AN EXAMINATION OF TWO CONTROL PROCESSES THAT OPERATE ONLINE DURING TARGET DIRECTED REACHING

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ABSTRACT

Examination of goal-directed aiming tasks has revealed that rapid, discrete human action is amendable to online control. This control affords humans a margin of error in movement planning and execution as well as a means of acquiring their goals when the body and/or the environment are extrinsically perturbed. For over a century, the models of online movement control that have best described the trajectories and outcomes of goal-directed reaches hold that these movements are composed of two distinct components. The first component moves the limb from its resting position towards the target. The second component is a corrective movement that is formed on the basis of a visual referencing of the moving limb and target positions. As such, the temporal and spatial characteristics of these discrete movement changes have been attributed to the limits of visual information processing. Furthermore, the absence of any discrete movement changes in the portions of movements outside of the temporal and spatial limits of vision led many investigators to conclude that first component impulses are ballistic and uncontrollable. However, recent studies involving environmental perturbation and within-subject trial-to-trial spatial variability analyses have evidenced that initial impulses are privy to online control. Because the corrections made early in movement impulses occur quicker than purely afferent visual information can be processed this form of control has been attributed to the use of forward anticipatory processes. The four studies presented here examine the nature of initial impulse control through kinematic analyses of reaches made to targets against various combinations of limb, target, and environment perturbations. This was done in order to evaluate anticipatory control's relationship with visually-regulated control and the relative influence the two processes have on the movement trajectory and performance outcome.

The first study examined target-directed reaches made against illusory moving background and target relocation perturbations. The results showed the presence of early anticipatory and late visually-regulated control. Non-interactive main effects of the two perturbations on outcome accuracy revealed that the processes operate independently.

The second study tested the applicability of an air discharging stylus as a tool for perturbing reach velocities. The results showed that the stylus effectively perturbed limb velocity and highlighted the presence of a limb forwarding response to either an advancing or hindering perturbation. The findings evidence the non-specific nature of anticipatory control responses.

The third study examined reaches made against combinations of actual limb velocity and target position perturbations. The interactive effect of the two perturbations on reach trajectories and outcome accuracy indicated that the perturbations were salient enough to prompt parallel operation of the two control processes. Again, the control of initial movement portions was highlighted by non-specific responses to the perturbations.

The fourth study examined reaches made against combinations of illusory and actual perturbations to both the anticipatory and visually-regulated control processes. Interestingly, performers withheld responses to the illusory perturbation unless they were also responding to an actual perturbation. This finding suggests that anticipatory control responses are biased during movement preparation. Furthermore, combined illusory and actual perturbations to target position had interactive effects on visually regulated control.

Overall, the studies evidence that target-directed movements are mediated by two modes of control. There is an anticipatory mode of control that operates continuously and, given that reaches are made within the spatial and temporal limits of visual processing, there is also a feedback driven discrete mode of control that overlaps with the continuous mode.

PREFACE

This thesis is comprised of four (4) manuscripts that have been, or are formatted to be, submitted for publication in refereed journals. These manuscripts are presented in the format requested by the journals to which they are being submitted except the figures and figure captions have been inserted directly in the text. All of the work presented here is original work. All data were collected between September 2005 and December 2007 in the Motor Control and Learning laboratories in the Department of Kinesiology at McMaster University. All experiments were designed and implemented by Lawrence Grierson with assistance from Dr. Digby Elliott and the supervisory committee of Dr. Tim Lee and Dr. James Lyons. All data were collected and analysed by Lawrence Grierson with the exception of the EMG data presented as a supplement to the second manuscript. These data were collected and analysed with the assistance of Claudia Gonzalez. All manuscripts were written exclusively by Lawrence Grierson under the guidance of Dr. Digby Elliott, with the exception of Claudia Gonzalez' contributions to the EMG methodology section of the second manuscript.

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Chapter 1

INTRODUCTION

The study of goal-directed movement began over a century ago with the publication of Robert S. Woodworth's (1899) "The accuracy of voluntary movement". This work laid an important foundation for modern accounts of speed-accuracy trade-offs, the relative contributions of central planning and online correction to movement success, and the processes that mediate manual performance asymmetries. But Woodworth's most influential contribution to movement control science was the two–component model of goal-directed aiming.

The Early Two-Component Model

In order to examine goal-directed action, Woodworth had performers draw speeded, pencil lines to targets that were a fixed width apart. The paper on which individuals performed these movements was fastened to a drum that rotated at a constant speed. In addition to allowing the examination of aiming accuracy, the use of pencil line drawings provided Woodworth a method for evaluating the spatiotemporal characteristics of movements. The lines drawn revealed that the initial portions of the movements were relatively rapid and stereotyped, and the portions of the movement nearer the target line were slower and marked with the presence of interruptions and greater variability. Woodworth controlled performers' movement times by having them act to the beat of a metronome and found that endpoint accuracy decreased as the speed of the movements increased. Interestingly, at short movement times, aims made with the aid of vision were performed no more accurately than those made without vision. Woodworth's interpretation of this finding was that vision regulates the control of goal-directed movement, but its use is constrained by an inherent processing time; that is, the time for the eye to recognize, the neural structures to transform, and the motor system to use the information. Woodworth interpreted his findings as evidence that the visuomotor processing time was approximately 450 milliseconds. However, his estimate was magnified by his methodology. Specifically, Woodworth's performers made back-and-forth movements with the goal of having the pencil reversal occur at the target. Notably, the return portion of these movements was made to a physical stop. As such, the aiming portion of the movements only comprised approximately half of the metronome cycle and led Woodworth to report a visuomotor processing time that was almost double what the data indicated (Carlton, 1992). Despite his miscalculation, the notion of a requisite visuomotor processing time served as the basis for the first two-component model of goal-directed aiming.

Woodworth's (1899) two-component model held that aiming movements to targets are composed of two distinct phases. The first component, the initial adjustment, was considered a ballistic movement responsible for the gross transport of the limb from its starting position to the vicinity of the to-be-attained target. Given the requisite time, the second component, or current control, used the available visual information to evaluate the relative locations of the limb and the target and initiate a second adjustment to reduce the remaining distance.

While Woodworth's two-component account of goal-directed aiming continued to be influential, his estimate of the visuomotor processing time was eventually challenged. Keele and Posner (1968) recognized that because Woodworth (1899) had experimented with a back-and-forth aiming task his calculation included both the time to travel between the start position and the target, as well as the time to reverse the pencil. As such, they experimented using a discrete aiming procedure. Performers practiced target-aiming movements of four specific durations: 190 ms, 260 ms, 350 ms, and 450 ms. Following practice, individuals performed these aims under conditions in which they retained the use of vision or vision was removed on movement initiation. The results showed that performers were able to acquire the target more effectively under the full vision condition for all movement times except 190 ms. Importantly, Keele and Posner's (190 ms-260 ms) estimate of visuomotor processing time gleaned from a discrete aiming task was roughly half that garnered from Woodworth's (1899) back-and-forth method.

The use of two-dimensional pencil lines allowed Woodworth to not only examine the accuracy outcomes of aims but also their trajectory characteristics. However, since the time of Woodworth (1899), advances in technology have provided motor control researchers with increasingly sophisticated ways of analysing movement. Nowadays, three-dimensional digital recording systems provide scientists the ability to finely and precisely track and measure the displacements of rapid goal-directed aims without having to engage in the time-consuming practice of manually digitizing reaches frame-by-frame through analog video footage. With tools like the Optotrak digital recording system (Northern Digital Inc., Waterloo, Ontario) displacement trajectories can be quickly generated, differentiated, and double-differentiated, for in-depth evaluation of their velocity and acceleration characteristics. Such systems have been instrumental in uncovering the presence of late-trajectory accelerations and extended deceleration phases, which provide evidence of the visually regulated movement amendments associated with classic two-component models of control. Furthermore, the examination of acceleration-deceleration profile symmetry has been used as an indicator of the central planning strategies that performers use when moving in environments of differing afferent feedback.

The Iterative Correction Model

Keele's (1968) iterative correction model explained the control of goal-directed aiming as the result of the cumulative operation of sequential motor programs. Motor programs are prearranged sequences of muscle commands that are executed without the influence of peripheral feedback (Keele, 1968). Keele proposed that the initial portion of a movement was the result of a motor program organized on the basis of the relative effector and target positions. Similar to Woodworth's initial adjustment component this program would persist unaltered. After approximately 200 ms, the performer would have had the time to process visual feedback regarding the moving limb and structure a second motor program designed to reduce the error of the first. For longer movements, a third corrective motor program would be executed, and so on. Assuming that more submovements related to greater accuracy, the iterative correction model predicted that slow movements would be performed with more success than fast movements. Though this model adequately coincided with mathematical accounts of speed-accuracy relationships (e.g., Fitts, 1954; Fitts & Peterson, 1964) subsequent studies employing high-speed film (Langolf, Chaffin, & Foulke, 1976) and sophisticated opto-electric technology (Elliott, Binstead & Heath, 1999) revealed that corrective submovements are not made at any regular temporal interval, but rather are locused in the latter portions of movements when the effector is near the target (Beggs & Howarth, 1970). As such, researchers reverted to single-correction (Beggs & Howarth, 1970; Woodworth, 1899) or open-loop (Schmidt, Zelaznik, Hawkins, Frank, & Quinn, 1979) models to describe goal-directed action.

The Impulse Variability Model

Schmidt and colleagues' (1979) impulse variability explanation of speed-accuracy relationships in goal-directed aiming differed from previous models in that it ignored the role of visual feedback to movement accuracy and outcome variability. Rather, this model was grounded in the positive linear relationship that exists between the magnitude of the force required to move the limb and the variability associated with this force generation. That is, a greater required force results in greater force variability. Schmidt predicted that, in the absence of feedback processing, longer and/or faster movements would be associated with proportionally greater variability in the motor program, and hence, the movement endpoint. This model effectively explained the relationship between movement time and variable error for very rapid movements (< 200 ms) (Schmidt et al., 1979) and for those made without vision (Wallace & Newell, 1983); however, its inability to explain longer visually-guided movements highlighted its disregard for the importance of visual and other sources of feedback in goal-directed aiming (Beggs & Howarth, 1970; Keele, 1968; Woodworth, 1899).

The Stochastic Optimized Submovement Model

The stochastic optimized submovement model (Meyer, Abrams, Kornblum, Wright, & Smith, 1988) amalgamated the ideas of the impulse variability model with the processing of online visual feedback inherent to two-component models. The stochastic optimized submovement model explained that the force of any aim directed towards the centre of a target would determine its endpoint variability. As such, movements of equal distance and duration will have endpoints that are normally distributed around the centre of the target. When the endpoint of a particular movement falls near one of the tails of the distribution it will be outside the target boundaries (e.g., an undershoot or overshoot) and a second submovement will be required. This corrective submovement will be structured on the basis of the available feedback. There will also be variability associated with this second movement and, as such, on some occasions an additional submovement will be required to hit the target. The stochastic optimized submovement model posits that performers attempt to strike an ideal compromise between the variations associated with making initial high-velocity submovements and the time associated with making corrective submovements late in the reach trajectory. By acknowledging the role of visual and proprioceptive feedback in movement regulation, this model succeeded in predicting both movement time and the spatial-temporal structure of both long and short duration movements. However, evidence has since indicated that initial movement endpoints are distributed short of targets (Elliott, Hansen, Mendoza & Tremblay, 2004; Lyons, Hansen, Hurding & Elliott, 2006), rather than around their centre.

Speed, Accuracy, and Energy Expenditure Optimization Models

Lyons et al. (2006) analyzed reaches made to targets that were positioned away from or towards the performer, and above or below the starting location. In all cases the initial movements undershot the target. However, the undershooting was greatest to targets located below the starting position. It has been reasoned that it is the differing costs of errors that drive performers to prepare initial movements that will initially undershoot a target (Elliott et al., 2004; Lyons et al., 2006). Because an initial movement that overshoots a target travels further and needs to overcome its inertia to reverse, performers favour target undershoots, to which necessary corrections may be incorporated with less cost to time and energy. As such, reaches to targets below the start positions were characterized by greater undershoots. Presumably this is because overshoots to these targets would require more costly amendments against gravity. In this way, the initial portions of goal-directed aiming movements seem to be organized such that the likelihood of the worse case outcome is minimized.

Performers' biases to adopting movement strategies that guard against worse case outcomes are also evident when they are uncertain of the feedback that will be available to them during a movement. When performers are aware that they will receive vision, reach trajectories will be characterized by asymmetrical velocity profiles, which indicate that more time is spent decelerating the limb towards the target. Presumably, performers quickly move the limb to the target vicinity and use the additional time evaluating the visual information to ensure accuracy. Conversely, when the performer is aware that vision will not be available during the reach, their increased reaction times indicate that they spend more time in movement preparation (Hansen, Glazebrook, Anson, Weeks & Elliott, 2006). As well, their aiming trajectories are reasonably symmetric even if vision becomes unexpectedly available.

