either with vision available during reaches (i.e., full-vision; FV) or not (no-vision; NV). In addition, optical prisms were applied during the NV trials to induce offline adaptation via terminal feedback. Lastly, to test for the contribution of terminal feedback alone, an additional control FV condition without the provision of terminal feedback was employed. The results indicated that VE and TAPV were sensitive to prism-induced, offline changes in performance, whereas $Z^2$ and pPower were not. Secondary analysis of the two FV conditions (i.e., with and without terminal feedback) indicated that $Z^2$ was more sensitive to terminal-feedback induced offline influences than pPower. Ultimately, the current study reaffirmed the importance of carefully considering offline influences on measures of online control and suggests that pPower may be the most suitable measure of online control.
4.3.2 Introduction

The identification, measurement, and quantification of online feedback utilization during goal-directed movements has been a goal in the field of motor control at least since the pioneering work of R. S. Woodworth (1899). Changes in the theoretical understanding of online control processes (e.g., Elliott et al., 2010) have fostered the continued development of measures of online trajectory amendments (e.g., Chua & Elliott, 1993; Elliott & Hansen, 2010; de Grosbois & Tremblay, 2016; Khan, Franks, & Goodman, 1998; Khan et al., 2003; Fitts, 1954; Messier & Kalaska, 1999; van Donkelaar & Franks, 1991; Walker, Philbin, Worden, & Smelcer, 1997; Zelaznik, Hawkins & Kisselburgh, 1983). Measures of online control can be loosely classified into two categories: 1) those computed across a number of trials (i.e., multiple-trial measures) within a given condition which include correlational measures (e.g., Elliott, Binsted, & Heath, 1999; Heath, 2005; Messier & Kalaska, 1999) and variability measures (e.g., Khan et al., 2003; Khan et al., 2006); and 2) those computed separately for each trial (i.e., within-trial measures), such as movement time (e.g., Fitts, 1954), time after peak velocity (e.g., Elliott, Carson, Goodman, & Chua, 1991), jerk-score (e.g., Tresilian, Stelmach, & Adler, 1997), and frequency domain analyses (e.g., de Grosbois & Tremblay, 2016).

Recently, de Grosbois and Tremblay (2016) examined the relative sensitivity of common measures of online control to performance changes associated with the presence of online vision during reaching. The analysis of effect sizes indicated that the most sensitive measure was a multiple-trial, correlational measure (i.e., the Fisher^2 transformed correlations or Z^2 values). However, given that such correlational measures are computed across a number of trials, performance changes between different vision conditions could naturally come about both through changes in online feedback utilization (e.g., Hansen, Tremblay, & Elliott, 2005) and in offline feedback utilization (e.g., Plamondon & Alimi, 1997).
Changes in both the planning and online control of reaching movements can become apparent when one manipulates the certainty of the availability of online visual feedback. For example, randomizing the availability of visual feedback across trials results in overall performance that differs from performance wherein visual feedback is blocked (e.g., Khan, Elliott, Coull, Chua, & Lyons, 2002). That is, in predictable situations, participants can prepare movements to minimize energy expenditure. Such a strategy results in shorter reaction times, shorter times to peak deceleration, and longer times after peak deceleration (e.g., Elliott, Hansen, Mendoza, & Tremblay, 2004). Because, $Z^2$ analyses are sensitive to changes in the symmetry of limb trajectories, this multiple-trial measure may also be sensitive to the offline control processes related to changes in planning strategies. Recently, de Grosbois and Tremblay (2015) examined the performance of participants under blocked full-vision, no-vision, and memory-guided no-vision viewing conditions. Under such a blocked condition presentation, participants were conceivably able to prepare their movements differently across conditions. The results indicated that the correlational measure (i.e., $Z^2$) yielded significantly greater evidence of online control in the no-vision relative to the memory-guided no-vision condition. Conversely, no such differences were observed for the pPower analyses. This discrepancy between the two measures could potentially be reconciled by at least two explanations. First, the correlational measures may have been more sensitive to performance-related changes in online control than the frequency domain analyses. That is, vision removed at movement onset may yield different online control mechanisms (i.e., memory-guided vs. no-vision conditions: e.g., Elliott & Madalena, 1987; cf., Franz, Hesse, & Kollath, 2009). That is, frequency domain analysis may be more prone to false negatives. In contrast, it is also possible that the multiple-trial, correlational measures were significantly more biased into false positives associated with changes in movement planning, which did not comparably contaminate the results of the within-trial, frequency analysis measure (i.e., pPower).

The purpose of the current study was to evaluate the degree to which common measures for the quantification of online control processes are susceptible to offline, planning-induced changes in limb trajectories. The main task for participants was the completion of discrete
reaching movements. Offline changes in reaching trajectories were induced primarily through a prism adaptation paradigm. Additionally, offline changes in reaching performance were induced and evaluated through the manipulation of terminal-feedback across two full-vision conditions. Performance was evaluated using two multiple-trial and two within-trial measures of online control. The two common multiple-trial measures employed were variable error in the primary movement axis (i.e., VE) and squared fisher transformed correlations of the position at 75% movement time vs. the position achieved at movement end (i.e., $Z^2$-values). The two within-trial measures included the time spent between peak limb velocity and movement end (i.e., TAPV) and a frequency domain analysis (i.e., pPower analysis; see de Grosbois & Tremblay, 2016; de Grosbois & Tremblay, 2015; de Grosbois & Tremblay, in press). In the pPower analysis, an optimally smooth acceleration profile is subtracted from the raw acceleration and the residual acceleration is subjected to a relative frequency content analysis. In this analysis, a greater contribution of pPower (i.e., frequency contributions) between 4 and 10 Hz have been observed in the presence vs. the absence of online vision during upper-limb reaching movements.

Four hypotheses were forwarded. First, it was hypothesized that providing terminal feedback with optical prisms would alter the end position reaching movements from trial-to-trial due to the prism adaptation (i.e., changes in constant error [CE]: see Redding & Wallace, 1997). Second, the comparison of performance in no-vision conditions with a full-vision condition was expected to yield evidence for differences in the contribution of online control for all four measures because each has been associated with online control. Third, it was hypothesized that the two multiple-trial measures (i.e., VE & Fisher²) would be more susceptible to the prism-induced, offline performance changes, as compared to the two within-trial measures (i.e., TAPV & pPower). That is, these multiple-trial measures would be relatively more biased into falsely reporting a relatively greater contribution of online control in the presence of prism-induced offline changes in performance. Fourth and last, when evaluating performance under full-vision conditions only, it was predicted that the provision of terminal feedback would solely influence multiple-trial measures of online control. These latter two hypotheses were predicted because participants were expected to modify their reaches on a trial-to-trial basis to a greater extent both
in the presence of prisms (e.g., Redding & Wallace, 1997) and when terminal feedback was provided (e.g., Roberts et al., 2013), which would be more apparent in the multiple-trial measures than within trials measures.

4.3.3 Methods

4.3.3.1 Participants

Eighteen participants completed the experiment (i.e., 4 males; 14 females; age range 18 to 35). All were right-handed, as determined by a modified version of a handedness questionnaire (Oldfield, 1971). Informed written consent was given by each participant prior to the beginning of the experimental trials. Monetary compensation was provided in the amount of $5 CAD upon completion of the protocol, which lasted approximately 30 minutes.

4.3.3.2 Materials and apparatus

Data collection was completed in a dimly lit room. The setup included a desk, upon which a custom aiming console was placed (i.e., console dimensions: length = 51 cm; width = 28 cm; height = 9 cm). Participants were seated at the table and the long axis of the aiming console was oriented parallel to their frontal plane (see Figure 4.3.1). A small square piece of Velcro™ (i.e., 1 by 1 cm) was affixed to the superior surface of the aiming console and served as the start position for the reaching movements. In addition, a chin-rest was affixed to the near edge of the table, in front of the participant. The height of the chin-rest was maintained at a constant level across all participants (i.e., approximately 29 cm above the surface of the aiming console) to ensure comparable effects of the optical prisms. The aiming console was positioned so that its short/left edge was aligned with the chin-rest and the participant's mid-saggital axis. The start position was located near the far right edge of the console, approximately 40 cm to the right of the chin-rest. Within the surface of the aiming console, a green light emitting diode (i.e., an LED) was affixed. The LED was positioned 30 cm to the left of the start-position, approximately 12 cm to the right of the chin rest. Importantly, because the LED was positioned below the aiming surface of the console, it was visible to participants only when illuminated. Also, a piezo-
electric buzzer (Mallory Sonalert Products, Inc., Indianapolis, IN, USA) was utilized to produce auditory cues (50 ms, 2900 Hz).

During the experiment, the visual information available to participants was manipulated in two ways. First, liquid-crystal goggles (i.e., PLATO, Translucent Technologies Inc., Toronto, ON, CA: Milgram, 1987) were worn by participants throughout the experiment. These goggles allowed for the control of the availability of visual information of the environment and can change from a transparent (i.e., glass-like or open) to a translucent state (i.e., milky-like or closed). Second, two sets of optical-prisms (i.e., 1 diopter and 12 diopter Press-On-Prisms, 3M, MN, USA) were affixed to custom plastic mounts and adhered to the surface of the goggles with Velcro™. At a constant viewing distance of approximately 40 cm, these two sets of prisms shifted the perceived location of the visual array to the right by approximately 0.7 cm and 8 cm, respectively. Thus, the 12-diopter prisms were utilized to induce offline changes in performance, and the 1-diopter prisms were utilized because they elicited a relatively comparable view through the goggles and thus served as a control condition (i.e., no large prism adaptations expected). To limit viewing to through the prisms only, a rectangular section of black felt was attached to the plastic mounts and to the goggles, between the participant's eyes and chin. Also, a third plastic mount was utilized, which did not have an optical prism affixed to it and served as an additional control condition (i.e., full-vision condition).

Both position and acceleration data of the moving limb were collected. The position of the tip of each participant's right-index finger was tracked using an optoelectric motion tracking system (Optotak Certus, Northern Digital Inc., Waterloo, ON, CA) using an infrared light emitting diode (i.e., IRED). Second, acceleration data were also obtained using a triple-axis accelerometer (i.e., MMA7361L; NXP Semiconductors, Eindhoven, Netherlands). Data from the accelerometer were acquired via a multi-function data acquisition card (i.e., model PCI-6042E, National Instruments Inc., Austin, TX, USA). The accelerometer was inserted into an orthotic wrist-brace worn by the participant on their right hand (i.e., model 225ZZ ; Life Brand, Toronto, ON, CA). Thus, an axis of the accelerometer was aligned with the primary movement axis. Both the position and acceleration data were concurrently sampled at 250 Hz. Custom MATLAB
scripts (The Mathworks Inc., Natick, MA, USA) controlled the data collection as well as the target LED, the piezo-electric buzzer, and the liquid-crystal goggles.

4.3.3.3 Design and procedures

The primary task of participants was to complete right-to-left reaching movements (i.e., inward direction) with their right index finger, as accurately as possible, towards the green target LED. Each trial began with the participant seated at the table, their head in the chin-rest, and their right-index finger on the start-position (see Figure 4.3.1). The target LED was illuminated and the goggles were open (i.e., transparent) for a variable foreperiod of 1 to 1.5 s. Next, an auditory go-signal (i.e., 50 ms in duration) indicated to the participant to begin their movement. Concurrent with the go-signal onset, the goggles were closed. Participants then completed their reaching movement to the previously seen target LED, with the instruction to focus on movement accuracy. In the full-vision conditions, the goggles then re-opened upon movement onset (i.e., first occurrence of limb velocity greater than 30 mm/s for 12 ms) and closed again upon movement completion (i.e., first occurrence of limb velocity less than 30 mm/s for at least 20 ms, following movement start). In the no-vision conditions, the goggles remained closed throughout the movement. Following the completion of their movement, participants were instructed to maintain their finger end-position until three more tones had sounded (see Figure 4.3.2). Note that the first tone (i.e., 50 ms) signalled the end of the 1.5-s data collection interval and the beginning of the 1-s terminal feedback interval. During the terminal feedback interval, the goggles were either open (i.e., providing terminal feedback) or closed (i.e., withheld feedback). A double-tone (i.e., two more tones, 50 ms in length, separated by 50 ms) sounded at the end of the 1-s terminal feedback interval, instructing the participant to return to the home position for the next trial.

Five unique sensory conditions were employed across a total of nine blocks of trials. These nine blocks were scheduled as two consecutive blocks in all but the last condition. The conditions differed from one another based on the availability of visual information during the reaching movement (i.e., FV and NV), during the post-movement terminal feedback interval.
(i.e., TF and noTF), and the magnitude of the diopter of the selected prism apparatus (i.e., 1-diopter [1D] and 12-diopter [12D]). Two conditions provided a baseline for the prism conditions and tested the influence of terminal feedback, and three conditions involved prisms and no online vision (see below). Adaptation was induced with the provision of terminal feedback because this sensory environment has been shown to facilitate offline adaptation (e.g., Bernier, Chua, & Franks, 2005; Heuer & Hegel, 2008; Redding & Wallace, 1997). As such, the five experimental conditions were performed in the following order: 1) full-vision during the movements, with terminal feedback (i.e., FV-TF); 2) full-vision during the movements, without terminal feedback (i.e., FV-noTF); 3) no-vision during the movements, with the 1D prism, with terminal feedback (i.e., NV-1D-TF); 4) no-vision during the movements, with the 12D prism and terminal feedback (i.e., NV-12D-TF); and 5) no-vision during the movements, with the 1D prism but without terminal feedback (i.e., NV-1D-noTF). Prior to the commencement of the first block of trials, participants completed 5 familiarization trials in the FV-TF condition. Also, the trials completed in first four conditions were organized as two 15-trial blocks. Prior to each successive block of 15 trials, the goggles were closed and the prism mount was removed. Then, unbeknownst to the participants, the mount was replaced with either the same, or a different mount, depending upon the upcoming condition. Participants were informed regarding changes in the availability of online vision and terminal feedback to be expected during each block of trials. An additional final condition block (i.e., NV-1D-noTF) consisted of five trials, and was solely added to confirm the presence of prism adaptation during the preceding NV-12D-TF condition. Ultimately, participants completed a total of 125 experimental trials.