The Initial Adjustment

Proteau and Masson (1997) performed an experiment that questioned the longstanding belief that the initial component of movements is ballistic and uninfluenced by the processing of online visual feedback. In their experiment performers moved a cursor across a computer screen to a target. Upon movement initiation, the background elements over which the cursor moved either remain stationary or shifted in the opposite direction. Interestingly, this procedure revealed that initial movement endpoints were completed significantly earlier when the background shifted. In a similar experiment, the background either remained stationary or shifted in the same direction as the movement. In this scenario, Proteau and Masson (1997) showed the initial movements performed over the moving background terminated after significantly greater amplitude displacement. The findings of both experiments were consistent with the interpretation that the moving backgrounds created illusory perceptions of limb velocity that influenced the progress of early aiming trajectories. Specifically, when the background shifted opposite the direction of the movement, limb velocity was overestimated and prompted an early limb deceleration. Conversely, when the background shifted in the same direction as the cursor movement, the limb was perceived as moving slower and, as such, limb deceleration began later. Importantly, Proteau and Masson (1997) showed that the early portions of goal-directed aims were not entirely ballistic. Seemingly, these trajectory portions could be influenced by concurrent information about limb velocity.

Furthermore, advances in digital recording and kinematic analysis have given rise to the method of within subject trial-to-trial spatial variability analysis. The underlying assumption in the analysis of movement spatial variability is that if the limb moves independently of online control, any error in the executed movement should grow until the limb comes under the supervision of late-trajectory, visually regulated processes. In this way, spatial variability of ballistic movements is expected to increase as the movement progresses. However, analyses of the within subject, trial-to-trial spatial variability of goal-directed reaches made under various conditions of practice and feedback (Khan & Franks, 2003; Khan et al., 2006; Hansen, Tremblay & Elliott, 2007; Hansen, Elliott & Tremblay, 2007) has shown that trial-to-trial spatial variability often does not increase, and in some cases decreases, during early portions of the trajectory. Importantly, such studies have been powerful in further disproving the notion that the initial components of goal-directed movements are ballistic.

Two Processes of Online Control

In addition to the well-documented process of discrete, feedback driven control that contributes to limb regulation late in the movement, the aforementioned evidence also suggests that there is a continuous form of control that makes amendments throughout the movement. The kinematic continuity of early reach trajectories suggests that these amendments result from graded changes in muscle force (Elliott et al., 1999). Because this form of control operates quicker than the minimum visuomotor processing time dictates, its alterations may be ascribed to an internal, forward modeling process. The forward modeled control perspective (Desmurget & Grafton, 2000; Wolpert & Davidson, 2005; see also von Holst, 1954) holds that when an individual executes a motor command, a copy of that command is simultaneously amalgamated with information concerning the performer's current state. This amalgamation serves to generate an internal representation of the predicted afferent information. As such, performers are provided with a method of rapidly evaluating whether movements are executed as intended. Presumably an ameliorative response is initiated when a mismatch between the expected and incoming afference is realized. However, forward modeled control does not fully explain how early movement corrections are formed appropriately. Current accounts of forward modeled control hold that the error detected between predicted and actual afference is fed through an inverse model, which mediates corrections on the ases of the performer's expected next state and the desired outcome (Desmurget & Grafton, 20). However, this process would require the time associated with visual information processin order to calculate the error. This requisite time renders inverse models an ineffective mediat f initial movement components.

Although there is a profusion of evide ighlighting the influence of afferent visual
ıformation on goal-directed aiming moveme clear that any conceptualization that
scribes movement outcomes and trajectorie ly an interaction between central planning
ocesses and temporally-constrained feedbac is overly simplified. This dissertation
scribes a series of kinematic analysis studies goal-directed aims are subjected to
nbinations of visual and physical perturbatio either quicker than or long enough for
ual feedback processing. This was done in or und a more accurate account of the

control of goal-directed reaching movement. Specifically, the possibility that these movements are controlled by two online processes is challenged.

Notably, in addition to the visual inputs performers receive, some of the perturbations used in this thesis impact proprioceptive afference. Although, the unique role of visual feedback processing in late-trajectory discrete control is well established (Elliott et al., 2001), the influence of proprioceptive feedback processing on early movement portions (Brown & Cooke, 1981; Larish, Volp, & Wallace, 1984; Sarlegna & Sainberg, 2007) should not be overlooked. Proprioception is integral in providing information regarding effector initial location (Ghez, Gordon, & Ghiraldi, 1995), and final position as well as, using these estimates to select desired motor commands (Scheidt, Conditt, Secco & Mussa-Ivaldi, 2005). It also represents a substantial portion of the information regarding performer state whose integration with efference copies is paramount to predictive forward modelled control. Though the present research focuses on the processing of visuomotor control, the operation of proprioceptive processes in response to physically applied movement perturbations can not be denied.

It is expected that perturbations that occur in sufficient time for information processing will elicit the discrete, late movement corrections that have been documented for over a century (Elliott et al., 2001; Mendoza, Elliott, Meegan, Lyons & Welsh, 2006; Mendoza, Hansen, Glazebrook, Keetch & Elliott, 2005; Woodworth, 1899). However, it is expected that perturbations that occur earlier than full information processing is possible will elicit the type of graded kinematic and spatial variability modifications that have been more recently noted (Desmurget & Grafton, 2000; Hansen et al., 2007; Proteau & Masson, 1997). Through a combination of late and early perturbations, the studies investigate whether the modifications represent a single process or two independent processes. That is, if the combined perturbations do not have an interactive influence on reach trajectory and accuracy than it may be concluded that they affect two distinct modes of control (Sternberg, 1969).

The studies begin by investigating the impact of combined illusory visual perturbations on aiming performance and progress on to evaluating the influence of more salient physical and veridical movement perturbations. Overall, the data are interpreted from a perspective that contends that goal-directed movements are pre-programmed (Keele, 1968) and are guarded against imprecision through an integration of continuous forward modeled control (Desmurget & Grafton, 2000) and temporally-constrained feedback control processes (Elliott et al., 2001).

The first study, "Goal directed aiming and the relative contribution of two online control processes", examined the kinematic profiles of movements made against combinations of illusory perturbations. The study's first experiment followed from Mendoza and colleagues (2005, 2006) and examined reaches made to targets that reconfigured to Müller-Lyer structures. The Müller-Lyer illusion creates a misperception of the target location relative to the hand and operated to affect the discrete, late trajectory control. In the study's second experiment, a moving background procedure, similar to that of Proteau and Masson (1997), was used to perturb the early limb control. The third experiment analyzed the relative impacts of these two perturbations when they were presented in tandem.

The second study, "Kinematic analysis of the early online control of goal-directed reaches: A novel movement perturbation study", examined the ability of a handheld compressed air stylus that discharged advancing and hindering blasts of air to perturb the early velocities of goal-directed reaches. This was done because the illusory misperceptions created by moving backgrounds must be somewhat offset by the processing of veridical proprioceptive information. By analyzing reaches made against the air perturbations under full and no vision conditions, the study also examined the necessity of visual information regarding the limb velocity for early online control.

The third study, "Kinematic analysis of goal-directed aims made against early and late perturbations: An investigation of the relative influence of two online control processes", replicated the procedures of the first study but replaced illusory velocity and target perturbations with actual perturbations. This was done in order to expand the investigation of the independence of the two online control processes. The study's first experiment perturbed early reaches to the aforementioned compressed air blast. The second experiment perturbed discrete late trajectory control by moving the target either closer to or further away from the performer upon movement initiation. The third experiment combined these two perturbations.

The fourth study, "A kinematic investigation of the structure of early trajectory ameliorations to goal-directed movements following early and late perturbations", investigated the early trajectory modifications that occur when performers act against two perturbations designed to impact the same online control process. The study's first experiment analyzed the kinematics of reaches made against the moving background illusion and the compressed air perturbation. It was hypothesized that if a priori knowledge of the possible perturbations affects the nature of the non-specific responses generated, then a single response would be prepared to deal with both perturbations. Or, if a priori knowledge does not influence the early and non-specific control, the resulting trajectory would represent the additive impacts of the responses to the two perturbations. The study's second experiment examined movements made to targets that undergo Müller-Lyer transformations and spatial relocations.

The overall goal of the four studies presented was to further the investigation of the nature of the early and continuous process of online regulation. Also, the studies sought to evaluate the relative contributions of this early control process and discrete late-trajectory control. The experiments are designed to pay particular attention to the differences in control manifested when movements are made against illusory and actual perturbations to the limb, target, and movement environment. This was done with the specific goal of determining the degree to which the operation of forward internal models could explain movement trajectories and outcomes.

Chapter 2

GOAL DIRECTED AIMING AND THE RELATIVE CONTRIBUTION OF TWO ONLINE CONTROL PROCESSES

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Running head: AIMING AND TWO ONLINE CONTROL PROCESSES

Goal Directed Aiming and the Relative Contribution of Two Online Control Processes

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Abstract

Kinematic investigations of rapid goal directed aiming suggest that the online control of movement occurs via two processes. One process involves a comparison of the visual information about the relative locations of the hand and target late in the trajectory. A second process has been proposed in which a movement's initial impulse is subject to online control. The Müller-Lyer illusion creates a bias in the perceived location of the target relative to the hand and impacts late adjustments to the movement trajectory. Displacing the background over which movements are performed, either in or opposite to the direction of the movement creates a mismatch between perceived and expected limb velocity thus affecting early online control. To investigate the relative influence of these two types of online control, kinematic analysis of participants' rapid goal directed movements was conducted. Upon movement initiation, the environment in which participants acted was manipulated such that they were exposed to a factorial combination of these perturbations. Results of the Müller-Lyer-only and moving background-only conditions replicated the previous evidence of late trajectory and early control adjustments, respectively. More interestingly, end movement accuracy measures yielded non-interactive main effects of the two perturbations suggesting the two forms of control operate independently.

Introduction

Over a century ago, Woodworth (1899) conducted a series of experiments in which subjects were required to make accurate movements under temporal constraints. He found aiming accuracy decreased as the speed of the movement increased. Interestingly, it was noted that at a particular speed the accuracy of movements made with vision was no different than movements made in the absence of vision. Woodworth posited that visual information is used in the control of rapid aiming movements but its use is constrained by an inherent visual processing time; that is the time to recognize, transform, and use the information to correct movement error. Speeded movements that terminate quicker than this visual processing time are uninfluenced by the availability of vision. From this empirical evidence, Woodworth forwarded the two-component model of limb control. This model held that goal-directed aiming movements consist of an initial impulse phase and, if time permits, a current control phase. The initial impulse phase was considered a ballistic, stereotyped movement responsible for moving the limb to the vicinity of the to-be-attained target while the control portion of the movement was mediated by the availability of visual feedback information and represented a "homing in" period in which the limb was brought to rest on the target.

Although several models rely on open-loop, feedforward processes to explain the speed-accuracy relationships (Plamondon, 1995; Schmidt, Zelaznik, Hawkins, Frank, & Quinn, 1979), two component models such as Woodworth's have generally been more successful in explaining not only movement outcomes (Beggs & Howarth, 1970; Fitts, 1954), but also the spatial and temporal characteristics of movement trajectories (Carlton, 1979; Meyer, Abrams, Kornblum, Wright, & Smith, 1988; see Elliott, Helsen, & Chua, 2001, for a review). Current versions of the two component model (e.g., Elliott, Hansen, Mendoza, & Tremblay, 2004; Meyer et al., 1988) hold that, as the distance to be traveled or the required speed of a movement increases, the impulses necessary to produce the movement also increase (Schmidt et al., 1979). With this increase, greater noise in the neuromuscular system is generated (i.e., force variability), such that the end-point variability of the initial ballistic portion of the movement increases. Response produced visual feedback from the limb is then utilized during the final portion of the trajectory to correct any errors associated with the errors generated during the execution of the original motor plan. Thus when the accuracy demands of the movement are high, movement trajectories are often characterized by either an extended deceleration phase or discrete discontinuities in the acceleration-deceleration profile late in the movement. These late departures from acceleration-deceleration symmetry are thought to represent online adjustments designed to bring the limb onto the target. Presumably these corrections are based on visual feedback about the position of the limb relative to the target (Elliott et al., 2001).

Although this discrete, feedback-based control makes an important contribution to limb regulation, over the last 15 years it has become increasingly apparent that on-line control may begin to operate very early in goal-directed aiming movements (Elliott, Binsted, & Heath, 1999; Elliott, Carson, Goodman, & Chua, 1991; Proteau & Masson, 1997). The examination of trial-to-trial spatial variability and central tendency at specific kinematic markers under various feedback (Hansen, Elliott, & Tremblay, 2007; Khan, Chua, Elliott, Coull, & Lyons 2002; Khan, Franks, Elliott, Lawrence, Chua, Bernier, Hansen, & Weeks, 2006) and practice (Hansen, Tremblay, & Elliott, 2005) conditions indicates that skilled performers can make very early modifications to their movement trajectories based on dynamic information about the limb's direction (Hansen et al., 2007) and velocity (Proteau & Masson, 1997). Evidence for this type of early control suggests that the initial phase of the movement may not be as ballistic as was originally thought (e.g., Beggs & Howarth, 1972: Woodworth, 1899).

The experiments presented here set out to determine the extent to which these two modes of on-line control interact, or perhaps co-vary, to influence movement accuracy. This was accomplished through three experiments which introduced perturbations designed to influence the perceived position of the target and the perceived velocity of the limb while measuring performance and trajectory outcomes. Experiment 1 was designed to affect the late type of discrete control associated with Woodworth's two-component model of limb control (i.e., error reduction based on a comparison between limb and target position). Following Mendoza and colleagues (Mendoza, Elliott, Meegan, Lyons, & Welsh 2006; Mendoza, Hansen, Glazebrook, Keetch, & Elliott, 2005), participants made rapid aiming movements away from the body to a small target defined by the intersection of three lines. Upon movement initiation, the target was changed to either a Müller-Lyer tails-in configuration, a Müller-Lyer tails-out configuration, or remained unperturbed. A tails-in configuration introduced at movement initiation has been shown to result in greater target undershooting compared to the control condition, while the tails-out configuration has the opposite effect. According to the hypothesized model of on-line control, this type of perturbation is expected to affect the perceived position of the target relative to the limb and thus result in a discrete adjustment to the movement late in the trajectory. Conversely, Experiment 2 was designed to create a mismatch between the expected and perceived dynamics of early limb movement. Specifically, this experiment employed the moving background perturbation of Proteau and Masson (1997); that is, the texture elements over which participants performed goal directed reaches were perturbed either in the direction of, or the direction opposite to, that of the movement. This perturbation is hypothesized to create a mismatch between the expected and perceived sensory consequences of the movement. Kinematic evidence from Proteau and Masson's (1997) work showed that when the background moves in the direction opposite to the movement the actor consistently terminates the initial phase of their movement earlier than normal, an adjustment consistent with an overestimation of initial limb velocity. Likewise, though to a lesser extent, the actor over extends the initial portion of their trajectory when the background moves in the same direction as the limb. While Proteau and Masson's study used two-dimensional computer displayed cursor movements controlled by a pressure lever and evaluated the spatial position of the initial phases of movements, Experiment 2 examined the overall outcome of natural reaches made in three-dimensional space. Through a combination of the perturbations presented in Experiments 1 and 2, Experiment 3 examined the relative influence of the two proposed forms of online visual control on accuracy and trajectory outcomes. This was done in order to determine if the impacts of these manipulations are independent or interact with each other (e.g., Sternberg, 1969).

General Apparatus and Dependent Measures

Throughout the course of the experiments, participants sat at a table on which rested a flat display screen. The resting home position from which participants initiated the pointing movements was a micro-switch mounted beside this display screen. The home position and the screen were at the participant's midline and all aiming movements were away from the body. Both the micro-switch and the display screen were connected to a computer that controlled the visual perturbations as well as data acquisition. At the beginning of each trial, the target that the participants moved to was presented on the display screen. In all experimental sessions this target was represented by an intersection of three yellow lines; a long (35cm) shaft line, which began at the location where the home position lay flush with the display screen, and two smaller (7 cm) tail lines. The tail lines contacted, at right angles, the end of the shaft line such that the initial target was configured as a "**T**". Participants prepared an accurate-as-possible movement to this target position and following a short (1000 ms) delay were cued to execute this movement by an auditory tone. This auditory go-signal was an 800 Hz *beep* emitted from two speakers also connected to the computer. Upon the initiation of the movement (i.e., the participant released the micro-switch) the initial target array could be perturbed as indicated by the procedures outlined in the individual experimental methods sections. Participants were notified that the target display may change and were instructed to complete their movement as accurately-as-possible, regardless of any perturbation.

Throughout the experimental session participants wore an infrared light emitting diode (IRED) on their right index finger. For each trial, the auditory tone triggered an Optotrak-3020 digital recording system that recorded the spatial position of the IRED for 2 seconds at 500 Hz.

Participants also wore liquid crystal goggles. These goggles served to occlude the participants' vision 500 ms after movement initiation. Participants were notified of this imminent occlusion and were instructed to complete their target directed movements while they still had vision. This manipulation ensured that participants made rapid movements so that any end position differences could not be attributed to speed-accuracy trade-offs (see Mendoza et al., 2006). Upon completing the movement, participants kept their pointing finger on their acquired target until the display screen cleared and the goggles returned vision. They then replaced their finger on the home position and prepared for the next trial. The computer also controlled the goggles. E-prime software monitored the position of the home switch as well as randomized the presentation order of the target configurations.

The spatial position data collected by the Optotrak-3020 system were filtered with an 8 Hz dual-pass Butterworth filter and run through custom software which calculated the displacement of the limb in the primary direction of movement (Hansen, Elliott, & Khan, in press). In addition to differentiating and double differentiating the displacement to acquire velocity and acceleration, this software also discerned the magnitude of the peak acceleration (PA), peak velocity (PV), and peak deceleration (PD) for each reaching movement as well as the spatial location of these kinematic events and the end position (END) of the movement. The Optotrak frames in which the limb velocity rose above or fell below 30mm/s, and remained as such for 70 msec identified the start and the end of the movement. Values for any dependent variable that fell more than 2.5 standard deviation units from the mean were considered outliers and were removed from the data sets prior to analysis.

The main performance variables for all experiments were reaction time (RT), movement time (MT) and constant error (CE). RT and MT reflect movement preparation and execution time respectively. CE is mean signed error in the primary direction of the movement and provides information about systematic undershooting (negative CE) and overshooting (positive CE) of the target. We also examined mean peak acceleration (PA), peak velocity (PV), peak deceleration (PD), as well as the time before and after peak velocity. In order to examine the impact of our perturbations as the movement unfolds, we also examined the mean amplitude of the movement at PA, PV and PD, as well as the within-participant standard deviation of this spatial position.

The underlying assumption in the analysis of variability at kinematic landmarks is that any error in the early execution of the planned movement, either due to the quality of the selection parameters or the inherent noise that exists in the neuromuscular system, will contribute to error in the motor output. Left unaltered by closed-loop control process this error should increase systematically as the movement progresses. If however variability at some point begins to decrease, the reduction in variability is taken to reflect the impact of online control (Khan & Franks, 2003; Khan et al., 2006).

Experiment 1

Method

Participants. The participants were 14 (7 male; 7 female) right-handed members of the McMaster University community. They had normal or corrected-to-normal vision and were naïve to the purpose of the study. Prior to participating, all individuals gave informed consent according to the guidelines of the McMaster University Office of Research Ethics.

Procedure. Participants performed a series of 120 trials in which they were instructed to make rapid, accurate pointing movements from a resting home position to a resting target position. Upon movement initiation the initial "T" target configuration (Figure 1A) was either perturbed to a Müller-Lyer tails-in configuration (Figure 1B), a Müller-Lyer tails-out configuration (Figure 1C), or remained unperturbed. The order of the perturbations was randomized with equal probability of each potential configuration (40 control figures, 40 tails-in figures, and 40 tails out figures). The tails-in configuration translated the 7 cm tail lines such that they intercepted the end of the shaft line at 45°. The tails-out configuration translated the 7 cm tail lines such that they intercepted the end of the shaft line at 135°. The actual place where the three lines intersected remained 35 cm away along the midline of the participant.

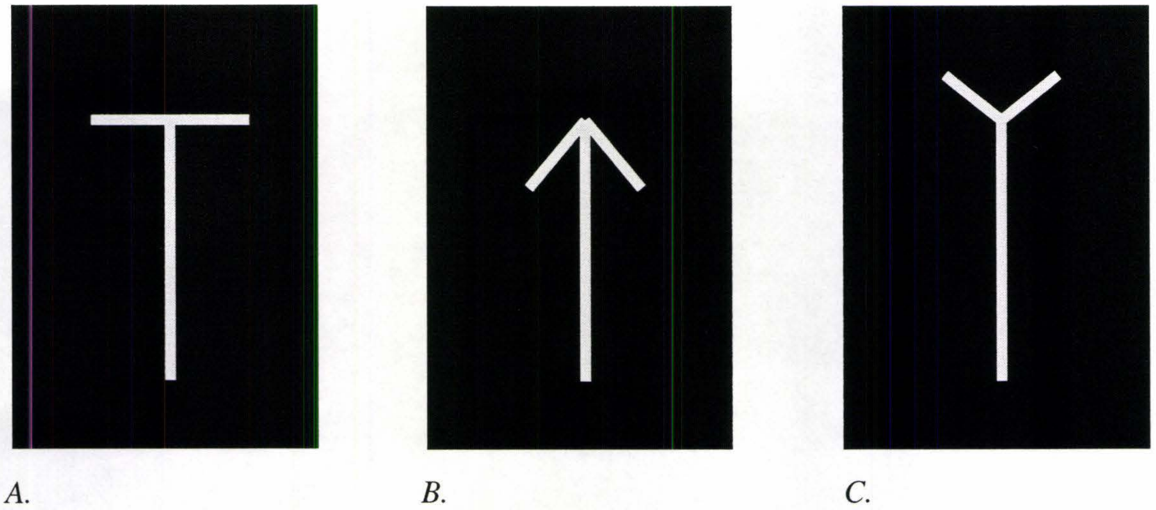


Figure 1. Depiction of Experiment One's (A) control, (B) tails in, and (C) tails out Müller-Lyer target figures.

Analysis. Each of the primary performance and kinematic variables was subjected to a one-way repeated measures analysis of variance to determine if any trajectory or accuracy differences can be attributed to processes related to the perception of the Müller-Lyer target perturbations. In order to determine how movement bias and variability changes as the movement unfolds mean movement amplitude and spatial variability were examined via a 3 condition (control, tails-in, tails-out) by 4 kinematic marker (PA, PV, PD, END) two factor repeated measures analysis of variance. The nature of any significant difference was determined via Tukey's HSD post hoc comparisons ($p < .05$).

Results and Discussion

Performance Outcomes. The results of the CE analysis revealed that end point accuracy was biased by the illusory perturbation, F (2, 26) = 14.14, MSE = 1.38, $p < .0001$. Post hoc analysis revealed greater undershooting for the tails-in and control configurations than the tails-out configuration. The difference between the tails-in configuration and the control configuration did not reach significance ($p = .07$). These findings are a replication of Elliott and Lee's (1995) and Mendoza and colleagues' (2006) investigations of the Müller-Lyer illusion and its effect on the visual control of goal directed movement (Figure 2). No significant reaction time (grand mean = 286 ms) or movement time (grand mean = 411 ms) differences were seen between any of the conditions.

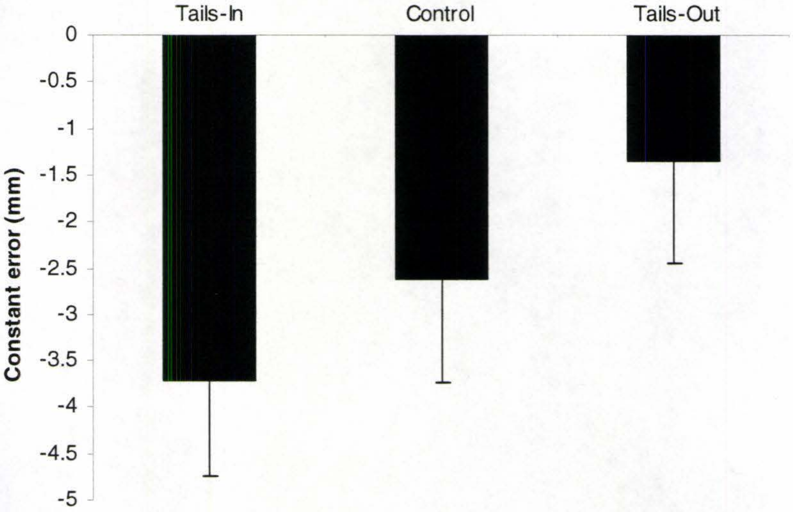


Figure 2. Constant Error (mm) plotted as a function of the Müller-Lyer condition (Experiment 1).

Magnitude of the Kinematic Events. Significant differences between the magnitudes of kinematic measures were elicited between conditions. Participants reached higher PA in the control condition relative to the tails-out configuration condition, $F(2, 26) = 4.11$, $MSE = 0.0001$, $p < .05$ (tails-in = 10.6 m/s^2; control = 11.2 m/s^2; tails-out = 10.1 m/s^2). Similar differences were seen for the measures of PV, $F(2, 26) = 9.33$, $MSE = 0.05$, $p < .001$ (tails-in = 3.49 m/s; control = 3.69 m/s; tails-out = 3.35 m/s), and PD, $F(2, 26) = 10.26$, $MSE = 0.0001$, $p < .001$ (tails-in = -6.2 m/s^2; control = -7.8 m/s^2; tails-out = -5.9 m/s^2). Although the acceleration, velocity and deceleration values obtained in the tails-in condition was less than the control condition and greater than the tails-out condition these differences were not significant. Though the manipulated perturbation is designed to affect the processing of spatial position at the end of the movement, it seems that participants notice a change in the visual context much earlier in the movement (i.e., PA), but the impact of that change is non-specific. There were no differences between the conditions in time to PV.