4.3.3.4 Data processing and analysis

First, regarding the analysis examining performance for the presence of adaptation and after-effects, constant error was calculated for each trial. That is, the location of the target was subtracted from the end point position of the finger. Constant error within a condition was calculated as the mean end point bias, relative to the target location (i.e., positive values indicating target overshoots).
Second, four main dependent variables were calculated. First, variable error in the primary movement axis (i.e., VE) was calculated as the within-condition standard deviation of the movement endpoints. Generally, smaller VE values can be associated with a greater amount of online control (e.g., Bernier, Chua, Franks, & Khan, 2006; Tremblay, Hansen, Kennedy, & Cheng, 2013). Second, time after peak velocity (i.e., TAPV) was calculated as the time in milliseconds elapsed from peak limb velocity until the end of the movement. Generally, longer TAPV values can be associated with a greater contribution of online control (e.g., Elliott, Carson, Goodman, & Chua, 1991; Soechting, 1984). Third, within-condition correlations were computed between the limb position in the primary movement axis achieved at 75% of movement time relative to the position achieved at movement end. These correlations were transformed to Fisher Z-scores and squared (i.e., $Z^2$: e.g., Bernier et al., 2006). Generally, lower squared correlation (i.e., $Z^2$ or $R^2$) values reflect a greater contribution of online control (e.g., de Grosbois & Tremblay, 2016; Heath, 2005). And fourth, the proportional frequency power of the acceleration variability (i.e., pPower) was calculated around a smooth acceleration profile (see de Grosbois & Tremblay, 2016; de Grosbois & Tremblay, 2015). This was achieved by fitting a 5th order polynomial to each acceleration profile. The MATLAB polyfit() function was used to generate the polynomial slopes and the residuals of this fit were determined by subtracting the associated polynomial computed via the MATLAB polyval() function. Subsequently, the power spectra were calculated via MATLAB's FFT() function using a transform length of 256 samples after applying a Hanning truncation window, yielding a frequency resolution of 0.97 Hz. The spectra were computed by multiplying the Fourier coefficients by their complex conjugates via the MATLAB conj() function and dividing by the transform length. Once calculated, the power at each resolvable frequency was normalized as a percentage of the total power up to the Nyquist frequency (i.e., 125 Hz). Additionally, because movement times below 512 ms would mathematically result in a lower resolvable frequency, all pPower data was binned to a lower frequency resolution (i.e., 1.95 Hz). Once calculated, both the frequency of and the magnitude of observable peaks in the pPower spectra were separately subjected to further analyses. Greater peak magnitudes in the pPower spectra below 10 Hz have been associated with greater contributions of online visuomotor control (e.g., de Grosbois & Tremblay, 2016; de Grosbois &
Tremblay, 2015). Additionally, given that secondary, higher frequency peaks have been previously observed at approximately 20 Hz (e.g., de Grosbois & Tremblay, 2015), the frequency spectra were evaluated up to 30 Hz.

To test the hypotheses outlined above, three sets of analyses were conducted. First, an analysis was conducted to assess the first hypothesis, evaluating performance for the presence of prism-induced after-effects, and thus prism adaptation. Constant error data in the primary movement axis was contrasted between last block of trials completed immediately before the NV-12D-TF condition (i.e., the NV-1D-TF) and the first block of trials completed immediately after the NV-12D-TF condition (i.e., the NV-1D-noTF). Importantly, both conditions contrasted employed the 1-diopter prisms and the latter withheld terminal feedback, which is common in assessments of prism-induced after-effects (e.g., Redding & Wallace 1997; Redding & Wallace 2008).

Second, the main analysis of the current study involved a 3 Vision Condition (FV-TF, NV-1D-TF, NV-12D-TF) repeated-measures ANOVA. This analysis was completed on the four selected measures of online control (i.e., VE, TAPV, $Z^2$, pPower). This analysis evaluated the second and third hypotheses, regarding the influence of online vision on online control and the influence of prism-induced adaptation on measures on online control.

Thirdly, an analysis was completed to contrast performance in the FV-noTF condition relative to the FV-TF condition for all four measures and was completed as a 2 Terminal Feedback (TF, noTF) repeated-measures ANOVA. This analysis was conducted to further evaluate the potential influence of offline processing on measures of online control via the provision of terminal visual feedback.

When necessary, Bonferroni corrections were applied to $p$-values on a family-wise basis. When more than one pairwise comparison was completed (i.e., paired samples t-tests), corrected $p$-values were reported as $p_{bcx}$ where 'b' indicates that the p-value has been Bonferroni corrected, and 'x' indicates the number of tests corrected for. Alpha was set to .05 for all analyses. Effect
sizes were reported as the generalized eta squared ($\eta_G^2$; see Bakeman, 2005; Olejnik & Algina, 2003). Statistical analyses were run using R (version 3.1.2; R-core Team, 2014) and ANOVAs were computed using the EZ package (Lawrence, 2013). All error bars depicted in figures represent within-subject 95% confidence intervals (see Loftus & Masson, 1994).

4.3.4 Results

Although the main hypotheses did not explicitly predict differences in movement time, such differences could be expected based on the chosen manipulations (e.g., Elliott et al., 1991). Accordingly, a supplementary analysis of movement times has been completed (see section 4.3.7.1).

4.3.4.1 Assessing the effect of the prism on movement end points

The analysis of end point bias in the primary movement axis (i.e., constant error) revealed a significant main effect of Condition, $F(1,17) = 79.87$, $p < .001$, $\eta_G^2 = .563$. The mean end point in the first block after the NV-12D-TF condition (i.e., NV-1D-noTF) yielded significantly greater overshooting (i.e., NV-1D-noTF: $M = 20.66$ mm, $SD = 9.92$) relative to the last block completed prior to the NV-12D-TF condition (i.e., NV-1D-TF: $M = 3.10$ mm, $SD = 5.33$). The presence of this aftereffect was evidence that participants significantly adapted to the prism during the NV-12D-TF condition. This adaptation and aftereffect can be easily observed when inspecting the right side of Figure 4.3.3, which reports the mean movement end point across all participants and trials.

4.3.4.2 Assessing the effect of online visual feedback and prism adaptation on measures of online control

The main analysis, comparing performance between the three TF-present conditions (i.e., FV-TF, NV-1D-TF, & NV-12D-TF) for VE yielded a significant main effect of Vision Condition, $F(2,34) = 86.55$, $p < .001$, $\eta_G^2 = .761$ (see Figure 4.3.4). Post-hoc pairwise comparisons indicated that the condition with online vision (i.e., FV-TF) condition yielded
significantly smaller VE values (i.e., $M = 3.6$ mm, $SD = 1.0$) relative to both no-vision conditions (i.e., NV-1D-TF: $M = 8.0$ mm, $SD = 1.3$, $p_{b3} < .001$; NV-12D-TF: $M = 9.8$ mm, $SD = 2.0$, $p_{b3} < .001$). Further, the 12D prism condition (i.e., NV-12D-TF) also yielded significantly larger VE$_{Prim}$ values relative to the 1D prism condition (i.e., NV-1D-TF; $p_{b3} = .005$).

The main analysis of $Z^2$ yielded a significant main effect of Vision Condition, $F(2,34) = 103.92$, $p < .001$, $\eta_G^2 = .716$ (see Figure 4.3.4). Post-hoc pairwise comparisons indicated that the full-vision condition (i.e., FV-TF) yielded significantly smaller $Z^2$ values (i.e., $M = 0.62$, $SD = 0.37$) relative to both no-vision conditions (i.e., NV-1D-TF: $M = 2.13$, $SD = 0.52$, $p_{b3} < .001$; NV-12D-TF: $M = 2.16$, $SD = 0.49$, $p_{b3} < .001$). The 1D no-vision and the 12D no-vision conditions did not exhibit significantly different $Z^2$ values (i.e., $p_{b3} > .999$).

The main analysis of TAPV$^6$, yielded a significant main effect of Vision Condition, $F(2,34) = 8.29$, $p = .001$, $\eta_G^2 = .023$ (see Figure 4.3.4). Post-hoc pairwise comparisons indicated that the 12D condition (i.e., NV-12D-TF) yielded significantly longer TAPVs (i.e., $M = 347$ ms, $SD = 84$) relative to both the one-diopter no-vision condition (i.e., NV-1D-TF: $M = 325$ ms, $SD = 85$, $p_{b3} = .024$) and the full-vision (i.e., (FV-TF: $M = 318$ mm, $SD = 79$, $p_{b3} = .014$). The full-vision condition and the one-diopter no-vision condition did not exhibit significantly different TAPV values (i.e., $p_{b3} = .606$).

Prior to any statistical evaluation of the proportional power spectra, the spectra themselves were qualitatively evaluated for the presence/absence of observable peaks. As can be seen in Figure 4.3.5, a first frequency peak (i.e., around 6 Hz), denoted the alpha peak (i.e., $\alpha_{peak}$), was observed in all conditions. Additionally, a secondary peak, denoted the beta peak (i.e., $\beta_{peak}$), was observed at relatively higher frequencies (i.e., around 18 Hz) for the two no-vision

6 Considering the changes observed in movement amplitude in response to the prism manipulation, one could surmise that the relative symmetry of the velocity profile would be a better indicator of online feedback utilization (i.e., the proportional time spent after peak velocity). However, an ANOVA performed on the proportion of time spent following peak limb velocity indicated no significant effect of Vision Condition, $F(2,34) = 1.81$, $p = .179$, $\eta_G^2 = .012$. 

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conditions. Both peaks were consistent with the results of de Grosbois and Tremblay (2015; see also de Grosbois & Tremblay, in press). The frequency and magnitude of these two peaks were computed using each participant's condition-specific, mean spectra, and contrasted across the three vision conditions using a repeated-measures ANOVA.

The analysis of frequency of the $\alpha$ peak resulted in a significant main effect of Vision Condition, $F(2,34) = 6.06, p = .006, \eta_G^2 = .095$. Pairwise comparisons across Vision Conditions yielded a significantly higher frequency for the $\alpha$ peak in the full vision condition (i.e., FV-TF: $M = 7.7 \text{ Hz, } SD = 2.1$) relative to both no-vision conditions (i.e., NV-1D-TF: $M = 6.3 \text{ Hz, } SD = 1.5, p_{b3} = .027$; NV-12D-TF: $M = 6.6 \text{ Hz, } SD = 1.9, p_{b3} = .024$). Additionally, no significant frequency difference was observed between the two no-vision conditions (i.e., $p_{b3} > .999$).

The analysis of the magnitude of the pPower at the $\alpha$ peak resulted in a significant main effect of Vision Condition, $F(2,34) = 17.10, p < .001, \eta_G^2 = .257$ (see Figure 4.3.4). Pairwise comparisons across Vision Conditions yielded significantly greater pPower in the full-vision condition (i.e., FV-TF: $M = 20.2 \% \text{, } SD = 5.7$) relative to both no-vision conditions (i.e., NV-1D-TF: $M = 14.9 \% \text{, } SD = 3.2, p_{b3} = .003$; NV-12D-TF: $M = 14.3 \% \text{, } SD = 4.5, p_{b3} < .001$). Additionally, no significant difference in $\alpha$ peak magnitude was observed between the two no-vision conditions (i.e., $p_{b3} > .999$).

Given that no $\beta$ peak was apparent for the FV-TF condition, the frequency of this peak was estimated via analysis of the two no-vision conditions only. The analysis revealed no significant effect of Vision Condition, $F(1,17) = 0.03, p = .859, \eta_G^2 < .001$. The grand mean frequency of the $\beta$ peak for the two no-vision conditions was 17.7 Hz ($SD = 0.7$). As such, the pPower at the nearest resolvable frequency, namely 17.58 Hz, was chosen to represent the magnitude of the $\beta$ peak for the full-vision condition in subsequent analyses.

The analysis of the magnitude of the pPower at the $\beta$ peak resulted in a significant main effect of Vision Condition, $F(2,34) = 5.92, p = .006, \eta_G^2 = .117$. Pairwise comparisons across levels of vision condition yielded significantly lower pPower in the full-vision condition (i.e.,
FV-TF: $M = 3.4 \%, SD = 2.1$) relative to the no-vision twelve-diopter (i.e., NV-12D-TF: $M = 5.1 \%, SD = 2.3, p_{b3} = .022$), but not the no-vision one-diopter condition (NV-1D-TF: $M = 4.7 \%, SD = 1.7, p_{b3} = .150$). Additionally, no significant difference was observed in $\beta_{\text{peak}}$ magnitude between the two no-vision conditions (i.e., $p_{b3} > .704$).

### 4.3.4.3 Assessing influence of terminal feedback on measures of online control

A summary of the means, standard deviations, and effect sizes associated with the last set of analyses can be found in Table 4.3.1. These analyses contrasted both between-trial and within-trial measures of online control.

The analysis of variable error in the primary movement axis (i.e., VE) yielded no significant effect of Terminal Feedback, $F(1,17) = 1.43, p = .247, \eta^2_G = .025$ (TF present: $M = 3.6$ mm, $SD = 1.0$; TF absent: $M = 4.0$ mm, $SD = 1.3$).

In contrast, the $Z^2$ analyses yielded a significant effect of Terminal Feedback, $F(1,17) = 4.65, p = .046, \eta^2_G = .113$. This main effect was driven by significantly lower $Z^2$ values when TF was present (i.e., $M = 0.62, SD = 0.37$) relative to when TF was absent (i.e., $M = 1.52, SD = 1.78$).

The analysis of the time spent following peak limb velocity (i.e., TAPV) failed to yield a significant effect of Terminal Feedback, $F(1,17) < 0.01, p = .996, \eta^2_G < .001$ (TF present: $M = 318$ ms, $SD = 79$; TF absent: $M = 318$ ms, $SD = 74$).

The analysis of frequency of the $\alpha_{\text{peak}}$ resulted in a significant main effect of Terminal Feedback, $F(1,17) = 10.82, p = .004, \eta^2_G = .090$. The mean frequency of the $\alpha_{\text{peak}}$ when TF was provided was significantly higher (i.e., $M = 7.7$ Hz, $SD = 2.1$) relative to when TF was not (i.e., $M = 6.6$ Hz, $SD = 1.5$). In contrast, the analysis of magnitude of the pPower of the $\alpha_{\text{peak}}$ did not result in a significant main effect of Terminal Feedback, $F(1,17) = 0.15, p = .701, \eta^2_G = .002$ (TF present: $M = 20.1 \%, SD = 5.6$; TF absent: $M = 20.6 \%, SD = 4.2$). Given the absence of an
observable $\beta_{\text{peak}}$ in the power spectra of the full-vision conditions, no analysis was completed in the higher frequency range.

4.3.5 Discussion

The main purpose of the current study was to evaluate the sensitivity of measures of online control to online vs. offline, trial-to-trial changes in reaching trajectories. To elicit differences in online control, participants completed reaching movements with and without online vision. And to elicit offline changes in reaching performance, optical prisms were employed with no-vision conditions with terminal-feedback provided. Four hypotheses were forwarded and evaluated. First, participants were expected to exhibit offline adaptation to the presence of the optical prisms. Second, all measures were expected to be sensitive to full-vision vs. no-vision changes in online control. Third and fourth, the multiple-trial measures of online control were expected to be sensitive to both prism-induced and terminal-feedback induced offline processes.

The first set of analyses indicated that participants significantly adapted to the prism manipulation. That is, when the optical prisms were applied, participants first undershot the target, but gradually improved their reaching accuracy through the use of the provided terminal feedback (see Figure 4.3.3). Additionally, this offline adjustment in performance was further supported by the presence of a significant after-effect in the final block completed without terminal feedback. That is, the presence of such after-effects can be confidently interpreted as evidence for significant offline prism adaptation (e.g., Redding & Wallace, 2008).