Mean Displacement. A significant main effect was seen for the displacement of the kinematic landmarks, F (3, 39) = 1374.8, MSE = 675.56, $p < .01$. The amplitude displacement at PA (19.4 mm) was significantly less than the amplitude displacement at PV (152.6 mm), which was less than that at PD (300.0 mm), which was less than that of the end position (346.8 mm) of the movement. This is a typical effect indicative of a movement that progresses smoothly from the home position to the location of the target with no reversals of direction. As no differences were manifested between conditions, it may be assumed that the differences manifested in CE arose late in the trajectory. This is consistent with the idea that a perturbation of the perceived position of the target will impact the final corrective stage of the movement.

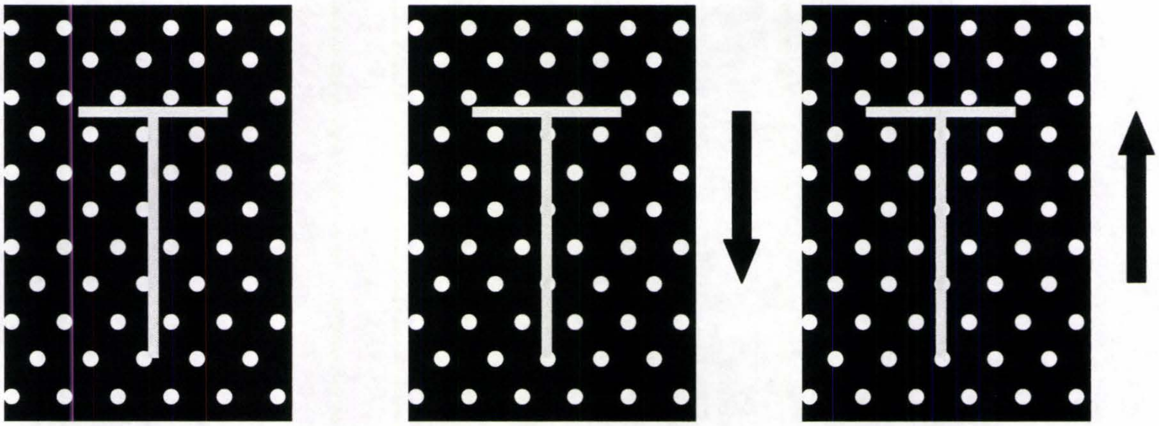
Spatial Variability. Analysis of the spatial variability at each kinematic landmark also produced a significant main effect, F (3, 39) = 10.28, MSE = 375.17, $p < .001$, with the variability increasing significantly from PA to PD before dropping to its lowest level at the end position of the movement (PA = 8.55 mm; PV = 16.43 mm: PD = 27.5 mm; END = 6.27 mm). This finding indicates that the participants exercised online control when the limb had reached the vicinity of the target.

Experiment 2

Method

Participants. The participants were the same 14 (7 male; 7 female) right-handed members of the McMaster University community tested in Experiment 1. Participants performed Experiment 1 and Experiment 2 in a counterbalanced fashion. They had normal or corrected-to-normal vision and were naïve to the purpose of the study. Prior to participating, all individuals gave informed consent according to the guidelines of the McMaster University Office of Research Ethics.

Procedure. Participants performed a series of 120 trials in which they were instructed to make rapid, accurate pointing movements from a home position to a stationary target position. The apparatus and recording techniques for Experiment 2 were identical to those of Experiment 1. At the beginning of each trial, the target that the participants moved to was presented on the display screen (Figure 3A). Rather than the target being displayed on a black screen it was surrounded by a background of white dots (1.5 cm diametre). These dots served as texture elements over which the movement was performed. Participants prepared an accurate-as-possible movement to this target position and, following a go signal, executed this movement. Upon the initiation of the movement the initial target remained unperturbed but the white dot background either translated down towards the participant (Figure 3B), up away from the participant (Figure 3C) or remained stationary. Participants were notified that the background display may or may not change and were instructed to complete their movement as accurately-as-possible regardless of any perturbation. The order of the perturbations was randomized with equal probability of each potential translation (40 stationary backgrounds, 40 downward backgrounds, and 40 upward backgrounds).



A. *B.* *C.*

Figure 3. Depiction of Experiment Two's (A) control, (B) downward, and (C) upward moving background target figures.

Analysis. The analyses and post hoc procedures were the same as Experiment 1.

Results and Discussion

Performance Outcomes. The analysis of the temporal measures showed a significant difference between the conditions for MT, F (2, 26) = 3.86, MSE = 49.51, p < .05, with the downward moving background taking significantly longer than the stationary condition. The upward moving background was intermediate to the two but did not differ significantly from either (downward = 459.8 ms; stationary = 452.3 ms; upward = 457.1 ms). This MT effect is attributed to an evaluative response that operates as a function of the task's increased visual complexity.

Such a response is characterized by trajectories that increase the amount of available sensory feedback processing time. No RT differences were noted (grand mean = 300 ms).

The CE analysis revealed significantly greater undershoots in the downward background condition, F (2, 26) = 4.86, MSE = 2.01, $p < .05$, than in the stationary background and upward background conditions (Figure 4). Once again this is consistent with the notion that under downward conditions, participants misperceived their limb to be moving faster than it really was. Similar to Proteau and Masson (1997), participants terminated their movements earlier to compensate for this higher perceived velocity. However, in order to insure that the impact of the perturbation is appropriately localized to the early portions of the trajectory, differences in the magnitudes and/or the spatial displacements of the early kinematic markers must be elicited.

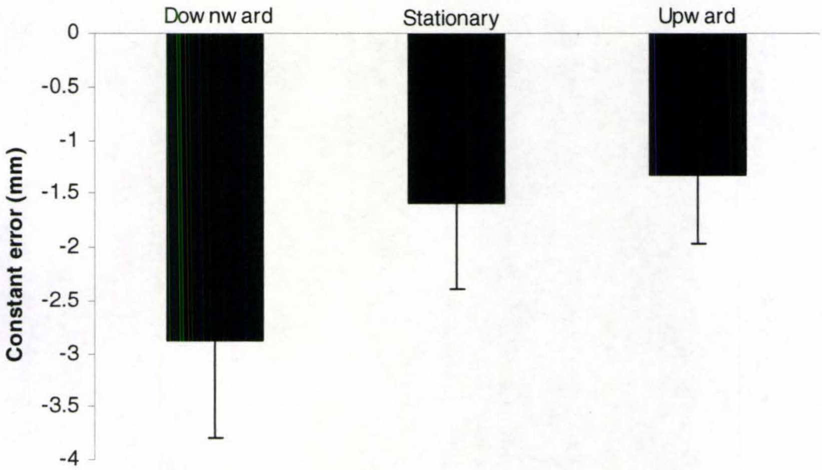


Figure 4. Constant error (mm) plotted as a function of moving background condition (Experiment 2).

Magnitude of the Kinematic Events. Differences between conditions were revealed in the magnitudes of PA, F (2, 26) = 5.48, MSE = 0.00007, $p < .05$, PV, F (2, 26) = 8.43, MSE = 0.04, $p < .05$, and PD, F (2, 26) = 4.93, MSE = 0.00007, $p < .05$. As was the case with the Müller-Lyer conditions, these differences occur early in the movement and were maintained as the movement unfolded. The PA obtained in the downward moving background condition was larger than both the measures obtained from the stationary condition and the upward moving background condition which were not significantly different from one another (downward = 10.8 m/s^2, stationary = 9.8 m/s^2, upward = 10.1 m/s^2). These differences maintained the same relative relationship at PV (downward = 3.59 m/s, stationary = 3.30 m/s, upward = 3.39 m/s) and PD (downward = -6.8 m/s^2, stationary = -5.8 m/s^2, upward = -6.1 m/s^2).

Interestingly, the downward moving background condition produced a series of results in which the participants increased the magnitude of their accelerations, velocities and decelerations. Operationally, it seems the individuals respond to the perturbation by speeding through the early trajectory. This response allows more time to be spent in deceleration where the unperturbed visual information regarding the relative hand and target positions can be better referenced. The downward background condition also elicited a significantly reduced time to PV, F (2, 26) = 5.84, MSE = 147.73, $p < .05$, compared to the other two conditions which did not differ significantly from one another (downward = 187.4 ms, stationary = 201.8 ms, upward = 199.9 ms).

Mean Displacement. Analysis revealed main effects for kinematic marker, F (3, 39) = 1280.8, MSE = 744.09, $p < .05$, and moving background, F (2, 26) = 6.32, MSE = 0.006, $p < .01$, as well as a kinematic marker by moving background interaction, F (6, 78) = 2.29, MSE = 15.85, $p < .05$ (Figure 5). Post hoc analysis of the interaction revealed that PD occurs after less distance traveled in the downward background condition than in the upward background condition and substantiates the idea that the perturbation affects early control processes. Presumably, when the background is perturbed downwards, participants perceive their limb to move faster than expected. This sensory mismatch leads to earlier deceleration of movements.

Spatial Variability. Once again this analysis revealed a main effect for kinematic marker, F (3, 39) = 31.36, MSE = 122.93, p < .01, as well as a kinematic marker by moving background interaction, F (6, 78) = 3.30, MSE = 5.90, p < .01 (Figure 6). As is evident in Figure 6, the variability for the stationary and downward background conditions increased systematically to PD before decreasing towards the end of the movement. In upward condition, spatial variability also increased from PA to PV but then leveled off, and at PD was significantly lower than the other two conditions, which did not differ. As one would expect, there was then a dramatic reduction in variability in all three conditions between PD and the end of the movement

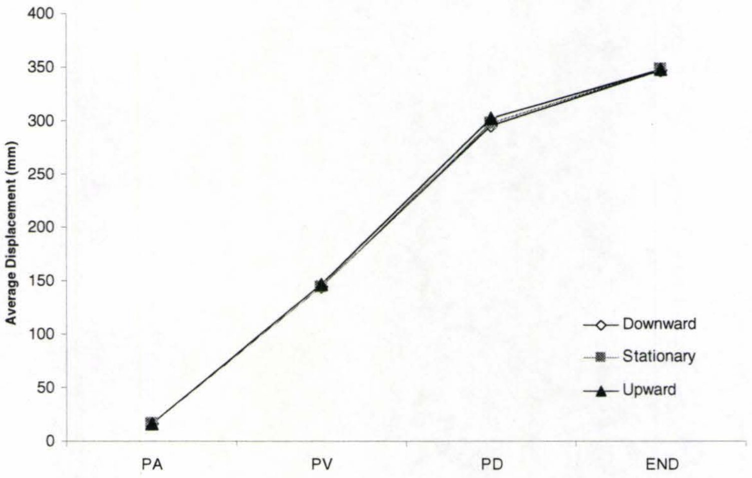


Figure 5. Mean displacement of peak acceleration (PA), peak velocity (PV), peak deceleration (PD), and the end position of the movement (END) in the primary direction of movement plotted as a function of moving background condition (Experiment 2).

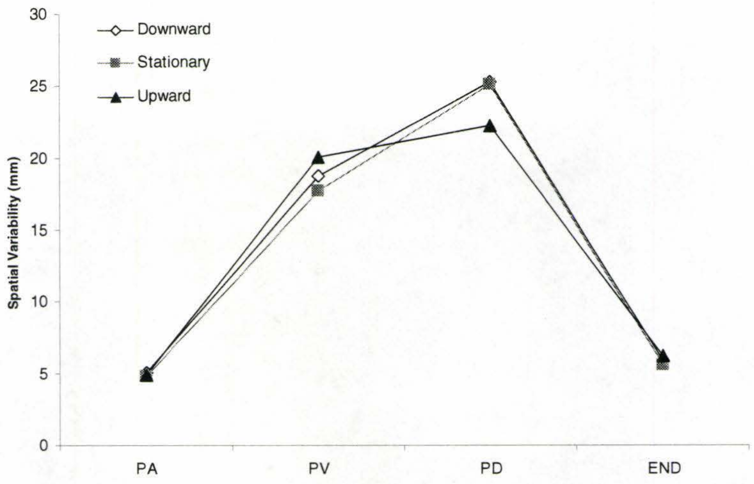


Figure 6. Mean spatial variability of peak acceleration (PA), peak velocity (PV), peak deceleration (PD), and the end position of the movement (END) in the primary direction of movement plotted as a function of moving background condition (Experiment 2).