Also, a validation of the influence of online vision on measures of online control was warranted. That is, analyses separately tested if the measures of online control were robustly sensitive to differences in visuomotor online control processes, even in the presence of significant offline contributions to performance. These contrasts resulted in the predicted pattern of results for VE (e.g., de Grosbois & Tremblay, 2016; Elliott & Hansen, 2010; Heath, Westwood, & Binsted, 2004; Khan & Franks, 2003; Zelaznik, Hawkins, & Kisselburgh, 1983),
Z² (e.g., Bernier, Chua, Franks, & Khan, 2006; de Grosbois & Tremblay, 2016), and pPower (e.g., de Grosbois & Tremblay, 2016; de Grosbois & Tremblay, 2015; de Grosbois & Tremblay, in press). That is, even in the presence of offline changes in performance, greater evidence for online control was obtained in full-vision relative to the no-vision conditions. An additional finding in the pPower analysis in the current study was the presence of a significantly higher frequency for the αpeak in the full-vision condition relative to the no-vision conditions. Recently, de Grosbois and Tremblay (2015; de Grosbois & Tremblay, in press) argued that the rate at which online control operates may be adjustable based on the time constraints of individual reaching environments. Such shifts in the rates of feedback utilization have been also observed for both manual tracking (e.g., Miall, 1996) and isometric force control (e.g., Sosnoff & Newell, 2005). A shift to higher rates of control in the presence of online vision may therefore represent an up-regulation of feedback utilization when vision was available during the reaching movements.

Also in the pPower analyses, a second significant difference, in the opposite direction to that of the magnitude of the αpeak, was observed for the magnitude of the βpeak between the FV and the NV-12D-TF condition. Given the observed increase in the βpeak magnitude in the absence of online vision, it is unlikely that it represented the contribution of a visually-mediated online control process (see also de Grosbois & Tremblay, 2015; de Grosbois & Tremblay, in press). The possibility remains that the βpeak represents the contribution of a non-visual online control process, which is consistent with the current results. As such, the nature of the βpeak should be examined in future studies employing manipulations of sources of sensory feedback other than vision. Nevertheless, no significant differences were observed between the pPower values at the βpeak for the two NV conditions.

In contrast to the other three measures, the analysis of the time following peak limb velocity (i.e., TAPV) indicated that participants spent longer times after peak velocity in the 12D no-vision condition (i.e., NV-12D-TF) relative to both the 1D no-vision (i.e., NV-1D-TF) and the full-vision condition (i.e., FV-TF). Thus, rather than the anticipated finding that visually-mediated online control results in a longer TAPV value (e.g., Elliott et al., 1991), the offline
influence of prism adaptation appeared to negate any measurable influence of online control on TAPV values. Notably, however, a failure to replicate the influence of online vision on TAPV values is not uncommon (e.g., de Grosbois & Tremblay, 2016; Heath et al., 2004). Indeed, it has also been reported that TAPV may be influenced by strategic efforts to produce accurate movements (e.g., Elliott et al., 1991). Thus, although changes in TAPV values may be attributable to visually-mediated online control, it may also be heavily influenced by offline trial-to-trial changes in performance (see also Plamondon & Alimi, 1997).

Regarding the main analysis of interest, it was hypothesized that the multiple-trial nature of the VE and $Z^2$ measures would make them particularly susceptible to the contributions of offline, prism-induced, trial-to-trial changes in performance. Partially contrary to this expectation, one within-trial measure (i.e., TAPV) and one multiple-trial measure (i.e., VE) of online control were significantly influenced by prism-induced, offline changes in performance. Furthermore, one within-trial measure (i.e., pPower) and one multiple-trial measure (i.e., $Z^2$) were relatively robust to the prism-induced offline changes in reaching trajectories.

In contrast to the prism-induced offline changes in performance, the analysis of the provision of terminal feedback under full vision conditions (i.e., FV-TF vs FV-noTF) indicated that neither VE nor TAPV reported changes in the online control of the associated reaching trajectories. Conversely, the analysis of the $Z^2$ values indicated a greater contribution of online feedback utilization when terminal feedback was provided relative to when it was withheld (i.e., without online vision). Although it may seem counter-intuitive for terminal feedback to have any direct influence on online control, it has been suggested that offline changes in planning can influence how online control is implemented. That is, Khan, Elliott, Coull, Chua, and Lyons (2002) suggested that under predictable conditions, individuals may plan their movements in such a way as to optimize their forthcoming online feedback utilization. In accordance with this idea, the multiple processes model of online control (e.g., Elliott et. al., 2011; 2017) posits that expected sensory consequences may be integrated into movement plans and thus influence their control. Thus, in the current study, the provision of terminal feedback may have altered the manner in which online feedback was utilized. The analysis of the frequency of the $\alpha_{\text{peak}}$ yielded
findings complementary to this explanation. That is, frequency of the $\alpha_{\text{peak}}$ significantly increased by the presence of terminal feedback. Similar increases in the frequency of the $\alpha_{\text{peak}}$ have been observed when reaches were spatio-temporally constrained (de Grosbois & Tremblay, 2015; de Grosbois & Tremblay, in press), and potentially represented an up-regulation of the rate of online visuomotor feedback utilization. In contrast to both the $Z^2$ and the $\alpha_{\text{peak}}$ frequency results, the analysis of the magnitude of the $\alpha_{\text{peak}}$ indicated no evidence of a change in the relative contribution of online visuomotor feedback processes on reaching performance. Given that no significant differences were observed regarding end point variability across the terminal-feedback conditions, it remains unlikely that differential contributions of online control were present across the two full-vision conditions. Thus, the $Z^2$ analysis may have been relatively more sensitive to the contributions of offline processes altering the manner in which online feedback was utilized. Importantly, when considering the magnitude of the pPower at the $\alpha_{\text{peak}}$, no such bias was present, indicating a comparable relative contribution of online control on reaching performance. Altogether, the results of the current study indicate that the $Z^2$ measure is likely more susceptible to biased estimates of online control induced by offline processes than the pPower analyses. Therefore, only the magnitude of the pPower analyses may provide a sufficient level of sophistication to optimally distinguish between the effects of offline vs. online control mechanisms.

4.3.6 Conclusion

In the current study, participants performed reaching movements that were influenced by online visuomotor feedback as well as offline feedback associated with both prism-adaptation and terminal feedback. The VE, $Z^2$, and pPower measures were successful in identifying the contributions of visuomotor online control in the presence of offline, trial-to-trial changes in performance. Conversely, the influence of offline processes biased TAPV values, above and beyond the influence of online vision. Although the VE measure was sensitive to the contribution of online control, it was also significantly biased by prism-induced, offline processes (i.e., planning mechanisms). Lastly, the provision of terminal-feedback within a full-
vision condition only influenced $Z^2$ and the frequency of the lower peak in the pPower spectra analysis, likely representing an influence of offline feedback on the implementation of online control. Ultimately, within the confines of the current study, the magnitude of the $a_{peak}$ in the pPower analyses appears to be the measure of online control that is most robust to the contributions offline processes to reaching performance.

4.3.7 Supplementary Analyses

4.3.7.1 Movement time analysis

Movement time was defined as the elapsed time between movement onset and movement end. The main analysis of movement time yielded a significant main effect of Vision Condition (Greenhouse-Geisser corrected), $F(1.4, 23.5) = 9.3, p = .002, \eta^2_G = .026$. Post-hoc pairwise comparisons indicated that the NV-12D-TF condition yielded significantly longer movement times (i.e., $M = 527$ ms, $SD = 112$) relative to both the NV-1D-TF (i.e., $M = 501$ ms, $SD = 111$), and the FV-TF (i.e., $M = 486$ ms, $SD = 100$) conditions ($p_{bs} < .018$). Additionally the NV-1D-TF and the FV-TF conditions did not differ significantly from one another.

The analysis of the influence of terminal feedback within full vision conditions on movement time did not yield a significant statistical effect, $F(1, 17) = 0.33, p = .573, \eta^2_G < .001$ (TF present: $M = 486$ ms, $SD = 100$; TF absent: $M = 482$ mm, $SD = 93$).
4.3.8 References


Table 4.3.1. Means, standard deviations (in parenthesis) and effect sizes associated with the comparisons across levels of terminal feedback within the full-vision conditions.

<table>
<thead>
<tr>
<th>Measure</th>
<th>Condition</th>
<th>Effect Size</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>FV-noTF (ms)</td>
<td>FV-TF (ms)</td>
</tr>
<tr>
<td>TAPV (ms)</td>
<td>318 (74)</td>
<td>318 (79)</td>
</tr>
<tr>
<td>(\alpha_{peak}) Frequency (Hz)</td>
<td>6.6 (1.5)</td>
<td>7.8 (2.1)</td>
</tr>
<tr>
<td>(\alpha_{peak}) Magnitude (%)</td>
<td>20.6 (4.2)</td>
<td>20.2 (5.7)</td>
</tr>
<tr>
<td>VE (mm)</td>
<td>4.0 (1.3)</td>
<td>3.6 (1.0)</td>
</tr>
<tr>
<td>(Z^2)</td>
<td>1.52 (1.78)</td>
<td>0.62 (0.37)</td>
</tr>
</tbody>
</table>

Note. * = \(p < .05\); ** = \(p < .01\)
Figure 4.3.1. A depiction of the experimental setup (Note. Not to scale).
Figure 4.3.2. An illustration of the trial progression in the main conditions. In all conditions, the goggles closed state was coincident with the auditory go-signal. The speaker symbols above the trace indicate the relative onsets of the auditory beeps.
Figure 4.3.3. The mean movement endpoint across participants as a function of trial. Each successive 30 trials were completed in a different viewing condition. The solid gray line represents the measured location of the target relative to the home position. The final five trials were completed with the 1D prisms and no terminal feedback to assess after-effects. The dashed vertical gray lines represent transitions from one condition to another. Solid black lines represent least-squares linear regressions computed across mean values within each block of trials.
Figure 4.3.4. The main analysis across the four primary measures of online control: a) Variable error (VE); b) Time after peak velocity (TAPV); b) Squared Fisher transformations of correlations of position at 75 % vs. 100 % of movement time ($Z^2$); and d) pPower magnitude analysis at the $\alpha_{\text{peak}}$ (pPower %). Error bars indicate within-subjects 95 % confidence intervals. * = $p_{\text{corrected}} < .05$
Figure 4.3.5. The pPower spectra for the three vision conditions in the main analysis. Note the two prominent peaks in the lower (i.e., $\alpha_{\text{peak}}$) and higher (i.e., $\beta_{\text{peak}}$) ranges of the spectra. Error bars indicate within-subjects 95% confidence intervals. * indicates that a significant main effect of Vision Condition was present at the associated peak.
4.4 Manuscript 4: Identifying the nature of the frequency peaks via manipulations of intention

As of March 9, 2017, this manuscript has yet to be submitted for publication
Accuracy instructions modulate the frequency content of ongoing reaching movements
4.4.1 Abstract

The current understanding of the online control of goal-directed action is multi-faceted in nature. In particular, both visual and non-visual processes can contribute to reaching performance and online control. Although the presence or absence of vision inherently alters the contribution of visual feedback to reaching performance, intentions to achieve accurate movements also influence reaching performance. Importantly the improvements associated with accuracy-based intentions may be due to changes in movement planning and/or online control. Furthermore, such improvements may influence both visual and non-visual processes. Using frequency domain analyses, the online contributions of such visual and non-visual sub-processes have been identified (e.g., de Grosbois & Tremblay, 2015; de Grosbois & Tremblay, 2016b; de Grosbois & Tremblay, in press). The purpose of the current study was to further understand the nature of these sub-processes, through the influence of online vision and intentions to complete accurate movements. To this end, reaching movements were completed in the presence of three manipulations. First, online vision was provided or withheld. Second, the predictability of visual information was manipulated through a blocked and randomized feedback scheduling. And third, high- and low-accuracy instruction sets were provided. The results indicated that the contribution of online visuomotor processes (i.e., visual sub-process) was increased by the presence of online vision and intentions to be accurate. In contrast, the non-visual sub-process was promoted in the absence of online vision, but suppressed with intentions to be accurate, when a randomized feedback schedule was implemented. Ultimately, this non-visual process was proposed to be associated with proprioceptive spinal feedback loops.
Accuracy-focused instruction sets differently modulate visual and non-visual contributions to online reaching performance

As early as the seminal contributions of Woodworth (1899), it has been reported that instructions to produce accurate movements have systematic influences on reaching accuracy. Inherently, such changes in reaching performance could theoretically stem from movement planning and/or online feedback utilization (i.e., online control). Hand-in-hand with theories of online control (e.g., Crossman & Goodeve, 1983; Howarth, Beggs, & Bowden, 1971; Meyer, Abrams, Kornblum, Wright, & Smith, 1988; see Elliott, Helsen, & Chua, 2001 for a review), many methodologies have been forwarded to quantify online feedback utilization. Many of these methodologies emerged via technological advancements that allowed for increasingly precise movement measurements.

Earlier work (e.g., Fitts, 1954; Keele & Posner, 1968) quantified movement accuracy solely based on target hits and misses. A presumption was that feedback acted as a servomechanism (e.g., Craik, 1947) and that the utilization of feedback would result in relatively more target hits. The invention of motion tracking systems led to the quantification of movement accuracy in terms of the spatial variability of the movement endpoints (e.g., Zelaznik, Hawkins, & Kisselburgh, 1983). In addition to the greater movement accuracy under conditions wherein feedback utilization likely took place, Woodworth (1899) also noted that the later portions of movements in the presence of vision also exhibited discontinuities, which likely came about through feedback utilization after movement onset. As such, online feedback utilization was initially associated with the presence of such movement discontinuities and researchers developed methodologies for their quantification (e.g., jerk score: see Tresilian, Stelmach, & Adler, 1997) and utility (e.g., index of error-correction effectiveness: see Khan, Franks, & Goodman, 1998). Subsequently, however, other researchers have shown that the mere presence of more discontinuities has not always been associated with greater endpoint accuracy (e.g., Elliot, Carson, Goodman, & Chua, 1991; Jeannerod, 1986; Poston et al., 2013).
The absence of discontinuities may not be confidently taken as evidence for the absence of contributions of online control mechanisms. For example, Pélisson, Prablanc, Goodale, and Jeannerod (1986) utilized a double-step reaching paradigm, where the target location was surreptitiously displaced during the initial orienting saccade. Nevertheless, participants corrected their ongoing movements, without any evidence of a discrete correction to the limb trajectory. Subsequently, Elliott et al. (1991) formalized the idea of feedback utilization in the absence of observable discrete corrections in what became known as the pseudocontinuous model of online control. In the pseudocontinuous model, corrective processes are completed in an iterative, overlapping fashion, which often results in a relatively smooth kinematic profile.

As a consequence of the difficulty in relying upon discontinuities for the quantification of online control, newer methodologies based on the variability associated with a series of trials have been developed (i.e., multiple-trial measures). These methodologies have focused on either the magnitude of the variability at different points across the movements (i.e., Khan et al., 2003; Khan et al., 2006; Hansen, Elliott, & Khan, 2008), correlations between kinematic markers across multiple movements (i.e., Bernier, Chua, Franks, & Khan, 2006; Heath, Westwood, & Binsted, 2004; Messier, & Kalaska, 1999), or correlations between the distance travelled up to, and following, peak limb velocity (e.g., Elliott, Binsted, & Heath, 1999). In general, the variability-based measures have been argued to be evidence for the contribution of online control when a significant decrease in variability was observed. That is, if online control processes are not intervening, then the variability across multiple movements should increase monotonically throughout the duration of movements. Considering the correlational methods involving kinematic markers, a greater predictability across many movements results in larger correlations, which has been taken as evidence of lesser contributions of online control. That is, because unique corrections are likely required on a trial-to-trial basis, their correlations across trials should be low. Critically, the displacement-based correlations of Elliott et al. (1999) assumed that participants finished their movements near the target. Thus, to complete an accurate movement, any relative overshooting or undershooting at peak limb velocity would need to be
corrected-for in the distance travelled after peak limb velocity. Such corrections would result in a negative correlation between the distance travelled to vs. travelled after peak limb velocity.