While analysis of the mean displacement of the kinematic marker showed no impact of the upward moving background, the modulation of spatial variability in this condition indicates that this perturbation also affects early online control. Thus, it seems that the downward and upward moving background conditions both affect early control; however, the kinematics of movements made against each perturbation reflect operational differences in how the visuo-motor system is affected by the perturbations. Trajectories made against the downward moving background emphasize the early initiation of the aim's homing-in phase while those made against the upward moving background operate to ensure more consistency in the location of limb throughout. These differences may stem from an incongruity in the relative difficulty in gleaning the qualities of the two perturbations. In the downward moving background condition the relative translation of the background array occurs in the same direction as expected. This visual similarity increases the difficulty in discerning the presence of a perturbation and amplifies the impact of the sensory mismatch. As such, a more conservative response strategy is adopted. It should also be noted that the strategy employed by participants against the downward background perturbation resulted in greater undershooting error than the upward background strategy. In any event, both results replicate the findings of Proteau and Masson (1997) and are evidence that the early portions of reaching trajectories are not entirely ballistic, but rather are under the influence of an online control process concerned with the dynamic characteristics of the movement.

Experiment 3

Method

Participants. The participants were 20 (10 male; 10 female) right-handed members of the McMaster University community. They had normal or corrected-to-normal vision and were naïve to the purpose of the study. Prior to participating, all individuals gave informed consent according to the guidelines of the McMaster University Office of Research Ethics.

Procedure. Participants performed a series of 90 trials in which they were instructed to make rapid, accurate pointing movements from a resting home position to a resting target position. The apparatus and recording techniques for Experiment 3 were identical to those of Experiments 1 and 2. At the beginning of each trial, the target that the participants moved to was presented on the display screen (Figure 7A). This target was represented by an intersection of the three yellow "**T**" configured lines displayed on a background of white dots. Participants prepared an accurate-as-possible movement to this target position and following a go signal executed this movement. Upon the initiation of the movement the initial target was either perturbed to a Müller-Lyer tails in configuration (Figure 7B), or a tails-out configuration (Figure 7C). Simultaneously, the grouping of white dots either translated down towards the participant, up away from the participant or remained stationary. Participants were notified that the target display and the background display may change and were instructed to complete their movement as accurately-as-possible regardless of any perturbation. The order of the perturbations was randomized with equal probability of each potential perturbation-translation combination (15 tails-in stationary background, 15 tails-out stationary background, 15 tails-in upward background, 15 tails-out upward background, 15 tails-in downward background, and 15 tails-out downward background).

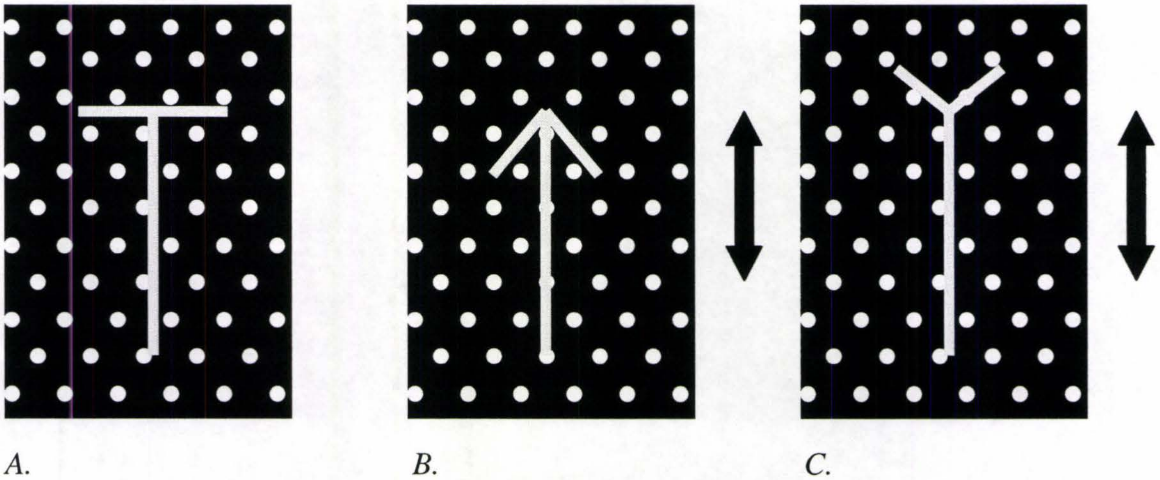


Figure 7. Depiction of Experiment Three's (A) control, (B) downward/upward tails in, and (C) downward/upward tails out Müller-Lyer and moving background target figures.

Analysis. Each performance and kinematic variable was subjected to a 2 Müller-Lyer condition (tails-in, tails-out) X 3 moving background condition (upward, stationary, downward) repeated measures analysis of variance. As in Experiments 1 and 2, for mean displacement and spatial variability, kinematic marker was also included as a 4-level independent variable (PA, PV, PD, END). Significant differences involving more than two means were examined using Tukey's HSD post hoc comparisons ($p < .05$).

Results and Discussion

Performance Outcomes. The CE analysis revealed main effects that replicated the effects of Experiments 1 and 2. The Müller-Lyer manipulation, F (1, 18) = 5.43, MSE = 2.88, $p< .05$, showed greater undershoots for the tails-in configuration than the tails-out configuration (Figure 8). The moving background manipulation, F (2, 36) = 12.82, MSE = 12.82, $p < .001$, showed greater undershoots for the downward background condition and greater overshoots for the upward background condition relative to the stationary condition and to each other (Figure 9). The lack of any interaction between these perturbations indicates that the online control processes that they are meant to interfere with are independent of one another and have an additive impact on movement accuracy (see Sternberg, 1969). No significant RT or MT differences were seen between any of the conditions (RT grand mean = 257 ms; MT grand mean = 510 ms).

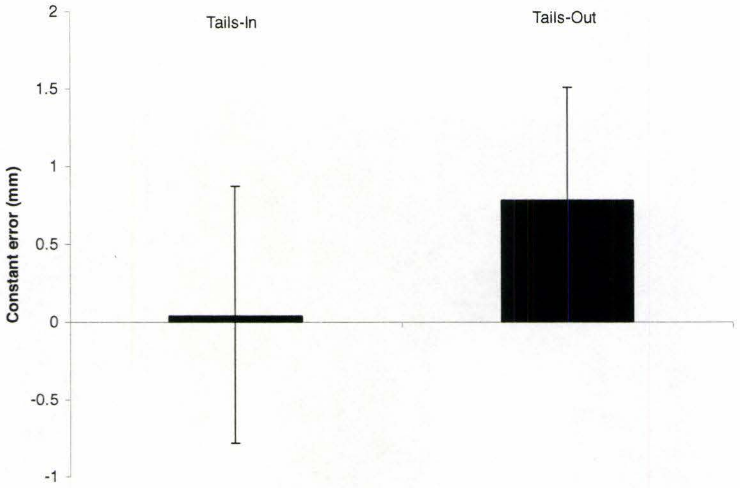


Figure 8. Constant Error (mm) plotted as a function of the Müller-Lyer condition (Experiment 3).

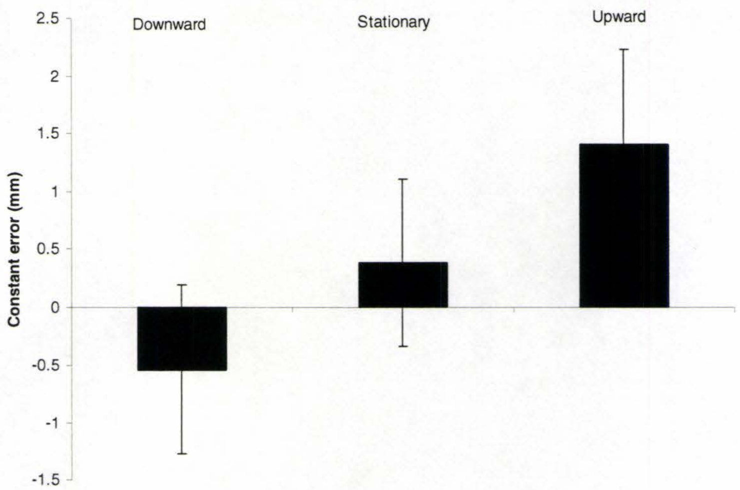


Figure 9. Constant Error (mm) plotted as a function of the moving background condition (Experiment 3).

Magnitude of the Kinematic Markers. No significant differences were elicited between the conditions for any of the magnitudes achieved at the kinematic markers. Also there were no differences in time to PV.

Mean Displacement. In addition to main effects for kinematic marker, F (3, 54) =1240.2, MSE = 2200.36, p < .01, Müller-Lyer condition, F (1, 18) = 5.58, MSE = 45.71, p < .05, and moving background condition, F (2, 36) = 5.46, MSE = 79.29, p < .01, an interaction between kinematic marker and moving background condition was revealed, F (6, 108) = 2.60, MSE = 60.35, p < .05. This interaction was driven by the difference in the displacement at PD (Figure 10). Specifically, participants had not moved as far by PD under downward moving conditions compared to upward and stationary conditions. As was the case in Experiment 2, this finding indicates that the initial portions of movements made against the downward moving background conditions were terminated sooner than they were planned. This again indicates early online control of the reach.

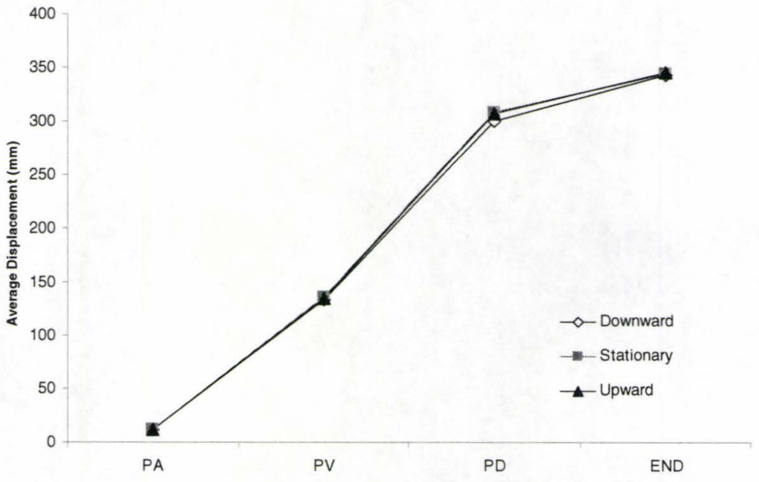


Figure 10. Mean displacement of peak acceleration (PA), peak velocity (PV), peak deceleration (PD), and the end position of the movement (END) in the primary direction of movement plotted as a function of moving background condition (Experiment 3).

Spatial Variability. In typical fashion, the spatial variability analysis yielded a main effect for kinematic marker, F (3, 54) = 34.65, MSE = 1042.02, p < .001. The results show that variability increased until PD before reducing at the movement end point, indicating late on-line control (PA = 6.31 mm; PV = 31.88 mm; PD = 39.72 mm; 4.70 mm).

General Discussion

These 3 studies sought to examine the relative contribution of two proposed processes of online control in goal-directed aiming. Using established kinematic methods (Elliott et al, 2001; Khan, Lawrence, Franks, & Buckolz, 2004), Experiments 1 and 2 replicated the findings of earlier work reporting evidence for late trajectory (Mendoza et al, 2005) and earlier control processes (Proteau & Masson, 1997), respectively. The illusory perturbations introduced in these studies not only manifested their influence on online control via outcome accuracy, but also via the temporal and spatial characteristics of aiming trajectories.

The impact of the Müller-Lyer illusions on movement accuracy is well-documented (e.g., Elliott & Lee, 1995) and have been attributed to a form of discrete control that is based on an allocentric evaluation of the relative location of the hand and target late in the movement trajectory (Heath, Neely, & Binsted, 2007). This form of control was documented over a century ago (Woodworth, 1899) and has served as a foundation for a number of two component accounts of limb control and speed-accuracy relations (e.g., Elliott et al., 2001; Meyer et al., 1988).

Experiment 2 extended Proteau and Masson's (1997) methods by examining 3-dimensional movements made against a moving background. This perturbation affects the perceived velocity of the moving limb and results in subsequent velocity modulation early in the movement. This form of control has recently been linked to the use of predictive or forward models that may exert influence on moving limbs quicker than is dictated by the inherent temporal constraints of purely sensory processing. The forward model perspective holds that when a motor command is executed a copy of that command is concomitantly integrated with information concerning the current state of the organism. This integration allows for a rapidly generated prediction of the forthcoming sensory feedback that can be used to evaluate errors in the executed command and to generate appropriate corrections. Whether or not this early control functions in a continuous fashion is not clear. In order for the CNS to maintain confidence in its modeled estimations a copy of the expected sensory feedback is compared against the actual sensory feedback. The error determined from this comparison is then used to modulate an inverse model, which generates appropriate corrections based on the expected next state of the organism and the desired final state of the organism (Davidson & Wolpert, 2005; Desmurget & Grafton, 2000; Miall & Wolpert, 1996; see also Von Holst, 1954). A perturbation such as a moving background purportedly causes a mismatch between expected sensory feedback and actual sensory feedback. Thus with the procedures examined here, there is at least some time lag associated with the processing of actual sensory feedback. Importantly, this dynamic form of control seems to be distinct from late corrective processes associated with the relative positions of the limb and the target.

In order to examine the combined influence of these two online control processes, Experiment 3 examined aimed movements made during combinations of the two perturbations. This study revealed an additive and non-interactive effect of the two perturbations on the accuracy of the movements. The non-interactive nature of these effects suggests that these two processes operate independently (Sternberg, 1969).