An alternative, within-trial approach for the measurement of iterative, pseudocontinuous corrective processes was developed by de Grosbois and Tremblay (2016a). This approach utilized analyses in the frequency domain (i.e., pPower analysis). de Grosbois and Tremblay (2016a) reasoned that a relatively stable visuomotor feedback time could be expected due to the relative stability of corrective reaction times across a range of movement parameters (e.g., Cressman, Cameron, Lam, Franks, & Chua, 2010; Saunders & Knill, 2003; Veyrat-Masson, Brière, & Proteau, 2010), and the overlap of these reaction times with the minimum time with vision that is required to observe a change in reaching performance (e.g., Zelaznik et al., 1983). The contribution of this relatively stable visuomotor influence on reaching performance was isolated by fitting a smooth acceleration profile (i.e., a minimum jerk trajectory: see Flash & Hogan, 1985) and evaluating the relative frequency content in the residuals. Overall, an increased relative contribution of the power at frequencies ranging between approximately 5 and 10 Hz has been associated with the presence relative to the absence of online vision (e.g., de Grosbois & Tremblay, 2016a; de Grosbois & Tremblay, 2015; de Grosbois & Tremblay, de Grosbois & Tremblay, 2016b; de Grosbois & Tremblay, in press). Additionally, performance differences between vision and no-vision conditions were also apparent at a second frequency peak (i.e., between approximately 17 and 20 Hz; see de Grosbois & Tremblay, 2015; de Grosbois & Tremblay, 2016b; de Grosbois & Tremblay, in press). This second peak was proposed to represent a non-visual process, contributing to reaching performance because its associated power increased in the absence, rather than in the presence of online vision. de Grosbois and Tremblay (2016b) proposed that this second peak may reflect a strategic change in the manner in which the reaching movements were planned and controlled.

Because reaching performance can be significantly influenced by instruction set (e.g., Adam, 1992; Elliott et al., 1991; Zhai, Kong, & Ren, 2004), the influence of strategic instruction sets could be used to further evaluate the nature of the frequency peaks observed in de Grosbois and Tremblay (2016b). Accordingly, the primary purpose of the current study was to investigate
how the intent to produce accurate movements influenced the relative contributions of the visual and non-visual control mechanisms attributed to the lower and higher frequency peaks reported in de Grosbois and Tremblay (2015; de Grosbois & Tremblay, 2016b; de Grosbois & Tremblay, in press). To this end, two experiments were completed wherein the scheduling of the availability of vision was either blocked (i.e., Experiment 1) or randomized (i.e., Experiment 2). Both experiments examined whether the contributions of these peaks to reaching performance were modifiable by online vision and voluntary intentions, through the use of two sets of instructions. Participants were instructed to either focus on being as accurate as possible (i.e., high-accuracy instruction) or to simply land in the general vicinity of the target (i.e., low-accuracy instruction). Analyses were completed on four measures of online control, namely; variable error, time after peak limb velocity, $Z^2$ correlations, and pPower (see Data Processing and Analyses for details). It was hypothesized that all measures would indicate greater contributions of online control when online vision was available (i.e., more with full-vision than with no-vision), and when instructed to be accurate (i.e., more with high-accuracy instructions than with low-accuracy instructions). Further, for the pPower analyses, it was hypothesized that if the lower frequency peak indeed represents the contributions of online visuomotor feedback processes modifiable by voluntary intentions, its relative contribution to reaching trajectories would therefore increase in the presence of online vision and to a further extent when participants were instructed to be accurate. Finally, and likewise, it was also hypothesized that if the secondary (i.e., higher) frequency peak represents a non-visual control process modifiable by voluntary intentions, its relative magnitude would increase in the absence of online vision, and to a greater extent when participants were instructed to be accurate. Alternatively, if the frequency peaks represents processes not under voluntary influence, then an accuracy-focused instruction set would not significantly increase their associated relative contributions.
4.4.2 Experiment 1 Methods

4.4.2.1 Participants

Twelve participants were recruited for Experiment 1 (5 males; 7 females; age range 18 to 31). All were right-handed as determined by a modified version of a handedness questionnaire (Oldfield, 1971). Informed written consent was obtained prior to the beginning of the experimental trials. Monetary compensation was provided in the amount of $5 CAD upon completion of the protocol, which lasted approximately 30 minutes.

4.4.2.2 Materials and apparatus

The experimental procedures were completed in a dimly lit room wherein participants sat at a desk in front of a custom aiming console (i.e., console dimensions: length = 51 cm; width = 28 cm; height = 9 cm). The console was oriented such that its long axis extended in the participant's medial-lateral plane (see Figure 4.4.1). Participants also positioned their head in a chin-rest, extending approximately 29 cm above the surface of the aiming console. The shorter edge of the aiming console was aligned with the centre of the chin-rest. A 1 cm by 1 cm of Velcro™ patch served as the home position and was positioned approximately 40 cm to the right of the chin rest. A green light emitting diode (LED) was located 30 cm to the left of the home position and below the surface of the aiming console. Notably, the LED became visible to participants only when illuminated. Also, a piezo-electric buzzer (Mallory Sonalert Products, Inc., Indianapolis, IN, USA) was utilized to provide an auditory go-signal during the experiment.

The availability of visual information of the environment was manipulated via liquid-crystal goggles (i.e., PLATO, Translucent Technologies Inc., Toronto, ON, CA: Milgram, 1987). The goggles could take two states: 1) transparent/open whereby they permitted vision of the environment; or 2) translucent/closed whereby they withheld vision of the environment.

Both position and acceleration data were collected during movements at a concurrent rate of 250 Hz. The position data was acquired using an optoelectric motion tracking system (i.e., Optotrak Certus, Northern Digital Inc., Waterloo, ON, CA), which tracked the position of the
participant's right index finger via an infrared light emitting diode (IRED). The acceleration data was acquired via a triple-axis accelerometer (i.e., MMA7361L; NXP Semiconductors, Eindhoven, Netherlands) embedded in an orthotic wrist-brace worn by the participant on their right hand (i.e., model 225ZZ; Life Brand, Toronto, ON, CA). One of the three axes of the accelerometer was oriented with the primary direction of movement (i.e., the medial-lateral axis). Data from the accelerometer was sampled with a multi-function data acquisition card (i.e., model PCI-6042E, National Instruments Inc., Austin, TX, USA). Custom MATLAB scripts (The Mathworks Inc., Natick, MA, USA) controlled the experimental procedures and devices.

4.4.2.3 Design and procedures

Each trial commenced with the participant resting their right-index finger at the home position. The target LED was illuminated and the goggles were open (i.e., transparent) for a variable foreperiod of 1 to 1.5 s, after which an auditory go-signal was sounded (i.e., 50 ms, 2900 Hz). Movement start was defined as the first occurrence of limb velocity greater than 30 mm/s for 12 ms following the go-signal. In the full-vision condition, the goggles remained open until movement end. Movement end was calculated as the first occurrence of a limb velocity less than 30 mm/s for 20 ms (i.e., four samples) following movement start. The no-vision condition progressed in a similar manner as the full-vision condition up to the moment of movement start, at which the goggles closed and remained closed for the remaining duration of the trial. In addition to the manipulation of the availability of vision, two instruction sets were employed.

In the high-accuracy instruction set, participants were told to try to be as accurate as possible, within a 400 to 500 ms movement time bandwidth. Note that the 500 ms duration was critical for the frequency analyses (see section 4.4.2.4 below) and that reaches taking more than 512 ms (or less than 400 ms) were re-run. In the low-accuracy instruction set, participants were told to land in the general vicinity of the target, still within the movement time bandwidth. This latter condition was conceptually comparable to the “automatic” condition employed by Woodworth (1899) in that online vision was available, but participants were instructed not to focus on completing accurate movements. The two vision conditions and the two instruction sets
were arranged in four blocks of 30 trials, preceded by ten full-vision familiarization trials. The four blocks were arranged in four different orders, which were counter-balanced across participants. Further, each participant completed either two blocks of full-vision followed by two blocks of no-vision or the reverse. Within the two blocks of each vision condition, the instruction sets were also counter-balanced.

4.4.2.4 Data processing and analysis

Based on previous work (i.e., de Grosbois & Tremblay, 2015; de Grosbois & Tremblay, 2016b) four dependent measures of online control were calculated and used to evaluate performance. Variable error (i.e., VE) was computed as the within-condition standard deviation of the movement endpoints in the primary movement axis. Smaller VE values have been attributed to a relatively greater contribution of online control to reaching performance (e.g., Tremblay, Hansen, Kennedy, & Cheng, 2013; see Elliott et al., 2010).

Time after peak velocity (i.e., TAPV) was computed as the number of milliseconds elapsed between the time peak limb velocity was reached and the time of movement end. Longer TAPV durations have been linked to more online control processes (e.g., Binsted, Brownell, Vorontsova, Heath, & Saucier, 2007; Elliott et al., 1991; Hansen, Glazebrook, Anson, Weeks, & Elliott, 2006; Soechting, 1984).

Third, a correlational measure of online control was computed. These, correlational measures were calculated as within-condition correlations across trials between the position attained at a proportion of movement time (i.e., 75% in this case), relative to the position achieved at movement end (e.g., Heath, 2005; Heath, Westwood, & Binsted, 2004). The correlations were then converted into Z-scores using a fisher-transform and then squared (i.e., Z²: e.g., Bernier et al., 2003; de Grosbois & Tremblay, 2016a; de Grosbois & Tremblay, 2015; de Grosbois & Tremblay, 2016b). Squared correlation (e.g., Z²) values that are smaller are interpreted as evidence of a greater contribution of online control to reaching performance (e.g., de Grosbois & Tremblay, 2015; Heath, 2005).
Lastly, proportional power spectra were computed from the acceleration profiles of each trial (i.e., pPower; see de Grosbois & Tremblay, 2016a; de Grosbois & Tremblay, 2015b; de Grosbois & Tremblay, 2016b). These spectra were attained via a four-step process. First, using the MATLAB polyfit and polyval functions, the best fitting 5th order polynomial was determined and computed for each acceleration trace. The best fitting polynomial was then subtracted from the acceleration trace yielding the fit residuals. These residuals were considered for further analyses based on two assumptions: 1) Reaching movements were planned as single, smooth profiles, with four bends (e.g., Flash & Hogan, 1985); and 2) The influence of feedback-based processes could be better evaluated in the associated residual variability (e.g., Noy et al., 2015). Second, a Hanning truncation window of the same length was multiplied by the residuals (e.g., Randall, 2008; Warner, 1998) and the data was converted into a frequency domain representation via a fast-fourier-transform (i.e., FFT; MATLAB fft function) with a transform length of 128 samples (i.e., movement times up to 512 ms). The output of the FFT was converted into a proportional power spectrum (i.e., pPower spectrum) representing the relative percent contribution of resolvable frequencies to the residual variance up to the Nyquist frequency of 125 Hz. The pPower spectra were subsequently evaluated qualitatively for observable peaks. Both the frequency and the relative magnitude of these observable peaks in the pPower spectra were separately subjected to further analyses. Such peaks were identified for each trial, and the associated mean frequencies and magnitudes were computed for each condition, for each participant. Greater relative magnitudes of observed peaks in pPower spectra at 10 Hz and below have been associated with a greater relative contribution online visuomotor control (e.g., the α peak; see de Grosbois & Tremblay, 2016a; de Grosbois & Tremblay, 2015b; de Grosbois & Tremblay, 2016b). Further, greater relative magnitudes of observed peaks in pPower spectra between approximately 17 and 20 Hz have been associated with the contribution of a non-visual process (e.g., the β peak; see de Grosbois & Tremblay, 2015b; de Grosbois & Tremblay, 2016b). Thus, to ensure the capture of both peaks, frequency spectra were evaluated up to 30 Hz.

The main analysis was computed separately for each of the four dependent variables as a 2 Vision Condition (full-vision, no-vision) x 2 Instruction Set (high-accuracy, low-accuracy)
repeated-measures ANOVA. In the event of a significant interaction between Vision Condition and Instruction Set, pairwise comparisons were completed across the two levels of each factor. In this case, a Bonferroni correction was applied to p-values based on the number of t-tests completed (i.e., 4). The corrected p-values have been reported in the results section as $p_{b4}$ where the 'b' indicated that a Bonferroni correction has been applied, and the '4' indicated the number of comparisons corrected for. Statistical significance was determined at $p < .05$ for all analyses. The effect size reported for each ANOVA was generalized eta squared ($\eta^2_G$; see Bakeman, 2005; Olejnik & Algina, 2003). The ANOVAs were computed using the EZ package (Lawrence, 2013) in the R statistics program (version 3.1.2; R-core Team, 2014). All error bars depicted in figures represent within-subject 95 % confidence intervals (see Loftus & Masson, 1994).

4.4.3 Experiment 1: Results

Although no explicit hypotheses regarding either end point accuracy or movement time were proposed, the expected influences of Vision Condition and Instruction Set on performance in general warranted the inclusion of these results in a supplementary analysis (see Section 4.4.9.1).

The analysis of variable error in the primary movement axis (i.e., VE) yielded a significant main effect only of Vision Condition, $F(1,11) = 97.93, p < .001, \eta^2_G = .529$. Performance in the full-vision conditions yielded significantly smaller VE values (i.e., $M = 4.68$ mm, $SD = 0.92$) relative to the no-vision conditions (i.e., $M = 8.59$ mm, $SD = 1.66$). No significant main effect or interaction involving Instruction Set were observed, $F_{s}(1,11) < 3.13, ps > .104, \eta^2_{Gs} < .085$.

The analysis of the time spent following peak limb velocity (i.e., TAPV) resulted in no significant effects or interactions, $F_{s}(1,11) < 1.78, ps > .110, \eta^2_{Gs} < .013$. The grand mean TAPV was 288 ms ($SD = 20$).

The analysis of the $Z^2$ correlations evaluating the relationship between the position achieved at 75% movement time relative to movement end yielded a significant main effect of
Vision Condition, $F(1,11) = 34.12, p < .001, \eta_G^2 = .454$. Performance in the full-vision only conditions yielded significantly smaller $Z^2$ values (i.e., $M = 0.29, SD = 0.15$) relative to the no-vision conditions (i.e., $M = 1.15, SD = 0.48$). No significant main effect or interaction involving Instruction Set were observed, $F$s(1,11) < 0.34, $p$s > .570, $\eta_G^2$s < .007.

Prior to the analysis of the pPower data, the spectra were qualitatively examined for observable peaks (see Figure 4.4.2, panel a). As in de Grosbois and Tremblay (2016b; see also de Grosbois & Tremblay, in press), two peaks were evident: 1) one in the relatively lower frequencies, denoted as the alpha peak ($\alpha_{Peak}$); and 2) one in the relatively higher frequencies, denoted as the beta peak ($\beta_{Peak}$). Analysis of the frequency of the $\alpha_{Peak}$ resulted in no significant effects or interactions, $F$s(1,11) < 4.32, $p$s > .062, $\eta_G^2$s < .035. The grand mean frequency of the $\alpha_{Peak}$ was 7.17 Hz ($SD = 0.62$). Because the interaction between Vision Condition and Instruction Set neared conventional levels of statistical significance, $F(1,11) = 4.32, p = .062, \eta_G^2 = .034$, post-hoc pairwise comparisons were completed across levels of each factor; however no significant differences were observed (i.e., $p_{hs} > .269$). Analysis of the relative magnitudes of the $\alpha_{Peak}$ resulted in main effects of Vision Condition, $F(1,11) = 13.18, p = .004, \eta_G^2 = .235$, and Instruction Set, $F(1,11) = 11.90, p = .005, \eta_G^2 = .022$ (see Figure 4.4.2, panel b). In the full-vision conditions, the relative magnitude of the $\alpha_{Peak}$ was significantly larger (i.e., $M = 25.37 \%, SD = 3.81$) as compared to the no-vision conditions (i.e., $M = 20.68 \%, SD = 4.43$). Additionally, the relative magnitude of the $\alpha_{Peak}$ was also significantly larger with the high-accuracy instruction set (i.e., $M = 23.66 \%, SD = 3.70$) relative to the low-accuracy instruction set (i.e., $M = 22.39 \%, SD = 3.36$). No significant interaction was observed between Vision Condition and Instruction Set, $F(1,11) = 0.42, p = .531, \eta_G^2s = .004$.

Because no observable $\beta_{Peak}$ was present for the full-vision conditions, the frequency of this peak was estimated based on the associated no-vision conditions. The resulting analysis of the frequency of the $\beta_{Peak}$ revealed no significant effect of Instruction Set, $F(1,11) = 1.73, p = .215, \eta_G^2 = .020$. The grand mean frequency for the $\beta_{Peak}$ in the no-vision conditions was 18.27 Hz ($SD = 0.80$). The nearest resolvable frequency (i.e., 17.58 Hz) was chosen to represent the relative magnitude of the $\beta_{Peak}$ in the forthcoming relative magnitude analysis for the two full-
vision conditions. The analysis of the relative magnitude of the $\beta_{\text{peak}}$ resulted in only a main effect of Vision Condition, $F(1,11) = 45.10$, $p < .001$, $\eta^2_G = .562$ (see Figure 4.4.2, panel c). Reaches completed in the full-vision conditions yielded a significantly smaller pPower magnitude at the $\beta_{\text{peak}}$ frequency (i.e., $M = 2.20\%$, $SD = 1.02$) relative to those completed in the no-vision conditions (i.e., $M = 4.81\%$, $SD = 1.21$). No significant main effect or interaction involving Instruction set were observed, $Fs(1,11) < 0.93$, $ps > .005$.

4.4.4 Interim Discussion

The primary purpose of Experiment 1 was to further evaluate the nature of the previously observed frequency peaks in the pPower spectra reported under full-vision and no-vision conditions. Prior to assessing this question directly, measures of visuomotor online control were evaluated to validate the influence of the experimental manipulations.

Firstly, endpoint variability was significantly decreased by the presence of online visual information, which was expected (e.g., Elliott et al., 1991; Heath, 2005; de Grosbois & Tremblay, 2015; Zelaznik et al., 1983). Unexpectedly, the instructions to be accurate did not result in significant decreases in endpoint variability (cf., Adams, 1992; Elliott et al., 1991; Zhai et al., 2004). However, the pattern of results was in the expected direction (e.g., high-accuracy instructions: $M = 6.07$ mm, $SD = 1.32$; low-accuracy instructions: $M = 7.20$ mm, $SD = 1.83$).

Secondly, the analysis of the time spent following peak limb velocity did not exhibit any significant effects or interactions. Although increased times spent following peak limb velocity (TAPV) has been associated with visual feedback utilization, this finding has not been consistently replicated (e.g., de Grosbois & Tremblay, 2015a; de Grosbois & Tremblay, 2015b; de Grosbois & Tremblay, 2016; Heath, et al., 2004). Second, the analysis of TAPV did not result in a significant effect of Instruction Set. It was expected that TAPV would increase with instructions to be accurate (e.g., Adam, 1992; Elliott et al., 1991). However, no significant differences were observed (i.e., high-accuracy instructions: $M = 291$ ms, $SD = 22$; low-accuracy instructions: $M = 286$ ms, $SD = 20$).
Thirdly, $Z^2$ correlational analysis of position at 75% movement time relative to position at movement end yielded a significant effect only of Vision Condition. That is, the presence of online visual information during movement yielded greater estimates of online control. Such an influence of online vision on this correlational measure was expected and has been replicated many times (e.g., de Grosbois & Tremblay, 2016a; de Grosbois & Tremblay, 2015; de Grosbois & Tremblay, 2016b; Heath, 2005; Heath et al., 2004; Khan, Lawrence, Franks, & Buckolz, 2004; Tremblay, et al., 2013; cf., Bernier et al., 2006). In contrast, the effect of Instruction Sets was not significant, although the observed pattern of means was in the expected direction (i.e., high-accuracy instructions: $M = 0.69$; $SD = 0.20$; low-accuracy instructions: $M = 0.76$, $SD = 0.47$). The reduced influence of instructions on performance, relative to previous studies (e.g., Adam, 1992; Elliott et al., 1991), may have stemmed from the added temporal accuracy demand in the current study. That is, participants were instructed to move with a movement time bandwidth between 400 and 500 ms. Thus, given the blocked nature of the Vision Condition scheduling, participants may have inadvertently placed a stronger emphasis on the temporal aspect of the task rather than the spatial aspect. Nevertheless, such an influence of the temporal demands did not interfere with the pPower analyses.

Fourth and last, analysis of the relative magnitude of the $\alpha_{\text{Peak}}$ indicated a significant increase in the contribution of online control processes in the presence of online vision relative to the no-vision conditions. Increased power at this peak has been previously associated with a greater relative contribution of visuomotor online control mechanisms (e.g., de Grosbois & Tremblay, 2015; de Grosbois & Tremblay, 2016b; de Grosbois & Tremblay, in press). Notably, and uniquely across all measures, the high-accuracy instructions also significantly increased the relative magnitude of the $\alpha_{\text{Peak}}$. Because the relative magnitude of the $\alpha_{\text{Peak}}$ can be modulated by intentions to be accurate, the association between the magnitude of the $\alpha_{\text{Peak}}$ and the contribution of online control mechanisms was strengthened. Also, the overall modulation of the relative magnitude of the $\alpha_{\text{Peak}}$ irrespective of level of Vision Condition indicated that the $\alpha_{\text{Peak}}$ may be influenced by both visual and non-visual control processes. Such an assertion is consistent with the fact that the differences, which have been observed between full-vision and no-vision
conditions, have been in the relative magnitude but not in the mere presence/absence of the peak. Potential mechanistic explanations include efferent outflow control, voluntary non-visual control, and proprioceptive control (e.g., Elliott et al., 2010). However, the relative contribution of distinct processes to the relative magnitude of the $\alpha_{\text{Peak}}$ is beyond the scope of the current study and studies manipulating proprioceptive feedback could prove insightful in future investigations.

In contrast, the analysis of the relative magnitude of the $\beta_{\text{Peak}}$ resulted in only a main effect of Vision Condition. That is, as previously reported (e.g., de Grosbois & Tremblay, 2015; de Grosbois & Tremblay, 2016b; de Grosbois & Tremblay, in press), the relative magnitude of the $\beta_{\text{Peak}}$ was larger in the absence of online visual information, as compared to when it was present. Given that the Instruction Set to be accurate did not significantly increase the relative magnitude of the $\beta_{\text{Peak}}$, it may represent a non-voluntary process, which may or may not be corrective in nature. However, the overall differences across conditions raised some doubts.

The meagre differences observed across levels of Instruction Set in Experiment 1 for most dependent variables could indicate that participants opted to plan their movements in a characteristically different manner across conditions. That is, the blocked scheduling of the vision conditions may have led to differences in movement planning across conditions, which in turn may have changed the implementation of the online control of the movements (e.g., de Grosbois & Tremblay, 2016). Indeed, it has been shown that motor planning mechanisms may influence online control processes (e.g., Khan et al., 1998; Khan, Elliott, Coull, Chua, & Lyons, 2002). As such, the results obtained in Experiment 1 may not solely reflect differences in online control because participants knew if online visual feedback would be available or not. For instance, participants were most likely able to better deal with the lack of online vision because they knew the condition prior to each trial and thus could still achieve a high degree of endpoint precision. Importantly, the pPower analysis has been shown to be relatively more robust to planning-induced changes on the quantification of the contribution of online control as compared to the other considered measures (de Grosbois & Tremblay, 2016). As such this motor planning explanation is both possible and probable.
The purpose of Experiment 2 was to evaluate this latter possibility by introducing a randomized scheduling of vision conditions. Such scheduling has been argued to result in a more comparable planning process across vision conditions (i.e., plan for the worst-case scenario; Elliott, Hansen, Mendoza, & Tremblay, 2004; Hansen et al., 2006). In that context, if the frequency peaks represent voluntary and intentional online control processes, then a randomized scheduling may allow for a more direct estimation of differences in the online control between conditions, without as much contamination from additional differences attributable to planning than with a blocked vision condition scheduling.

4.4.5 Experiment 2: Methods

Twelve new participants were recruited for Experiment 2 (5 males; 7 females; age range 18 to 36). The methodologies employed were identical to Experiment 1, with the following exception. In Experiment 2, only two main blocks of trials were completed. Each block consisted of 60 trials within an instruction set and with the vision condition of upcoming trials pseudo-randomly selected. The trial ordering was pseudo-randomized in that the same vision condition could not be repeated on more than two consecutive trials. This manipulation was employed to prevent carry-over effects of repeated vision conditions (e.g., Cheng, Luis, & Tremblay, 2008). Thus, for Experiment 2, two block orders were counter-balanced across participants. Again, participation included a total of 130 trials, lasting approximately half an hour.

4.4.6 Experiment 2: Results

Although no explicit hypotheses regarding either end point accuracy or movement time were proposed, the expected influences of Vision Condition and Instruction Set on performance in general, warranted the inclusion of these results in a supplementary analysis (see Section 4.4.9.2).

The analysis of variable error in the primary movement axis (i.e., VE) yielded a significant main effect only of Vision Condition, $F(1,11) = 43.72, p < .001, \eta_p^2 = .273$. 
Performance in the full-vision conditions yielded significantly smaller VE values (i.e., $M = 4.63$ mm, $SD = 1.64$) relative to the no-vision conditions (i.e., $M = 6.85$ mm, $SD = 1.15$). No significant main effect or interaction involving Instruction Set were observed, $F_{s(1,11)} < 3.03$, $ps > .101$, $\eta^2_{G}s < .080$.

The analysis of the time spent following peak limb velocity (i.e., TAPV) resulted in a significant effect of Vision Condition, $F(1,11) = 7.33$, $p = .020$, $\eta^2_G < .068$. Performance in the full-vision conditions yielded significantly longer TAPV values (i.e., $M = 294$ ms, $SD = 15$) relative to the no-vision conditions (i.e., $M = 286$ ms, $SD = 14$). No significant main effect of Instruction Set was observed, $F(1,11) = 1.90$, $p = .195$, $\eta^2_G = .024$. Additionally, because the interaction between Vision Condition and Instruction Set neared conventional levels of significance, $F(1,11) = 4.74$, $p = .052$, $\eta^2_G = .009$, post-hoc pairwise comparisons were completed. This subsequent analysis revealed that a sole significant difference was observed in the high-accuracy Instruction Set, indicating significantly longer TAPV values in the full-vision relative to the no-vision condition (i.e., full-vision: $M = 298$ ms, $SD = 15$; no-vision: $M = 287$ ms, $SD = 14$; $p_{st} = .025$). The contrast between vision conditions did not reach significance in the low-accuracy Instruction Set (full-vision: $M = 290$ ms, $SD = 18$; no-vision: $M = 285$ ms, $SD = 16$; $p_{st} = .565$).

The analysis of the $Z^2$ correlations evaluating the relationship between the position achieved at 75% movement time relative to movement end yielded a significant main effect only of Vision Condition, $F(1,11) = 23.10$, $p < .001$, $\eta^2_G = .220$. Performance in the full-vision conditions yielded significantly smaller $Z^2$ values (i.e., $M = 0.39$, $SD = 0.34$) relative to the no-vision conditions (i.e., $M = 0.88$, $SD = 0.36$). No significant main effect or interaction involving Instruction Set were observed, $F_{s(1,11)} < 1.85$, $ps > .602$, $\eta^2_{G}s < .050$.

As was the case in Experiment 1, alpha ($\alpha_{peak}$) and beta peaks ($\beta_{peak}$) were observable in the spectra (see Figure 4.4.3, panel a). Analysis of the frequency of the $\alpha_{peak}$ resulted in no significant effects or interactions, $F_{s(1,11)} < 1.61$, $ps > .231$, $\eta^2_{G}s < .027$. The grand mean frequency of the $\alpha_{peak}$ was 6.92 Hz ($SD = 0.49$).
Analysis of the relative magnitude of the $\alpha_{\text{peak}}$ resulted in a main effect of Vision Condition, $F(1,11) = 26.98, p < .001, \eta_G^2 = .223$. In the full-vision conditions, the relative magnitude of the $\alpha_{\text{peak}}$ was significantly larger (i.e., $M = 31.82 \%, SD = 3.10$) relative to the no-vision conditions (i.e., $M = 28.39 \%, SD = 2.70$). Also, the main effect of Instruction Set did not reach conventional levels of statistical significance, $F(1,11) = 3.59, p = .085, \eta_G^2 = .059$ (see Figure 4.4.3, panel b). However, the pattern of means was consistent with the Experiment 1 findings (i.e., high-accuracy instruction set: $M = 30.91 \%, SD = 3.11$; low-accuracy instruction set: $M = 29.30 \%, SD = 2.98$). Additionally, no significant interaction between Vision Condition and Instruction Set was observed, $F(1,11) < 0.01, p = .989, \eta_G^2 < .001$.

Because no observable $\beta_{\text{peak}}$ was present for the full-vision conditions, the frequency of this peak was estimated based on the two no-vision conditions. The analysis revealed no significant effect of Instruction Set, $F(1,11) = 0.16, p = .694, \eta_G^2 = .003$. The grand mean frequency for the $\beta_{\text{peak}}$ in the no-vision conditions was 17.75 Hz ($SD = 0.95$). The nearest resolvable frequency (i.e., 17.58 Hz) was chosen to represent the relative magnitude of the $\beta_{\text{peak}}$ in the forthcoming analysis for the two full-vision conditions.

The analysis of the relative magnitude of the $\beta_{\text{peak}}$ resulted in main effects of both Vision Condition, $F(1,11) = 108.45, p < .001, \eta_G^2 = .647$, and Instruction Set, $F(1,11) = 8.51, p = .014, \eta_G^2 = .152$ (see Figure 4.4.3, panel c). Reaches completed in the full-vision conditions yielded a significantly smaller $\beta_{\text{peak}}$ (i.e., $M = 1.47 \%, SD = 0.42$) relative to the no-vision conditions (i.e., $M = 3.60 \%, SD = 0.84$). Additionally, reaches completed under the high accuracy instruction set yielded a significantly smaller $\beta_{\text{peak}}$ (i.e., $M = 2.20 \%, SD = 0.51$) relative to the low accuracy instruction set (i.e., $M = 2.86 \%, SD = 0.83$). Additionally, no significant interaction between Vision Condition and Instruction Set was observed, $F(1,11) < 0.01, p = .988, \eta_G^2 < .001$.