Examination of goal-directed action studies which have used illusory Müller-Lyer target figures to investigate the role of allocentric coding of visual cues in movement control (Elliott &

Lee, 1995) has recently led Heath and colleagues (2007) to suggest that a unitary visual input of aggregated egocentrically and allocentrically referenced visual information is essential for specifying target location in peripersonal space. While this hypothesis accounts for the strong effect of target information on manual aiming and has served to counter the Perception-Action (Milner & Goodale, 1995) and Planning-Control (Glover, 2004) models that emphasize the importance of only egocentric coding during movement execution, it is inconsistent with the present results. Because the eyes typically foveate the target during movement execution (Binsted & Elliott, 1999), the initial portions of aiming trajectories are only available for processing by the peripheral visual field. Therefore contributions to the improvement of performance assessed peripherally are not involved in the direct evaluation of relative positions of the hand and target, as is the case with the assessments made by the central visual field late in the movement. That is, visual information gleaned from the peripheral visual field is associated with an egocentric frame of reference concerned with the actual and expected dynamic properties of the moving limb early in the trajectory. Conversely, the visual information concerning the relative spatial positions of the hand and target late in the movement trajectory that is available to central vision must be gleaned via an allocentric frame of reference (Heath et al., 2007). Via our combined perturbation manipulation we show these two modes of visual information processing do not represent an amalgamated egocentric and allocentric visual input. Rather, the non-interactive main effects on constant error, suggest that processing of visual information occurs on two independent levels, with central vision evaluating cues from an allocentric space-coordinate system for target acquisition and peripheral vision navigating the transport of the effector toward the target based on visual information mapped onto an egocentric body-centred reference frame concerned with elements of movement and direction (Paillard, 1982). Although dynamic control based on our perceived velocity manipulation appeared to begin earlier, it is quite possible, and even probable, that at some point in the trajectory these two forms of control proceed in parallel. With this in mind, it is important to note that the presence or absence of late trajectory control depends on the effectiveness of not only the initial movement plan but also early dynamic control. That is, in terms of overall accuracy outcome, any effect of the moving background perturbation on movement trajectory may be somewhat neutralized by the efforts of the late control process; albeit, not necessarily in its entirety. As such it is not unreasonable to suppose that a combination of perturbations could be developed which would elicit an interaction between these two levels of visual processing.

A corollary and interesting finding that emerged from the data was the presence of an early decrease in the kinematic magnitude of PA, and subsequently PV and PD, in the Müller-Lyer perturbation conditions. This early kinematic difference suggests that a non-specific recognition of change in the environment prompts a conservative movement adjustment. With respect to the conceptualization of current two-component models of goal directed aiming, it seems this early form of online control may serve a supervisory function, acting to influence initial movement impulses only when the need arises. A mechanism such as this is supported by non-perturbed movements' adherence to an impulse-variability relationship common to ballistic action (Khan & Franks, 2003; Schmidt et al., 1979). Furthermore it is consistent with the proposition that individuals plan and execute control strategies that optimize movement efficiency and minimize the costs of errors (Elliott et al., 2004). Modeling of a supervisory control mechanism may also provide insight into the greater pronunciation of the perturbation effects of the downward moving background relative to its upward moving counterpart.

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Chapter 3

KINEMATIC ANALYSIS OF EARLY ONLINE CONTROL OF GOAL-DIRECTED REACHES: A NOVEL MOVEMENT PERTURBATION STUDY

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Running Head: A NOVEL MOVEMENT PERTURBATION STUDY

Kinematic analysis of early online control of goal-directed reaches: A novel movement perturbation study

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Abstract

A novel perturbation device was developed and tested. With a hand held stylus, under blocked vision and no vision conditions, performers reached to a target represented by the intersection of perpendicular lines. The stylus was connected to an air compressor and engineered such that eighty milliseconds following movement initiation reaches were randomly perturbed by a short air burst either in the direction of, or opposite to, the movement. Spatial position analysis of the limb at early kinematic landmarks revealed that the single direction bursts were successful in advancing and hindering the movement progress. Furthermore, within subject trial-to-trial variability analysis indicated that performers adopted different control strategies for dealing with the perturbations depending on the availability of vision. In addition to validating the compressed air perturbation apparatus as a tool for examining movement control, the present findings suggest that a continuous form of online control is exercised during the early portions of the aiming trajectories. Presumably this form of control may be mediated by visual or proprioceptive information.

Kinematic analysis of early online control of goal-directed reaches: A novel movement perturbation study

Woodworth's (1899) two-component model holds that goal-directed movements are composed of a ballistic phase responsible for the transport of the limb to the vicinity of the target and a second phase that involves the use of visual information regarding the location of the limb and the target to reconcile any errors in the late stages of the movement trajectory. These two phases were named the initial impulse phase and current control phase, respectively. However, over the last fifteen years, investigations into the trial-to-trial spatial variability and central tendency at specific kinematic landmarks have called the ballistic nature of the initial impulse into question (Hansen, Tremblay, & Elliott, 2005; Hansen, Elliott, & Tremblay, 2007; Khan, Elliott, Coull, Chua, & Lyons, 2002; Khan, Franks, Elliott, Lawrence, Chua, Bernier, Hansen, & Weeks, 2006; Proteau & Masson, 1997).

Utilizing a moving background technique, Proteau and Masson (1997) provided kinematic evidence that individuals terminate initial impulses earlier when the texture elements over which two-dimensional aims were performed translated in the direction opposite to that of the movements. Presumably this occurs because participants misperceive their limb as moving too quickly and thus terminate their movement earlier. Though to a lesser extent, Proteau and Masson (1997) also showed that moving the background in the same direction as the limb resulted in an over-extension of the impulse. Additional moving background research involving reaches made in three dimensional space has replicated Proteau and Masson's early initial impulse termination finding while showing an early reduction in within subject trial-to-trial variability when the background texture elements translate in the same direction as the limb (Grierson & Elliott, under review). In each case these responses suggest that initial impulses are not ballistic actions but, rather, are subject to online control. These adjustments are consistent with the interpretation that early trajectory control is mediated via perception of the velocity of the moving limb (Khan et al., 2006).

Limb velocity misperception creates a mismatch between expected afference and actual visual afference, and as such affects the individual's ability to exert online control via forward predictive models. The forward model perspective holds that through an integration of an efferent motor copy and information regarding the current state of the organism, a prediction of sensory reafference can be rapidly generated for comparison against the intended movement and outcome. While this can be used to generate rapid movement corrections, referencing of actual afferent feedback is necessary to attenuate any error that may exist in the comparison. Through perturbing the perception of actual limb velocity the moving background causes a mismatch between the actual and expected afference such that unnecessary corrective commands are executed.

While the forward model interpretation has been sufficient for describing the nature of corrections made during the early portions of goal directed reaches Whitney, Westwood, and Goodale (2003) have recently reported evidence that the perceived velocity of the hand may not be essential to the moving background's effects. Specifically, they showed that the effect of the background persists even when the individual has no vision of the moving limb. This finding prompted the conclusion that "the influence of motion on reaching is not due to the visual representation of hand speed or location" (Whitney et al., 2003, p. 871).

While the aforementioned research has provided evidence that individuals can make online adjustments to the early portions of goal directed reaches, the nature of the control process is less clear. Importantly, the perturbations employed in this work have been exclusively illusory.

That is, changes to the visual environment have been manipulated to investigate the effects that the visual information gathering and transformation process has on the execution of motor plans. In order to gain a fuller understanding of the role of perceived limb velocity to the process of early online control it is prudent to investigate the motor modifications executed when the dynamic properties of the limb experience an actual perturbation.

In this study, a novel procedure was developed to examine the performers' ability to rapidly adjust to a physical limb perturbation introduced early in a goal-directed aiming movement. Using a hand held stylus participants made reaches to a target represented by the intersection of two perpendicular lines. This customized stylus was connected to an air compressor (Campbell Hausfeld, DK755100A5 0605, South Pasadena, California) and engineered such that shortly following movement initiation the velocity of reaches was perturbed by a short burst of air either in the direction of, or the direction opposite to, the movement. Participants made these reaches with full vision and under conditions in which vision was eliminated on movement initiation.

In order to first verify the applicability of this compressed air perturbation tool, analysis of the magnitude and amplitude displacement of kinematic landmarks should reveal the appropriate advancement and hindrance of the limb movement. Secondly, these analyses should provide insight into the control processes employed to offset these disturbances to the expected trajectory of the limb. If initial impulses are not subject to online control then the early trajectories of perturbed reaches should reflect the applied perturbation and this bias should persist until the movement progresses into the current control phase late in the movement (Khan & Franks, 2003). Conversely, any rectifications to the amplitude displacement at specific kinematic landmarks or reduction in spatial variability during perturbed trials should be taken to reflect the influence of early online control processes. However, if Whitney and colleagues' (2003) suggestion that vision of the limb's velocity and location are irrelevant, no differences should be apparent between vision and no vision trials. As such, any online control that is exerted early in the trajectory must be attributed to the propriomotor system. If visual information regarding the hand's speed and location influence the early online control process, then kinematic analysis of the early portions of the reach trajectories will yield differences between the vision and no-vision conditions. Furthermore, should such differences be found, comparison of the vision and no-vision trials will serve to highlight the individual roles that visual and proprioceptive information play in the mediation of this early online control.

Methods

Participants

Ten (5 male, 5 female) members of the McMaster University community volunteered to participate in the study. All participants were self-proclaimed right-handers and gave informed consent of their participation according to the guidelines set out by the McMaster University President's Committee on Ethical Consideration in Human Experimentation. Participants were awarded five dollars (CND) for their participation.

Experimental Apparatus and Procedure

Individuals sat comfortably in front of a flat display screen placed on a table top. The screen served as the target aiming surface. A microswitch was mounted flush to the screen edge closest to the participant. This microswitch was the home position from which reaches were initiated.

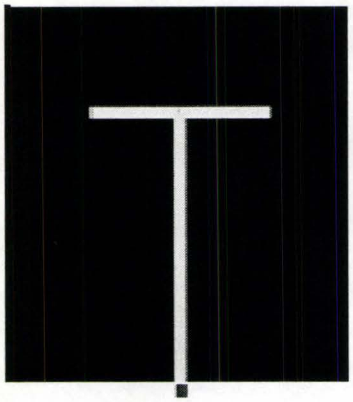

Figure 1. Depiction of target figure. The small square represents the microswitch home position.

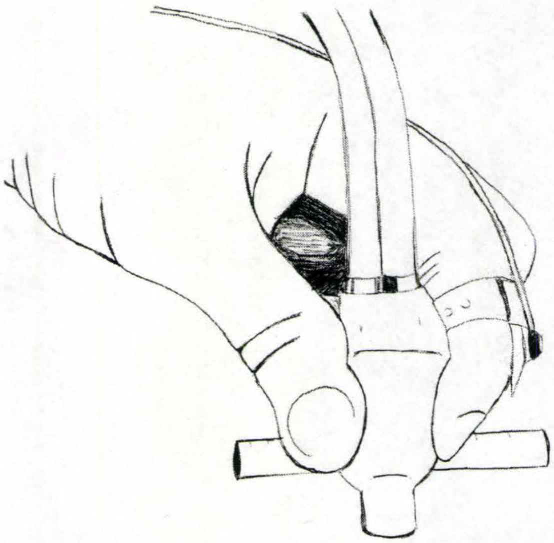

Figure 2. Depiction of the compressed air stylus.

Throughout the course of the experiment participants made goal-directed aiming movements to a target defined by the point of intersection of a 25 cm line and a perpendicular 10 cm line. These lines were arranged such that they formed a "**T**" configuration (Fig. 1). All aims were performed with a custom made handheld stylus (Fig. 2). This stylus was mounted to an air compressor and engineered with two small polyethylene tubes for the systematic expulsion of air blasts in both the direction of movement and the direction opposite to the movement. The air was released from the compressor at 100 psi and represented a 3.45 N perturbation to the movements. The stylus was also mounted with a small microswitch which participants were required to depress throughout the course of the study. This microswitch served to fix the handgrip used by participants across trials as well as provide a safeguard deactivation mechanism for the immediate cancellation of air expulsion. Individuals wore an infrared light emitting diode (IRED) on the finger responsible for the depression of this microswitch. The spatial location of this IRED was recorded on each trial at 500 Hz for 2 seconds by an Optotrak-3020 digital recording system (Northern Digital Inc., Waterloo, Ontario, Canada). Additionally, participants wore liquid crystal goggles (Translucent Technologies, (Translucent Technologies, Toronto, Ontario, Canada) such that their vision could be systematically occluded.