4.4.7 Discussion

The main methodological difference between Experiment 1 and Experiment 2 was a change from blocked to randomized vision condition scheduling. This change was implemented to increase
the relative influence of online control mechanisms on performance because it was assumed that under randomized scheduling, participants would plan consistently for the worst-case scenario of not having online visual feedback available (e.g., Elliott et al., 2004; Hansen et al., 2006). Thus, the purpose of Experiment 2 was to re-evaluate the effectiveness of various online control measures, while controlling for potential planning differences across vision conditions, which may have attenuated expected changes in online control processes across levels of Instruction Set. Analyses of variable error and $Z^2$ correlation measures in Experiment 2 resulted in a pattern of results similar to that of Experiment 1. That is, online vision availability mediated these measures of online control whereas the instruction set manipulation did not. Thus, as with Experiment 1, the temporal constraints associated with the movement time bandwidth may have led to smaller than expected changes in performance in response to changes in instruction set. In contrast to Experiment 1, the analysis of TAPV in Experiment 2 yielded a significant main effect of Vision Condition. Furthermore, pairwise comparisons indicated that it was only in the high-accuracy instruction condition that TAPV was lengthened in the full-vision relative to the no-vision condition. Such a difference is consistent with the conventional view of longer TAPV representing a greater contribution of online control (e.g., Elliott et al., 1991). The lengthening of the TAPV may have occurred only in Experiment 2 because participants were planning not to have online vision, but were provided with it. That is, participants likely incurred a cost associated with using online visual feedback when they had not planned to. These results and explanation are in line with the findings of Kennedy, Bhattacharjee, Hansen, Reid, and Tremblay, 2015; see also Tremblay et al., 2013; cf., Hansen et al., 2006).

Analysis of the relative magnitude of the $a_{Peak}$ revealed a similar pattern of findings to that of Experiment 1. That is, the relative magnitude of the $a_{Peak}$ was larger in the presence relative to the absence of online visual information. In contrast to Experiment 1, no significant effect of Instruction Set was observed. However, the pattern of the means, and the size of the difference between the two instruction sets were consistent with the findings of Experiment 1. Supplementary analyses conducted with experiments as a between-subjects factor supported this assertion (see Section 4.4.9.3). Overall, the analysis of Experiment 2 was consistent with that of
Experiment 1, with the addition of an anticipated TAPV finding, and a novel $\beta_{\text{Peak}}$ magnitude finding.

The analysis of the relative magnitude of the $\beta_{\text{Peak}}$ replicated the main effect of Vision Condition observed in Experiment 1 and elsewhere (e.g., de Grosbois & Tremblay, 2015a; de Grosbois & Tremblay, 2015b; de Grosbois & Tremblay, 2016). That is, a $\beta_{\text{Peak}}$ of greater relative magnitude was observed in the no-vision relative to the full-vision conditions. In contrast to Experiment 1, a main effect of Instruction Set was observed. That is, when the high-accuracy instruction set was provided, the relative magnitude of the $\beta_{\text{Peak}}$ was significantly smaller relative to the low-accuracy instruction set conditions. It was hypothesized that if the $\beta_{\text{Peak}}$ represented a control mechanism modifiable by voluntary intentions, it would increase in both no-vision conditions and when participants were instructed to be accurate. Instead, the relative magnitude of the $\beta_{\text{Peak}}$ increased with no-vision conditions and decreased when accuracy was stressed in the instructions. Given that this reduction in the $\beta_{\text{Peak}}$ was irrespective of vision condition, it is unlikely that increases in the relative magnitude of this peak represent increases in the contribution of a voluntary non-visual control mechanism. Rather, an alternative explanation is warranted.

Instead of viewing the presence of the $\beta_{\text{Peak}}$ as evidence for a control-related process, a parsimonious alternative is that its absence reflects the contribution of an inhibitory process. That is, under full-vision conditions, oscillations normally associated with this secondary peak were presumably suppressed to achieve a high level of movement accuracy. When online vision was not available, the decrease in contribution of visuomotor online control processes lessened this suppression. Further, when visual feedback was randomized, intentions to be accurate also significantly decreased the relative magnitude of the $\beta_{\text{Peak}}$. Although it is often stated that, under randomized visual feedback schedules, participant plan for the worst-case scenario (e.g., Elliott et al., 2004), the current results indicate that it may not be so simple. Given that under blocked visual feedback scheduling (i.e., Experiment 1), the $\beta_{\text{Peak}}$ was consistently larger in the no-vision conditions relative to the full-vision condition, a worst-case scenario prediction for Experiment 2 (i.e., randomized vision condition schedule) would be an overall $\beta_{\text{Peak}}$ magnitude comparable in
size to the no-vision conditions of Experiment 1. However, this was not the case. Instead, the relative magnitude of the $\beta_{\text{Peak}}$ decreased in Experiment 2 relative to Experiment 1 (see supplementary analyses in section 4.4.9.3). That is, it appeared as if participants were preparing to use visual feedback by suppressing the relative magnitude of the $\beta_{\text{Peak}}$, irrespective of the vision condition. Although the hypothesis of inhibition of the $\beta_{\text{Peak}}$ during movement fit the observed data, such suppression has also been supported by preliminary neurophysiological data.

Fink et al. (2014) examined reaching in mice and found evidence that presynaptic inhibition of interneurons in the spinal cord were important for the maintenance of smooth reaching behaviours. When the specific GABA-ergic interneurons were genetically ablated, the mice exhibited forelimb oscillations in the 18 to 22 Hz range during movement. The authors argued that the interneurons normally reduced the gain of proprioceptive spinal feedback loops during movement. Although the current experiment examined human reaching behaviours, such an inhibitory process is consistent with the data described above. This idea of a modulation of short-latency spinal reflex pathway in a task-specific manner has previously been observed for mechanical perturbations of a reaching limb (e.g., Mutha, Boulinguez, & Sainburg, 2008). As such, it is likely that the $\beta_{\text{Peak}}$ represents the contribution of proprioceptive feedback loops, which can be suppressed via online-vision during reaching and/or overt intentions to complete accurate movements.

4.4.8 Conclusion

The current study sought to evaluate the influence of online vision and intentions to produce accurate movements on visual and non-visual contributions to online reaching performance. It was hypothesized that if the two observed frequency peaks represented visual (i.e., the $\alpha_{\text{Peak}}$) and non-visual (i.e., $\beta_{\text{Peak}}$) online control processes modifiable by voluntary intentions, then their relative contributions to the trajectories of reaching movements should increase in the presence (i.e., the $\alpha_{\text{Peak}}$) and the absence (i.e., $\beta_{\text{Peak}}$) of online vision, respectively. Additionally, high-accuracy instructions were predicted to further facilitate the respective contributions of the visual process (i.e., under full-vision conditions) and the non-visual process
(i.e., under no-vision conditions). In agreement with the first hypothesis, the relative magnitude of the $\alpha_{\text{Peak}}$ increased in the presence of online visual information and also when participants were given high-accuracy instruction sets. However, this instruction-based modulation was more robust when vision conditions were blocked. In contrast, the results associated with the $\beta_{\text{Peak}}$ indicated that its relative magnitude increased in the absence of online vision, as anticipated, but decreased with instructions to be accurate. Notably, this instruction-based modulation was only observed when vision conditions were randomized. Thus, unlike the $\alpha_{\text{Peak}}$, the presence or absence of the $\beta_{\text{Peak}}$ does not represent the direct contribution of an online control process, but rather, it likely represents the suppression of proprioceptive spinal feedback loops, which may otherwise interfere with the production of smooth accurate movements. Further, its observed modulation under randomized trial scheduling indicates that participants were preparing for the possible opportunity to use online visual feedback.

4.4.9 Supplementary Analyses

4.4.9.1 Experiment 1: Mean end point performance and movement time analyses

The analysis of the mean end point performance for Experiment 1 yielded no significant effects or interactions, $F$s(1,11) < 2.16, $p$s > .160, $\eta_G^2$s < .060. The grand mean end point position was 307.8 mm ($SD = 5.8$).

Likewise, the analysis of movement time for Experiment 1 yielded no significant effects or interactions, $F$s(1,11) < 3.20, $p$s > .101, $\eta_G^2$s < .013. The grand mean movement time was 450 ms ($SD = 8$).

4.4.9.2 Experiment 2: End point accuracy and movement time analyses

The analysis of the mean end point performance for Experiment 2 yielded a significant main effect of Vision Condition, $F$(1,11) = 13.10, $p = .004$, $\eta_G^2$s = .247. The full-vision condition
yielded a significantly farther mean end point position (i.e., $M = 309.9$ mm, $SD = 2.8$) relative to the no-vision condition (i.e., $M = 303.3$ mm, $SD = 7.6$).

The analysis of the movement time performance for Experiment 2 yielded a significant main effect of Vision Condition, $F(1,11) = 5.92$, $p = .033$, $\eta_{G}^2 = .092$, and a significant Vision Condition by Instruction Set interaction, $F(1,11) = 6.18$, $p = .030$, $\eta_{G}^2 = .016$. Post-hoc pairwise comparisons of the interaction between Vision Condition and Instruction Set yielded a single significant difference wherein a significantly longer movement time was observed for the full-vision condition relative to the no-vision condition in the high accuracy instruction set condition only. (i.e., full-vision: $M = 455$ ms, $SD = 13$; no-vision: $M = 445$ ms, $SD = 10$; $p_{bs} = .026$).

4.4.9.3 Omnibus analyses of all dependant variables across both Experiment 1 and Experiment 2 with the addition of a between-subjects factor “Experiment”

Although the main analyses focused on within experiment differences, between experiment differences could be informative. As such, each dependent measure, including the supplementary variables of mean end point and movement time, were subjected to a mixed-design ANOVA, which consisted of the same statistical model as the previous analyses with the addition of the between-subjects factor of Experiment (i.e., Experiment 1: Blocked Scheduling, Experiment 2: Random Scheduling). Only significant effects including this between-subjects factor were subject to post-hoc analysis to avoid redundancy.

The analysis of mean end point location in the primary movement axis yielded significant main effect of Vision Condition, $F(1,22) = 6.90$, $p = .015$, $\eta_{G}^2 = 122$, and Instruction Set, $F(1,22) = 5.32$, $p = .031$, $\eta_{G}^2 = 013$. Participant's end points were significantly further in the full-vision condition (i.e., $M = 309.9$ mm, $SD = 3.3$) vs. the no-vision condition (i.e., $M = 304.5$ mm, $SD = 9.7$). Participant's end points were also significantly further in the low accuracy instruction set condition (i.e., $M = 308.0$ mm, $SD = 5.5$) vs. the high accuracy instruction set condition (i.e., $M =$
306.3 mm, SD = 5.5). No significant effects including the between-subjects factor of Experiment were observed, $F_{(1,22)} < 2.38, ps > .136, \eta_g^2{s} < .006$.

The analysis of variable error yielded significant main effect of Vision Condition, $F(1,22) = 139.78, p < .001, \eta_g^2 = .413$, and Instruction Set, $F(1,22) = 6.15, p = .021, \eta_g^2 = .081$. Also, a significant interaction was observed between Vision Condition and Experiment, $F(1,22) = 10.63, p = .004, \eta_g^2 = .051$. Participant's exhibited significantly smaller variable error values in the high accuracy instruction set condition (i.e., $M = 5.6$ mm, $SD = 1.3$) vs. low accuracy instruction set condition (i.e., $M = 6.7$ mm, $SD = 2.0$). Post-hoc analysis of the significant Vision Condition by Experiment interaction was completed via pairwise comparisons across levels of Experiment. These comparisons indicated that no significant difference was present between the two Experiments for the full-vision conditions (i.e., Experiment 1: $M = 4.7$ mm, $SD = 0.9$; Experiment 2: $M = 4.6$ mm, $SD = 1.6$; $t(22) = .09, p_{b2} > .999$). However, significantly greater variable error values were attained in Experiment 1 versus Experiment 2 for the no-vision conditions (i.e., Experiment 1: $M = 8.6$ mm, $SD = 1.7$; Experiment 2: $M = 6.8$ mm, $SD = 1.1$; $t(22) = 2.98, p_{b2} = .014$).

The analysis of movement time only yielded a significant interaction between Vision Condition and Experiment, $F(1,22) = 9.10, p = .006, \eta_g^2 = .051$. Post-hoc analysis of the significant Vision Condition by Experiment interaction was completed via pairwise comparisons across levels of Experiment. These comparisons indicated that no significant differences were present between the two Experiments for either the full-vision (i.e., Experiment 1: $M = 448$ ms, $SD = 8$; Experiment 2: $M = 455$ ms, $SD = 10$; $t(22) = -1.77, p_{b2} = .183$), or the no-vision conditions (i.e., Experiment 1: $M = 451$ ms, $SD = 9$; Experiment 2: $M = 448$ mm, $SD = 9$; $t(22) = 0.97, p_{b2} = .686$).

Likewise, the analysis of time after peak limb velocity only yielded a significant interaction between Vision Condition and Experiment, $F(1,22) = 7.52, p = .012, \eta_g^2 = .022$. Post-hoc analysis of the significant Vision Condition by Experiment interaction was completed via pairwise comparisons across levels of Experiment. These comparisons indicated that no
significant differences were present between the two Experiments for either the full-vision (i.e., Experiment 1: $M = 287$ ms, $SD = 18$; Experiment 2: $M = 294$ ms, $SD = 15$; $t(22) = -1.09$, $p_{b2} = .571$), or the no-vision conditions (i.e., Experiment 1: $M = 290$ ms, $SD = 23$; Experiment 2: $M = 286$ mm, $SD = 14$; $t(22) = 0.46$, $p_{b2} > .999$).

The analysis of the $Z^2$ correlations evaluating the relationship between the position achieved at 75% movement time relative to movement end yielded only a significant main effect of Vision Condition, $F(1,22) = 56.89$, $p < .001$, $\eta_G^2 = .343$. Reaches completed in the full-vision condition yielded significantly lower $Z^2$ values (i.e., $M = 0.34$, $SD = 0.26$) relative to the no-vision condition (i.e., $M = 1.02$, $SD = 0.44$). Notably, because the interaction between Vision Condition and Experiment neared conventional levels of statistical significance, $F(1,22) = 4.11$, $p < .055$, $\eta_G^2 = .036$, post-hoc analysis of this interaction were completed via pairwise comparisons across levels of Experiment. These comparisons indicated that no significant differences were present between the two Experiments for either the full-vision (i.e., Experiment 1: $M = 0.29$, $SD = 0.15$; Experiment 2: $M = 0.39$, $SD = 0.34$; $t(22) = -0.88$, $p_{b2} = .778$), or the no-vision conditions (i.e., Experiment 1: $M = 1.15$, $SD = 0.48$; Experiment 2: $M = 0.88$, $SD = 0.36$; $t(22) = 1.54$, $p_{b2} = .276$).