Participants began each trial with full vision and the stylus depressing the home position. Following a brief '*ready*' image, the tabletop screen changed to display the target image. A variable foreperiod (1000 ms – 1500 ms) ensued after which an 800 Hz beep from computer mounted speakers prompted the participants to make a rapid movement to the intersection of the displayed lines. On a majority of the trials (60 out of 90 trials) these aiming movements were unperturbed. However, the remaining thirty trials were subject to one of three possible perturbations; a 100 ms forward air blast (10 out of 90 trials), a 100 ms backward air blast (10 out of 90 trials), or simultaneous and offsetting 100 ms forward and backward blasts (10 out of 90 trials). Based on previous work from our lab, the timing of this blast was such that it occurred at the approximate time of the movement's peak acceleration in the primary direction of movement (i.e., 80 ms after movement initiation) (Grierson & Elliott, under review). Participants were notified that their movement might be perturbed and were instructed to complete their movement as accurately-as-possible, regardless of any perturbation.

Participants performed two counterbalanced blocks of trials; one block in which movements were made with vision and one block in which vision was occluded following movement initiation. For trials performed with vision, participants were notified that following the onset of movement vision would be available for 500 ms, after which time the goggles would occlude. They were instructed to use this time to complete their aims as accurately as possible. Under the no vision condition, the goggles occluded vision immediately upon the onset of movement (i.e. release of the home position microswitch). Upon completing the movement, participants kept the stylus on the target until the display screen cleared and the goggles returned vision. They then replaced their finger on the home position and prepared for the next trial (self-paced). In each block the order of all trials was completely randomized. In total each participant performed 180 trials.

The target display, liquid crystal goggles, computer speakers, Optotrak-3020 digital recording system trigger, and the compressed air expulsion were all controlled via a program developed using E-Prime software (Psychology Software Tools Inc., Pittsburgh, PA, USA).

Displacements in the primary direction of the movement were filtered with an 8 Hz dual-pass Butterworth filter and then differentiated and double differentiated to obtain velocity and acceleration. Custom software identified the magnitude of the peak acceleration (PA), peak velocity (PV), and peak deceleration (PD) for each reaching movement, as well as the spatial location of these kinematic events and the end position (END) of the movement. The Optotrak frames in which the limb velocity rose above or fell below 30mm/s, and remained as such for 70 ms identified the start and the end of the movement. Values for any dependent variable that fell more than 2.5 standard deviation units from the mean were considered outliers and were removed from the data sets prior to analysis.

The performance variables examined were reaction time (RT), movement time (MT), constant error (CE), and variable error (VE). We also examined mean peak acceleration (PA), peak velocity (PV), peak deceleration (PD), as well as the time before and after peak velocity. In order to provide insight into the impact of the perturbations as the movement unfolds, analysis was also conducted on the mean amplitude of the movement at PA, PV and PD, as well as the within-participant standard deviations of these spatial positions.

The primary dependent variables were analyzed using a 4 perturbation condition by 2 vision condition repeated measures analysis of variance. All significant effects involving more than two means were decomposed using the Tukey HSD, $p < .05$ procedure.

Results and Discussion

Performance Outcomes

For movement time there was a main effect for perturbation condition, $F(3,27) = 10.78$, $p < .001$. Aims made against the backward blast (582 ms) took significantly longer than those made in the forward blast (537 ms), bi-directional blast (538 ms), and no blast (537 ms) conditions. There were no MT differences between the latter three conditions. This difference in movement time represents the hindering nature of the backward blast perturbation. The MT analysis also yielded a perturbation condition by visual condition interaction, $F(3, 27) = 5.42$, $p < .001$. Under both vision and no vision conditions, individuals took significantly longer to complete movements made against the backward blast; however, visually guided movements made against the backward blast were performed significantly quicker than backward blasted movements made without vision. Conversely, the forward blasted movements were performed quicker in the no vision condition than the vision condition (Fig. 3). While the hindering nature of the backward blast and the facilitating nature of the forward blast serve as likely reasons for the MT effects without vision, it appears that visual information offers support to a control process that partially nullifies the effects of these two perturbations. Specifically, visually-guided movements made against forward blasts were slowed and visually-guided movements made against backward blasts were sped up. There were no reaction time differences between conditions (grand mean = 377 ms).

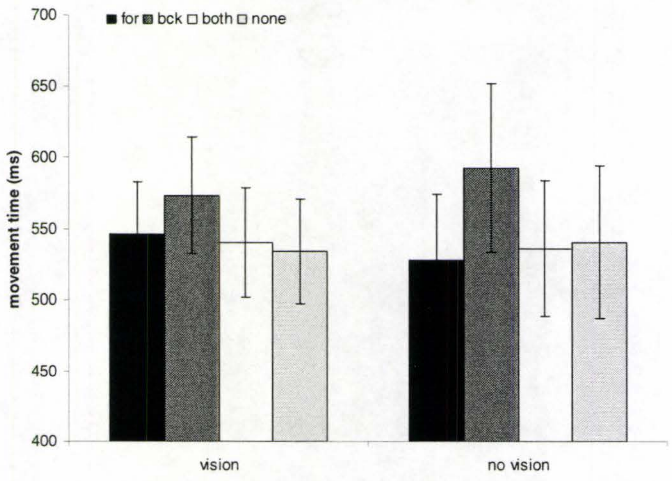

Figure 3. Mean movement time and standard error (ms) plotted as a function of the compressed air condition (forward blast (for), backward blast (bck), bidirectional blast (both), unperturbed (none)) and vision condition.

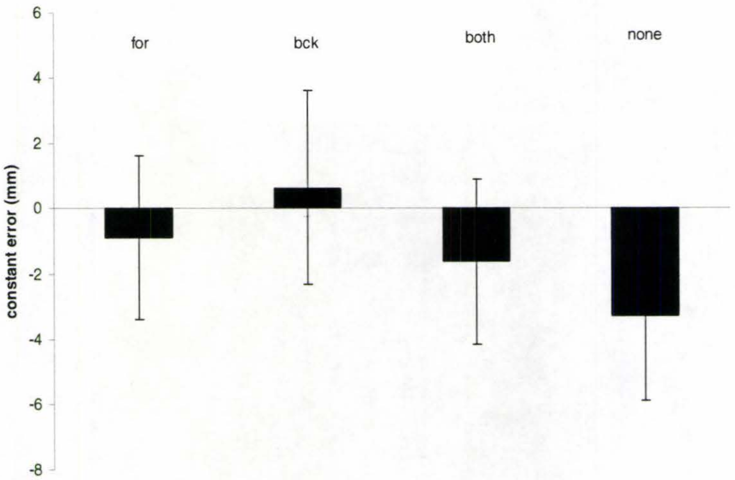

Figure 4. Mean constant error and standard error (mm) plotted as a function of the compressed air condition (forward blast (for), backward blast (bck), bidirectional blast (both), unperturbed (none)).

The results of the constant error (mean signed error in the primary direction of the movement) analysis yielded a main effect for perturbation condition, F (3,27) = 7.28, p < .001. Interestingly, individuals were more accurate on perturbed trials. Post hoc analysis revealed that unperturbed aims produced a greater undershooting error (negative CE) than did the forward blast and backward blast conditions. When the movement was perturbed equally in both directions the resulting constant error was intermediate to the no blast condition and the single blast conditions, but not statistically different from either (Fig. 4). That there was very little endpoint bias for both the single direction perturbation conditions is consistent with the notion that individuals modify their movements following perturbation. No differences in constant error were apparent between visual conditions.

The variable error analysis, however, revealed a main effect for visual condition, F (1,9) = 14.45, p < .01, in which the outcomes of movements made in the absence of vision (8.1 mm) were significantly more variable than those made with vision (6.1 mm). Thus while the CE analysis suggests visual information is not necessary to execute the aforementioned perturbation rectifications, the increased outcome variability in its absence indicates that this afferent information contributes to movement accuracy. These effects on outcome performance may be more related to vision's role in late trajectory control than the early trajectory processes that the perturbations are designed to induce.

Effects at Peak Acceleration

The air compressor perturbation device was engineered such that it applied a 3.45N burst of air to movement trajectories as the limb reached its peak acceleration. The perturbation onset lag of 80ms was determined via examination of the means of peak accelerations collected from previous research involving similar movements. Examination of the mean times to peak acceleration (ttPA) from this study's bi-directional blast condition and the unperturbed condition (81.7ms and 84.9 ms, respectively) show that this temporal lag was appropriate for the perturbation device to impact the intended portion of the reach. The longer mean ttPAs for the forward blast (104.7 ms) and the backward blast (101.6 ms) conditions confirm the impact of the perturbations. Analysis of time to peak acceleration (ttPA) revealed a significant perturbation condition main effect, $F(3, 27) = 3.66$, $p < .05$, which showed the time to peak acceleration to be longer when movements were forward blasted than when they were made against offsetting bi-directional blasts.

Analysis of the amplitude displacement at peak acceleration indicated a main effect for perturbation condition, $F(3, 27) = 3.06$, $p < .05$, and post hoc investigation of this effect indicated that the amplitude displacement of the limb at peak acceleration was further in the forward blast conditions as compared to the unperturbed conditions (Fig. 5).

No differences in the magnitude of peak acceleration (PA) were revealed between any of the perturbation or vision conditions (grand mean = 54 m/s^2).

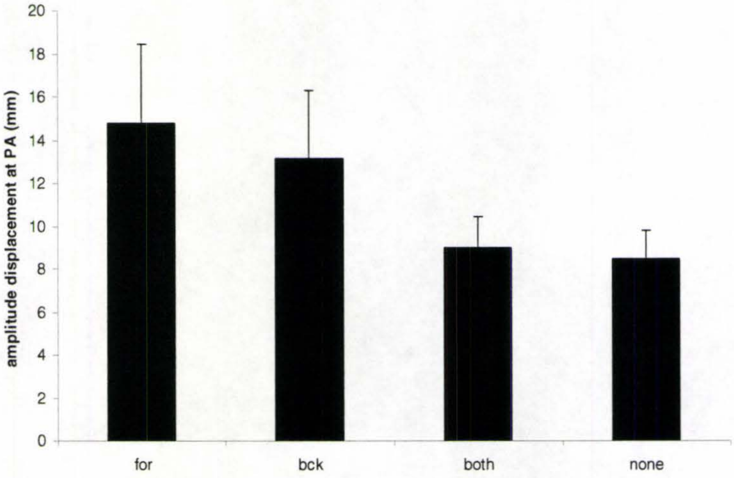

Figure 5. Mean amplitude displacement and standard error at PA (mm) plotted as a function of the compressed air condition (forward blast (for), backward blast (bck), bidirectional blast (both), unperturbed (none)).

With increased force applied to the limb in the primary direction of its trajectory, an unattended movement would be expected to achieve an increased magnitude of peak acceleration in temporal concord with the onset of this force application. However, the significant increase in this condition's ttPA and the lack of any difference in the magnitude of PA suggests that the limb does not fully accept the perturbation. Rather, the impact of the applied force is seemingly offset by some aspect of motor system.

With a backward blasted movement a similar trend occurs. If unattended the hindering nature of this perturbation is expected to reduce the magnitude of PA, shorten the amplitude displacement of the limb at PA, and to do so shortly following the onset of the perturbation. Rather, the ttPA and amplitude displacement, though not significantly different, is intermediate to the forward blast condition and the unperturbed conditions, while the magnitude of PA is no different than it is in any case. Again, it seems that the dynamic influence of the perturbation is being offset; and almost immediately (~ 20ms).

These findings evidence a rapid control mechanism concerned primarily with the maintenance of pre-set dynamic qualities of the moving limb and which operates primarily on early and non-specific information. Likely such a mechanism is primed in preparation of the possibility of a perturbation, and as such is influenced by the knowledge that a perturbation may occur. Similar findings were found in trajectory analysis of movements made to Müller-Lyer figures whose configurations changed upon movement initiation. In these cases a reduction in peak acceleration was noted for movements made to altered target figures, regardless of the nature of the alteration (Grierson & Elliott, under review).

As the forward blast operates to advance the limb in the same direction as it is already moving, portions of the dynamic impact of this perturbation may be incorporated into the ongoing movement with little cost to efficiency. In contrast, in order to overcome the force hindrance, movements made against the backward blast involve the generation of additional muscular output. Such differences in the functional operation of this rapid control mechanism, reflected in the increased prevalence of significant differences in ttPA and amplitude displacement of PA for the forward blasted conditions, suggest that, though seemingly driven by non-specific information, the control system prepares primarily to offset the influence of the backward blasts.

Effects at Peak Velocity

Analysis of time to peak velocity (ttPV) revealed no significant differences between any of the perturbation or visual conditions. The means for each perturbation condition (forward blast = 224.7 ms, backward blast = 237.6 ms, bi-directional blasts = 227.2 ms, unperturbed = 224.7 ms) indicate that, in all cases, peak velocity was not reached until after the compressed air had ceased to discharge.

Analysis of the amplitude displacement in the primary direction of movement at peak velocity yielded a significant visual condition by perturbation condition interaction, F (3,27) = 3.31, $p < .05$. Post hoc investigations into this effect revealed that, in the absence of vision, movements made against the forward blast perturbation reached peak velocity after greater amplitude displacement than unperturbed or backward blasted movements. Additionally, the forward blasted movements performed without vision reached peak velocity after further spatial displacement than when performed with vision. No differences existed between perturbation conditions when the movements were made with the benefit of vision (Fig. 6).