Analysis of the frequency of the $\alpha_{\text{Peak}}$ resulted in no significant effects or interactions and only the interaction between Vision Condition and Instruction Set neared conventional levels of statistical significance, $F(1,22) < 3.82$, $p = .063$, $\eta_G^2 < .018$. Post-hoc analysis of this interaction were completed via pairwise comparisons across levels of Vision Condition and Instruction Set, and revealed no significant differences, $t_s(23) > 2.19$, $p_{bs} > .155$. Notably, no significant effects including the between-subjects factor of Experiment were observed, $F_s(1,22) < 1.24$, $ps > .278$, $\eta_G^2$s < .032.

Analysis of the of the relative magnitude of the $\alpha_{\text{Peak}}$ resulted in significant main effects of Vision Condition, $F(1,22) = 31.35$, $p < .001$, $\eta_G^2 = .227$, Instruction Set, $F(1,22) = 9.68$, $p = .005$, $\eta_G^2 = .035$, and Experiment, $F(1,22) = 31.28$, $p < .001$, $\eta_G^2 = .470$. The relative magnitude of the $\alpha_{\text{Peak}}$ was greater in the full-vision (i.e., $M = 28.60\%$, $SD = 4.73$) vs. the no-vision condition.
(i.e., $M = 24.53\%, SD = 5.33$). Also, the relative magnitude of the $\alpha_{\text{Peak}}$ was greater in the high-accuracy instruction set (i.e., $M = 27.29\%, SD = 4.98$) vs. the low-accuracy instruction set condition (i.e., $M = 25.84\%, SD = 4.70$). Lastly, the relative magnitude of the $\alpha_{\text{Peak}}$ was greater in Experiment 2 (i.e., $M = 30.10\%, SD = 2.67$) vs. Experiment 1 (i.e., $M = 23.03\%, SD = 2.48$).

Given the relative absence of an apparent $\beta_{\text{Peak}}$ across both Experiments 1 and 2, the analysis of the frequency of the $\beta_{\text{Peak}}$ was restricted to the no-vision conditions (i.e., within-subjects factor of Instruction Set, and a between-subjects factor of Experiment). This analysis resulted in no significant effects or interactions, $F_s(1,22) < 2.11$, $p_s > .160$, $\eta^2_G < .074$.

Analysis of the of the relative magnitude of the $\beta_{\text{Peak}}$ resulted in significant main effects of Vision Condition, $F(1,22) = 116.63$, $p < .001$, $\eta^2_G = .591$, Instruction Set, $F(1,22) = 8.71$, $p = .007$, $\eta^2_G = .041$, and Experiment, $F(1,22) = 10.23$, $p = .004$, $\eta^2_G = .187$. The relative magnitude of the $\beta_{\text{Peak}}$ was greater in the no-vision (i.e., $M = 4.20\%, SD = 1.19$) vs. the full-vision condition (i.e., $M = 1.84\%, SD = 0.85$). Also, the relative magnitude of the $\beta_{\text{Peak}}$ was greater in the low-accuracy instruction set (i.e., $M = 3.22\%, SD = 0.96$) vs. the high-accuracy instruction set condition (i.e., $M = 2.81\%, SD = 0.95$). Lastly, the relative magnitude of the $\beta_{\text{Peak}}$ was greater in Experiment 1 (i.e., $M = 3.51\%, SD = 0.90$) vs. Experiment 2 (i.e., $M = 2.53\%, SD = 0.56$).
4.4.10 References


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doi:10.3200/JMBR.36.3.339-351

doi:10.1037//0033-2909.127.3.342


doi:10.1037/h0055392


doi:10.1037/cjep2006019


Figure 4.4.1. A depiction of the experimental setup (Note. Not to scale).
Figure 4.4.2. The main findings of Experiment 1. a) The mean pPower spectra of the four conditions for Experiment 1; b) The relative magnitude of the $\alpha_{\text{Peak}}$; and c) the relative magnitude of the $\beta_{\text{Peak}}$ across experimental conditions in Experiment 1. * indicates $p < .05$. Error bars represent within-subject 95% confidence intervals.
Figure 4.4.3. The main findings of Experiment 2. a) The mean pPower spectra of the four conditions for Experiment 2; b) The relative magnitude of the $\alpha_{\text{Peak}}$; and c) the relative magnitude of the $\beta_{\text{Peak}}$ across experimental conditions in Experiment 1. * indicates $p < .05$. Error bars represent within-subject 95% confidence intervals.
5 General Discussion

The overall purpose of the current dissertation could be subdivided into two major goals: 1) to develop and test a novel methodology for the quantification of online control; 2) to gain a further theoretical understanding of the underlying mechanisms governing the online control of simple reaching movements. These goals were achieved via five experiments organized into four manuscripts.

The experiment reported in the first manuscript examined the possible utility of frequency domain analyses for the segregation of performance between full-vision and no-vision conditions. That is, the first experiment examined performance wherein a relatively greater contribution of online control was expected (i.e., a full-vision condition) relative to another condition (i.e., a no-vision condition). The results of this first experiment indicated that frequency domain analyses were sensitive to visually-mediated changes in online control. Additionally, this analysis proved to be the most sensitive of the within-trial measures examined. Importantly, however, between-trial correlational measures appeared to be able to best dissociate performance between full-vision and no-vision conditions.

The experiment reported in the second manuscript sought to take advantage of an inherent advantage of frequency domain analyses over existing measures of online control to elucidate the potential presence and contribution of distinct sensorimotor control processes contributing to reaches. The basic rationale was that if distinct control processes mediate performance differences, then their influence should be apparent at unique frequencies of iteration. Conversely, traditional online control analyses have been inherently limited to binary decisions, albeit graded ones indicating relative changes in control as a whole, rather than the contributions of separable, distinct processes. Given that modern models of online control posit the existence of numerous distinct processes, such an evaluation was warranted. In this second experiment, a full-vision condition and two distinct no-vision conditions were employed. These no-vision conditions differed in that vision of the environment was either removed upon movement onset or two seconds prior to the go-signal. Importantly, previous evidence suggested
that these two conditions may rely upon different control mechanisms. With vision removal at movement onset, a more visually-mediated control was expected based in part on visual persistence (e.g., Elliott & Madalena, 1987). With vision removal two seconds prior to a go signal, an inefficient proprioceptive control mechanism was expected (e.g., Elliott et al., 1991). Notably, however, the results of the second manuscript were not completely consistent with the aforementioned hypotheses. That is, although the results reported in the second manuscript provided evidence for a secondary, non-visual control mechanism, through the presence of a second higher frequency peak, this additional process did not distinguish performance between the two no-vision conditions. Rather, the secondary peak distinguished the full-vision from both no-vision conditions. Given that the secondary peak was prominent only in the absence of online vision, the associated process was deemed to be inherently non-visual in nature, and likely represented proprioceptive-based process. Nevertheless, according to the frequency domain analyses forwarded in the first manuscript, there was no evidence that the two no-vision conditions differed in their online control mechanisms. Yet, trajectory and endpoint performance differences did exist between the two no-vision conditions. Ultimately, it was proposed that these performance differences might have come about through the influence of offline changes in performance. This hypothesis thus inspired the experiment reported in the third manuscript, which examined the relative sensitivities of measures of online control to offline processes.

The experiment reported in the third manuscript experimentally induced offline trial-to-trial changes in performance using optical prisms and terminal feedback. Only the frequency domain analyses were found to be both consistently sensitive to changes in online control, while remaining relatively robust to the offline changes in performance. Correlational analyses were found to be sensitive to online control and robust to graded offline changes in performance induced by the prisms. In contrast, the correlational analyses were also sensitive to the less consistent offline corrections induced by terminal feedback. Importantly, and consistent with the second experiment, a secondary frequency peak was observed in all no-vision conditions, irrespective of the magnitude of the shift in visual information induced by the prisms. Thus, changes in offline processes did not significantly influence the relative magnitudes of either the
lower or higher frequency peaks. The findings of the experiment reported in the third manuscript strengthened the notion that the performance differences observed across the no-vision conditions in the second manuscript were due to offline changes in performance. Nevertheless, the specific nature of the secondary frequency peak remained unresolved.

The purpose of the two experiments reported in the fourth manuscript was to seek further support in favour of the association between the observed frequency peaks from the previous experiments and online control processes. This purpose was accomplished through two main manipulations. First, vision conditions were either presented in a blocked (i.e., Manuscript 4, Experiment 1; see section 4.4.2) or a randomized (i.e., Manuscript 4, Experiment 2; see section 4.4.5) schedule. Because it was anticipated that participants would prepare for the worst-case scenario under randomized vision scheduling (e.g., Elliott et al., 2004), random scheduling was to control for possible planning differences across vision conditions and to better isolate the relative contributions of online control mechanisms. In addition, two instruction sets were implemented: one stressed movement accuracy and one did not. Both the availability of online vision and high-accuracy instructions led to an overall increase in the contribution of the lower frequency visuomotor process. In contrast, irrespective of vision condition scheduling, the higher frequency non-visual process increased its relative contribution in the absence of relative to in the presence of online visual information. However, this contribution decreased with a high-accuracy instruction set, when visual conditions were provided in a randomized scheduling. Thus, the studies reported in the fourth manuscript provided further evidence that the lower frequency peak represented an active online visuomotor mechanism. In contrast, the secondary, non-visual frequency peak likely represented a non-visual process, which can be inherently suppressed in the presence of online vision and can also be voluntarily suppressed in the absence of online vision. A speculative mechanism for the non-visual process was the potential for presynaptic inhibition of proprioceptive reflex loops. Altogether, the four manuscripts of the current dissertation directly lead to both significant methodological and theoretical contributions to the field of motor control.
5.1 Implications for the quantification and measurement of online control

Although the primary purpose of the experiment reported in the first manuscript was to evaluate the potential utility of frequency domain analyses for the identification of performance differences mediated by online visual feedback utilization, a secondary purpose was to compare this novel methodology with existing measures of online control. Particular interest was given to the distinction between single-trial and multiple-trial measures of online control. Specifically, it was hypothesized that multiple-trial measures may inherently be sensitive to both online and offline mechanisms. The findings of this initial manuscript identified a subset of online control measures that were more thoroughly examined across the remaining studies (i.e., across a number of sensory environments and experimental manipulations). These measures included two multiple-trial variables (i.e., variable error and \(Z^2\) correlations of position at 75% movement time relative to position at movement end), and two single-trial variables (i.e., time-after-peak-velocity and the novel frequency domain analysis). Overall, these analyses indicated that a simple distinction between single-trial and multiple-trial measures of online control was not sufficient to explain the differences observed between measures. That is, not all measures fared equally well under all conditions. A summary of the relative performance of the herein utilized measures of online control can be found in Table 5.1.
Table 5.1. Comparison of the sensitivities of the measures of online control across the studies.

<table>
<thead>
<tr>
<th>Type</th>
<th>DV</th>
<th>Online Vision</th>
<th>Offline Changes</th>
<th>Intentions to be Accurate</th>
<th>Distinct Contributions of unique processes</th>
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<td>Within-trial</td>
<td>TAPV</td>
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<td>Within-trial</td>
<td>pPower</td>
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<td>Between-trial</td>
<td>VE</td>
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<td>Between-trial</td>
<td>$Z^2$ @ 75% MT</td>
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Note. * indicates that significant effects were observed in the theoretically predicted direction. “~” indicates that some evidence was observed but it was not consistent across experiments.

First, the patterns of results for the two multiple-trial measures differed significantly across the experiments. Both VE and $Z^2$ analyses were capable of quantifying the increased contributions of online control under standard full-vision and no-vision reaching environments. However, in the presence of prism-induced offline changes in performance, the VE measure was no longer sensitive to the contribution of online control, whereas the $Z^2$ measure remained sensitive. Furthermore, although VE was robust to offline changes in performance induced via terminal-feedback, the $Z^2$ analysis was significantly influenced by them. Notably, in the current
studies, neither measure was sensitive to intentions to be accurate, and neither could quantify the independent contributions of distinct control processes.

Second, the two single-trial measures also differed in their performance across the included experiments. That is, TAPV was found to be modestly sensitive to the contributions of online control, however, it was also sensitive to prism-induced offline changes in performance. TAPV also exhibited a modest increase in response to instructions to focus on accuracy. However, it was not sensitive to the relative contributions of separate mechanisms contributing to performance. Conversely, the frequency domain analyses were sensitive to online control, robust to offline influences, modestly sensitive to the influence of intention, and capable of discerning the relative contributions of distinct processes.

Using the suggestions outlined by Bakeman (2005) for classifying the magnitude of the generalized eta squared effect size\(^7\) (i.e., \(\eta_G^2\); 0.2 >= small, 0.13 >= medium, 0.26 >= large), the size of the effect of online vision in the frequency domain analyses at the lower frequencies (i.e., alpha peak frequencies) varied from just below the small criterion to just below the medium criterion (i.e., \(\eta_G^2 = 0.014\) to 0.235). The experiment-wise average effect size for this lower frequency process was overall medium (i.e., \(\eta_G^2 = 0.129\)). The effect sizes associated with the presence of the secondary non-visual process (i.e., the \(\beta_{\text{peak}}\) frequencies) ranged from just below the medium criterion to well above the large criterion (i.e., \(\eta_G^2 = 0.117\) to 0.647). The experiment-wise average effect size for the higher frequency process was overall large (i.e., \(\eta_G^2 = 0.391\)). In contrast, the effect sizes of the \(Z^2\) correlational analysis ranged in its effect size from just above the small criterion (i.e., \(\eta_G^2 = 0.047\)) to well above the large criterion (i.e., \(\eta_G^2 = 0.716\)). Notably, the analysis of \(Z^2\) correlations averaged a large effect size of (i.e., \(\eta_G^2 = 0.420\)).

Altogether, the current dissertation succeeded in the development and testing of a frequency domain approach to the quantification of online feedback utilization, which included a

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\(^7\) Because generalized eta squared (i.e., \(\eta_G^2\)) is calculated utilizing a larger error term than partial eta squared (i.e., \(\eta_p^2\)), estimates of \(\eta_G^2\) tend to be smaller than those of \(\eta_p^2\) (e.g., Bakeman, 2005).
novel focus on the residual variability in the acceleration profiles following the fitting of a smooth 5th order polynomial. These frequency domain analyses successfully dissociated performance across conditions wherein online feedback utilization was expected to differ. Importantly, this sensitivity was found to be the greatest among existing within-trial measures of online control. This sensitivity to online control processes was also immune to offline, trial-to-trial changes in performance. All other measures considered did exhibit sensitivity to such offline changes. In addition to the sensitivity of frequency domain analyses to the contributions of online control, only the frequency analyses were able to explicitly identify the unique contributions of multiple processing contributing to the same trajectory. That is, both a visual and a non-visual process were identified in manuscripts 2 to 4. Ultimately, the dissertation improved upon the existing literature in that it resulted in a novel measure of online feedback utilization, which was also relatively robust to offline influences, and could successfully identify distinct processes contributing to reaches.

5.2 Implications for the theoretical and mechanistic understanding of online control

5.2.1 On the possibility of an iterative control process

Beyond the methodological contributions associated with the development of a novel approach for the quantification of online control during reaching, the outcomes of the herein contained experiments also led to significant theoretical contributions to the field of motor control. First, the frequency domain analyses provided evidence for the contribution of an iterative control processes because these analyses break signals down into rates or iterative influences.

Theories of motor control have posited the potential influence of iterative processes since the work of Craik (1947). Such a view is in line with Crossman and Goodeve (1983), who suggested that corrective processes operative in a serial iterative manner. Likewise, Elliott et al. (1991) argued that the contribution of overlapping corrective processes may often lead to
relatively smooth kinematic profiles. Such smooth corrective responses have been observed for target location perturbations occurring relatively early in the trajectory (e.g., Pélisson et al., 1986; see also Desmurget et al., 2001) and subsequently many researchers have argued for the continuous monitoring of sensory information during reaches (e.g., Proteau et al., 2009; Saunders & Knill, 2003). However, the evidence put forth in favour of a continuous control process was negative evidence because it was built upon an absence of significant trajectory discontinuities. The fact that frequency domain analysis was sensitive to performance differences mediated by changes in the contribution of online control indicates that an iterative control process contributed to the accurate performance of reaches. As well, the positive evidence of iterative control also challenges other theoretical perspective regarding online control mechanisms.

Meyer et al. (1988) argued against the probability of continuous corrective processes in favour of less frequent and discrete corrections, based on the presumption that many corrections would be energetically wasteful. However, considering that muscles impart forces upon the limbs to move them, the system could be considered as a second-order system (i.e., controlling trajectories via changes in acceleration because force equals mass times acceleration while mass is constant). When learning to control a second-order system, participants have been found to optimize their behaviour by making smaller corrections more often rather than larger fewer corrections (e.g., Hancock, 1996; Pew, 1966). Importantly, such a finding does not discount or downplay the importance of other potential corrective responses, such as impulse regulation or the many types of discrete corrections described by Meyer et al. (1988) and others. Rather, the idea of an iterative mode of control could serve to complement the current understanding of a multi-faceted, multiple-process view of online control (e.g., Elliott et al., 2010).

5.2.2 On the mode of visual feedback utilization

One important novel element arose through the analyses of the results of the current dissertation. That is, given that frequency domain analyses break signals down into sine and cosine waves, the frequencies observed could represent the contributions of an iterative pulsatile
process (i.e., acceleration-deceleration pairs), operating at the reported frequencies or the contribution of an iterative, graded process (i.e., either accelerations or decelerations) acting at twice the associated frequencies (see 4.1.4.2). Importantly, both types of corrective processes have been proposed to exist (i.e., discrete vs. graded corrections; e.g., Meyer et al., 1988). When considering the possibility of an iterative graded process (i.e., acting at twice the observed frequencies), the current data generated from movements to 30 cm targets could be associated with latencies of corrections ranging from 64 to 80 ms (i.e., frequencies ranging from 7.8 to 6.25 Hz, respectively). Such estimates are roughly consistent with the fastest visually-mediated corrective reaction times of 75 ms reported by Fautrelle, Prablanc, Berret, Ballay, and Bonnetblanc (2010). In contrast, the data corresponding with the performance to a 10-cm target distance were inconsistent with the possibility of a graded process. That is, the iterative rates consistent with the observed frequency of 9.55 Hz were significantly shorter in duration (i.e., 53 ms) than any previously observed visuomotor processes. Ultimately, a parsimonious explanation for the observed reaching behaviour towards all target amplitudes examined would be a mode of iterative pulsatile control similar to that described by Crossman and Goodeve (1963/1983). That is, corrective processes acting in acceleration/deceleration pairs (i.e., rather than graded accelerations/decelerations) with iterative rates of 128 to 160 ms (i.e., frequencies ranging from 7.8 to 6.25 Hz, respectively). Notably, such iterative rates are consistent with many estimates of the duration of visuomotor feedback time during reaching (e.g., Carlton, 1981; Knill & Saunders, 2003; Zelaznik et al., 1983). This singular mechanism explanation for the different rates observed to be associated with visuomotor feedback processes suggests that a flexible mechanism, capable of high iteration rates, was responsible for the observed differences (cf., contributions of distinct relatively fast-automatic and/or relatively slow-voluntary processes; e.g., Day & Lyon, 2000).

5.2.3 On the rate of visual feedback utilization

Although a visual corrective reaction time of approximately 100 ms has become a relatively standard estimate (e.g., Carlton, 1992), the results of the current dissertation could be interpreted as evidence that the online control may not normally operate at this proposed
maximal rate. Rather, online corrections likely normally proceed at slower rates but the rate can increase to a value close to this estimated maximal rate when task demands restrict the time available to complete corrections. Evidence for such similarly flexible rates of feedback utilization has been observed in manual tracking tasks, such as Miall (1996), who found that increasing the tracking speed led to corrections at significantly faster rates. Flexibility in the rates of online feedback utilization has also been observed when providing feedback in an intermittent fashion during an isometric force tracking task (e.g., Sosnoff & Newell, 2004). Thus, although it has been argued that iterative corrective processes may be energetically wasteful (e.g., Meyer et al., 1988), the cost associated with implementing such a strategy may also be minimized by reducing the rate at which feedback is utilized when task constraints permit such a strategy. Ultimately, the current set of studies indicates that although participants can utilize corrective processes at rates up to around 10 Hz (i.e., at least 9.5 Hz in manuscript 2), they may only do so when successful task performance requires it.

5.2.4 On the possibility of multiple distinct online processes contributing to reaching performance

Many distinct processes have been described and implicated in the control of goal-directed movement (e.g., Elliott et al., 2010). It was hypothesized that frequency domain analyses would be sensitive to the contributions of such processes, based on the assumption that each would require a distinct latency at which it could act. Although significant evidence exists in favour of multisensory integration during perceptual judgements completed at rest (e.g., Ernst & Banks, 2002), the evidence is much more equivocal during the completion of goal-directed reaching movements (e.g., Körding & Wolpert, 2004; cf., Loria et al., 2016; Tremblay & Nguyen, 2010). Overall, the current dissertation found evidence for multiple parallel-acting processes rather than a wholly integrative utilization of online feedback.

Overall, across the studies included in the current dissertation, two distinct frequency peaks were observed. The lower, \( \alpha_{\text{peak}} \) was consistently greater in relative magnitude in conditions wherein online vision was available relative to conditions without online vision. This
association was taken as evidence that visuomotor online control processes exert their influence at the associated frequency range (i.e., approximately 6 to 10 Hz). Evidence supporting the association between this peak and the contributions of online control were also attained through the observed insensitivity of offline mechanisms, the modest increases in contributions with intentions to be accurate, as well as the implementation of randomized visual feedback schedules. Thus, the increased contributions to the $\alpha_{\text{peak}}$ in the presence of online vision likely represent the contributions of a visuomotor online control process.

In addition to the $\alpha_{\text{peak}}$, a second, higher frequency $\beta_{\text{peak}}$ was observed in conditions wherein online visual information was not available. More specifically, the relative contributions to the frequency domain representation increased in the no-vision conditions relative to the full-vision conditions. Given this association, the contributions of the $\beta_{\text{peak}}$ were attributed to a non-visual mechanism. Arguably, a likely alternative candidate could be a proprioceptive mechanism. Indeed, manipulations of proprioceptive information have been shown to influence reaching performance (e.g., Cordo, Gurfinkel, Bevan, & Kerr, 1995; Steyvers et al., 2001). Evidence for an online nature of the process associated with the $\beta_{\text{peak}}$ was attained by the relative invariance of its contribution in the presence of offline changes in performance. Further, intentions to be accurate resulted in a significant reduction in the contribution of the $\beta_{\text{peak}}$ to performance, under a randomized vision schedule. Had the $\beta_{\text{peak}}$ represented the contribution of an error-reducing non-visual online control mechanism, it was hypothesized that the contribution would have increased with intentions to be accurate, particularly in the no-vision conditions. Thus, the $\beta_{\text{peak}}$ instead likely represented a process which is/was actively inhibited to promote accurate reaching performance, especially when online vision was available. One candidate explanation is the contribution of peripheral spinal reflex pathways. These pathways have been found to exert oscillations at comparable frequencies and their influence has been proposed to be limited during movement via presynaptic inhibition (e.g., Fink et al., 2014; Scott & Crevecoeur, 2014). Notably, this explanation does not discount the possible utility of such reflex processes in the absence of superseding top-down influences. Nevertheless, the $\beta_{\text{peak}}$ likely represented the unique contribution of a secondary non-visual process, which exerts its influence during reaching and is
not quantifiable using conventional measures of online control. Therefore, at least some visual and non-visual information available online during reaching performance is utilized relatively separately and not integrated into singular feedback mechanisms.

5.3 Limitations

Although the utility of frequency domain analysis was supported across the four manuscripts that contributed to the current dissertation. A number of important caveats must be acknowledged, the majority of which come about through the very nature of the analysis itself.

First, frequency domain analysis computed via a Fast Fourier Transform is inherently sensitive to cyclical or iterative processes acting at a relatively constant rate (e.g., Bracewell, 1986). Although many types of online corrections and online corrective processes have been proposed and observed, the current body of work is inherently sensitive only to relatively continuous, or at least temporally stable iterative processes (i.e., a stationary signal; e.g., Bracewell, 1986). Therefore, the currently implemented analyses were more consistent with behaviours predicted by iterative models of online reaching performance such as the iterative corrections model of Crossman and Goodeve (1963/1983), the pseudocontinuous model of Elliott et al. (1991) and the impulse regulation process of the multiple processes model of Elliott et al. (2010). In contrast, the currently utilized analyses were potentially insensitive to more discrete processes likely coming about via irregularly-timed discrete submovements (e.g., Meyer et al., 1988), voluntary control processes (e.g., Day & Lyon, 2000), or more traditional ideas of online control such as the limb-target regulation of the Elliott et al. (2010) multiple processes model. This inherent sensitivity to iterative processes could have contributed to the finding of only a singular visuomotor latency in the current dissertation. Importantly, such a finding does not refute the expected contributions of a multiple online visuomotor processes to reaching performance.

Second, the frequency resolution of an FFT is limited by the length of the associated signal (e.g., Bracewell, 1986). Thus, the specificity of the latencies associated with the identified frequencies attributable to the contributions of visual and non-visual online processes are at best
an approximation. Improved estimates of the associated latencies could be theoretically possible by employing longer and longer duration reaching movements, however, such movements quickly become unnatural and may no longer represent normal reaching behaviour. This methodological limitation was exacerbated to a degree by the application of this analytical approach with discrete reaching movements. Thus, research employing reciprocal aiming movements (e.g., Fitts, 1954) may provide an avenue to estimate the latencies associated with the identified processes.

The last limitation of the current body of work to be acknowledged stemmed from the choice of evaluating a normalized/proportional power spectra. It has been argued that the most valid way to compare distinct signals that differ in magnitude is by examining the relative contributions (i.e., normalized power) to the signals in question (e.g., Warner, 1998). Such an approach was applied for the current analyses due to the potential presence of both intra- and inter-individual changes in accelerations between movements that could dramatically increase the variability in the raw signal. Further, because online visual feedback utilization is but one of many possible sources of oscillatory variability during movement (e.g., biomechanical properties of the limb [e.g., Elble & Koller, 1990]; signal-dependent and signal-independent noise [e.g., van Beers et al., 2004]), the normalized spectra represented the overall impact of this online feedback processes. A consequence of this choice in methodological approach however, is a loss of information regarding the absolute contribution of any particular process to overall variability. Thus, the associated changes in the relative magnitudes of the different contributions to the overall variability cannot necessarily be interpreted directly in isolation of one another. Rather, the changes in relative contributions may come about through explicit changes in either individual processes, or in-coincident changes in multiple contributions. The associated analyses of the relative magnitudes of contributions cannot inherently dissociate between these alternatives. However, given the likely supplemental nature of multiple contributions to reaching performance, changes in the relative contributions likely still represent the best approach available.
5.4 Conclusions

The main purpose of the current dissertation was to evaluate the potential utility of frequency domain analysis for the quantification of the online control of upper-limb reaching movements. Through this purpose, both methodological and theoretical contributions to the field of motor control were sought. The methodological goal was achieved through the apparent sensitivity of frequency domain analyses to the contributions of online control processes to reaching movements. Further, this sensitivity was maintained even in the presence of experimentally-induced, offline changes in performance. Notably, frequency domain analyses fared better than other common measures of online control with regards to the degree of robustness observed to influence from such offline processes. Importantly, the other measures of online control that were considered did not fare as well in these regards. Lastly, only frequency domain analyses were able to identify and quantify the relative influence of multiple online processes contributing to reaching performance. Thus, frequency domain analysis represents a novel and effective means to evaluate the contributions of online control to reaching performance.

In addition to the methodological contributions, a number of theoretical contributions were achieved as well. First, because frequency domain analyses were sensitive to the online contributions of visuomotor processes, those processes inherently exerted an iterative influence on reaching performance. Second, the rate at which these visuomotor processes exerted their iterative influence was found to be flexible. That is, when movements of shorter amplitudes were completed (i.e., less time available to correct the trajectory), the rate of online corrections increased. Third, frequency domain analyses were able to identify the distinct contributions of two unique visual and non-visual processes, which contributed to online reaching performance. Current models of online feedback utilization predicted the contribution of multiple online processes, yet direct evidence from a single measure had not been demonstrated until now. Altogether, the characteristics of frequency domain analyses allowed for novel affirmation and insight into the multi-faceted nature of online reaching performance.
6 References


Appendix 1

MATLAB frequency domain analysis script

function
[ppower_spectra,raw_power_spectra,frequency_bins,fitted_function,fit_residuals,function_fit] = ppower_analysis(input_data,sampling_hz,transform_length,poly_order)

% Step 1: Fit a polynomial to the trajectory to remove trends associated with
% the primary sub-movement (in this case, since we are analyzing an
% acceleration trace; typically use a 5th order polynomial [4 bends].

samples = [1:length(input_data)];

% fitting a nth order polynomial to the data
[data_fit s mu] = polyfit(samples,input_data,poly_order);

% generate the polynomial from the weights determined in polyfit
fitted_function = polyval(data_fit,samples,[],mu);

%(get OLS residuals from the polynomial fit);
fit_residuals = input_data-fitted_function;

% Determine the R2 fit of our polynomial fit
input_data_grandmean = mean(input_data);
SSTotal = sum((input_data-input_data_grandmean).^2);
SSresiduals = sum(fit_residuals.^2);
function_fit = 1 - (SSresiduals/SSTotal);
%% Step 2: Pre-process the input data residuals for the FFT analysis
% Using a Hanning window to pre-process the data (tapers the edges of the
% data window for a cleaner FFT output (i.e., less spectral leakage)
% NOTE: there are other windowing functions available such as hamming, and chebwin (see
MATLAB help)
data_length = length(input_data);
window = hanning(data_length,'periodic');
x = window.*detrend(fit_residuals,'constant');

%% Step 3: Compute the FFT of the preprocessed residuals
fs = sampling_hz;
m = data_length; % Window length
% if transform length is not specified in advance, you should use next power of 2
n = transform_length;%pow2(nextpow2(m));
y = fft(x,n); % DFT
f = (0:n-1)*(fs/n); % Frequency range
p = y.*conj(y)/n; % Power of the DFT

% only taking the first half of the FFT output (because it mirrors itself) + 1 because there is an
additional 'zero' frequency bin
half_length = n/2+1;
frequency_bins = f(1:half_length);

% calculate the final power spectra as the proportional power
total_power = sum(p(1:half_length));
raw_power_spectra = p(1:half_length);
ppower_spectra = (raw_power_spectra./total_power)*100;
return