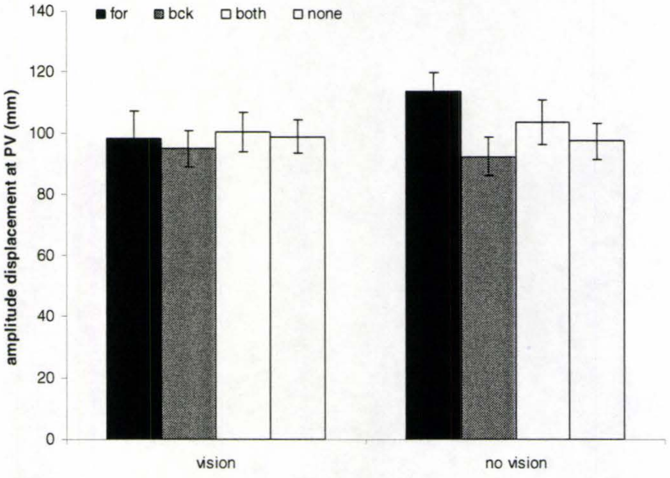

Figure 6. Mean amplitude displacement and standard error at PV (mm) plotted as a function of the compressed air condition (forward blast (for), backward blast (bck), bidirectional blast (both), unperturbed (none)) and vision condition.

The analysis of the magnitude of peak velocity (PV) revealed a significant main effect, F (3, 27) = 18.62, p < .0001, in which forward blasted movements (2.40 m/s) achieve higher peak velocities than backward blasted (2.08 m/s), bi-directionally blasted (2.14 m/s), and unperturbed movements (2.13 m/s).

The lack of any spatial difference between perturbed movements made with vision suggests that the processing of visual information operates to rectify any spatial discrepancy caused by the perturbation in the early portions of the trajectory. Conversely, in the absence of any visual information, the increase in the amplitude displacement for forward blasted movements manifested at peak acceleration is left unaltered by, and maintained at, peak velocity. Additionally, the artifacts of the early influences of the forward blast perturbation are further represented in the increased magnitude of peak velocity for the forward blasted movements. These findings are relevant in highlighting the presence of continuous visuomotor control.

Effects at Peak Deceleration

Analysis of the time to peak deceleration (ttPD) yielded a significant perturbation condition main effect, F (3,27) = 7.17, p < .01. Post hoc examination of this effect revealed that movements made against the forward blasts took less time to reach peak deceleration than those made against backward blasts (forward blast = 425.1 ms, backward blast = 488.8 ms, bi-directional blast = 459.1 ms, unperturbed = 454.6 ms).

The analysis of amplitude displacement in the primary direction of movement at peak deceleration revealed no differences between any of the visual or perturbation conditions (grand mean = 235 mm).

The magnitude of peak deceleration (PD) analysis revealed a perturbation condition main effect, F (3,27) = 12.11, $p < .0001$, and a visual condition by perturbation condition interaction, F (3, 27) = 3.00, $p < .05$. Post hoc analysis showed the main effect to be the result of a greater peak deceleration for forward blasted movements (57.6 m/s^2) than the other three conditions (backward blast = 42.8 m/s^2, bi-directional blast = 45.5 m/s^2, unperturbed = 38.5 m/s^2). Post hoc analysis of the interaction effect confirms this result. However, in the instances in which there is no vision the forward blasted and bi-directionally blasted movements achieve higher peak decelerations than their visual condition counterparts. Additionally, the without vision bi-directionally blasted movements achieve higher peak deceleration than unperturbed movements made without vision (Fig. 7).

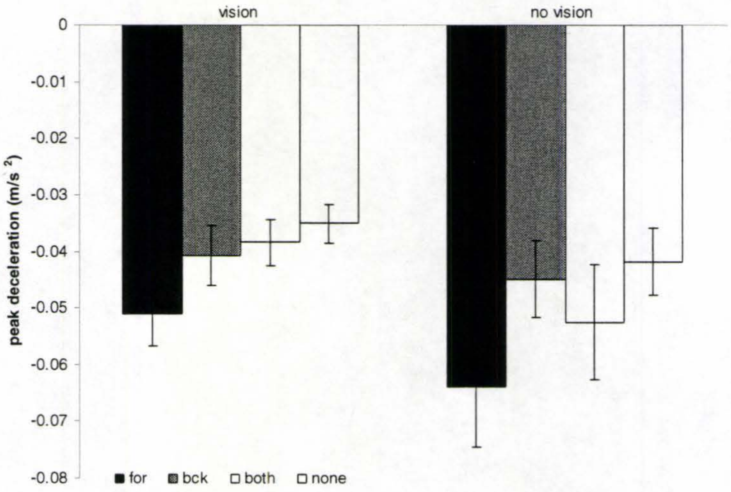

Figure 7. Mean peak deceleration and standard error (m/s^2) plotted as a function of the compressed air condition (forward blast (for), backward blast (bck), bidirectional blast (both), unperturbed (none)) and vision condition.

The bi-directional blast condition was incorporated into the experimental procedure as a control condition designed to highlight any effects that the sound of the air perturbation device had on the control processes executed by the participants. As the offsetting nature of the bi-directional blast condition exposed the moving limb to no actual perturbation any differences between the bi-directional and unperturbed conditions for any of the dependent measures must be attributed to the influence of processing the sound of the released air. Analysis of all dependent measures revealed no differences between these two conditions except for the aforementioned vision condition by perturbation condition interaction. While this finding suggests that the auditory afference created by the perturbation device contributes to the amount participants decelerate when blindly approaching their target the lack of any differences on any other measure provides sufficient confidence that the bi-directional condition is an appropriate control. By responding to the non-informative auditory information in this cautionary manner, the sensorimotor system seemingly switches from an early trajectory strategy intent on advancing the limb through the possibility of a hindering blast perturbation to a late trajectory strategy concerned with preserving the planned movement course in light of a potential limb-advancing perturbation.

In the cases in which the limb is actually advanced by a forward blast, in order to ensure that it obtains an appropriate spatial location for the accurate execution of late trajectory control processes, the motor system requires an increased deceleration to offset the additional limb velocity generated by the perturbation. Interestingly, the decreased time to peak deceleration for this condition, coupled with the consistently obtained amplitude displacement at peak deceleration, regardless of perturbation condition or presence of visual information, reflects the motor system's attenuation to the control of the dynamic properties of the limb for the purpose of obtaining such a planned outcome position. Failure to show any difference in this spatial location, for any condition, suggests that sensory redundancy in the motor system allows for compensation when one sensory modality is degraded. However, in the presence of vision, perturbed and unperturbed limbs reach a consistent spatial location as early as peak velocity, such that visuomotor processes may act to reduce the remaining distance between the moving limb and the target at the onset of limb deceleration. In terms of efficiency, ensuring that the limb obtains a normalized location to initiate this control process is beneficial.

Spatial Variability at Each of the Kinematic Markers

The underlying assumption in the analysis of spatial variability at the kinematic landmarks is that any error inherent in the execution of the planned movement will contribute to error in the motor output. Left unaltered by closed-loop control process this error should increase systematically as the movement progresses, and as such, the within participant trial-by-trial spatial variability should also increase. Conversely, a reduction, or no increase, in variability is taken to reflect the impact of online control processes (Khan & Franks, 2003; Khan et al., 2006).

A perturbation condition (forward blast, backward blast, bi-directional blast, unperturbed) by visual condition (vision, no vision) by kinematic marker (PA, PV, PD, and end of the movement (END)) repeated measures analysis of variance conducted on the participants' reach trajectories yielded a significant perturbation condition main effect, $F(3, 27) = 4.96$, $p < .01$, a significant kinematic marker main effect, $F(3, 27) = 29.67$, $p < .00001$, and a significant kinematic marker by visual condition interaction, $F(3, 27) = 10.9$, $p < .0001$.

Post hoc analysis of the perturbation main effect revealed that backward blasted movements were more variable than the bi-directionally blasted or unperturbed movements. Investigation into the kinematic marker main effect showed spatial variability to increase significantly from peak acceleration to peak velocity, and to decrease significantly as the movements moved from peak deceleration to the end of the movement. That there is no systematic increase in variability between peak velocity and peak deceleration is indicative of the operation of a continuous early trajectory control process. Interestingly, examination of the kinematic marker by visual condition interaction revealed that when vision was available the variability findings are typical for movements controlled under solely late trajectory closed-loop processes; that is, spatial variability increases significantly from peak acceleration to peak velocity, and from peak velocity to peak deceleration, before decreasing significantly at the end of the movement. However, in the absence of vision, the movement increases in variability from peak acceleration to peak velocity, before significantly decreasing to peak deceleration and again as the movement approaches its completion (Fig. 8). That this occurs regardless of any perturbation suggests the movements are planned differently when the subject knows that vision will not be available (Hansen, Glazebrook, Anson, Weeks, & Elliott 2006).

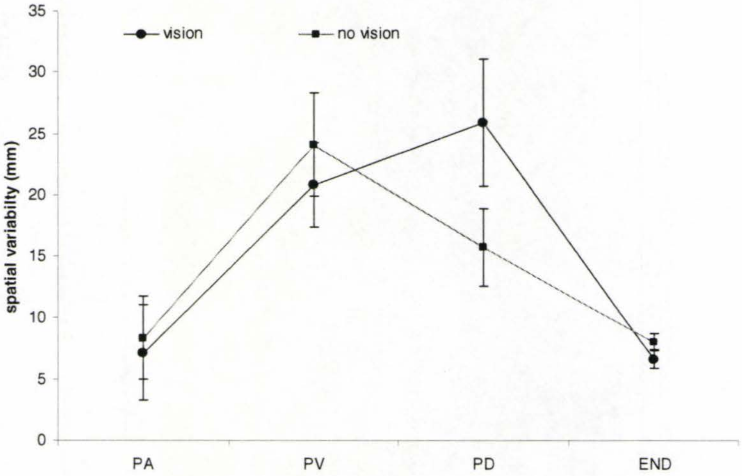

Figure 8. Mean spatial variability and standard error (mm) for each visual condition (vision, no vision) plotted as a function of kinematic event (peak acceleration (PA), peak velocity (PV), peak deceleration (PD), and movement endpoint (END)).

A Supplementary EMG Experiment

The aforementioned results intrigued us with the apparent presence of a non-specific response to the early compressed air perturbation. However, some uncertainty remained regarding the ability of the movement kinematics to fully describe the control processes involved. Since the optoelectric camera recorded the movement of a single marker affixed to the index finger of the acting hand, the possibility exists that differences between conditions could represent only control managed across the wrist joint. That is, the impacts of the forward or backward air blast may have been dampened or exacerbated at this most distal joint. As such, for a fuller understanding of the movement, we recorded and compared the muscular activities of the agonist and antagonist pairs at each of the pertinent joints involved in this complex aiming movement: the shoulder, the elbow, and the wrist.

Through measurement of the muscle activation patterns throughout perturbed and unperturbed movements we aimed to further characterize the nature of early movement control. If the system operates a non-specific response to the perturbation we expect to see a similar activation pattern across the muscle groups regardless of the perturbation's directional impact. Conversely, if the kinematic data has mistakenly evidenced the performers' use of the distal wrist joint as a non-specific response to manage the perturbation impact, discriminating EMG activities at the shoulder and the elbow will highlight the control executed at these joints.

Additionally, we sought to investigate the influence of a priori knowledge of the possible perturbation on movement planning and execution. In order to do this, we designed the experiment such that performers were exposed to blocks of trials in which they could expect a forward blast perturbation, a backward blast perturbation, either a forward or a backward perturbation, or no perturbation at all. We hypothesize that the manner in which individuals prepare and execute their movements would be contingent on the particular perturbation block under which they are performing. That is, when the perturbation direction was predictable, it was expected that the response to the compressed air perturbation would be structured with characteristics designed to offset that particular impact. However, in the instances that the perturbation was unpredictable it was expected that the response elicited would not discriminate across perturbations and as such be composed primarily of components to offset the more hindering backward blast perturbation.

Methods

Four (2 males, 2 females) right handed, informed and consenting (McMaster University President's Committee on Ethical Consideration in Human Experimentation) volunteers performed all trials while holding the compressed air stylus and sitting at the previously described experimental set-up. Performers wore an infrared light emitting diode (IRED) on the index finger of their aiming hand. The participants first performed a pre-test block of ten trials in which they made rapid aiming movements from the home position to the target intersection with no possibility of a compressed air perturbation. The following three blocks of trials exposed performers to a 3.45 N predictable forward air blast, a 3.45 N predictable backward air blast, or a 3.45 N unpredictable air blast. These three experimental blocks were randomized for each performer. In the predictable forward air blast block, a blast of air was discharged randomly from the stylus (10 out of 30 trials) in the direction opposite to that of the movement. In the predictable backward air blast block, a blast of air was randomly discharged from the stylus (10 out of 30 trials) in the direction of the movement. In the unpredictable perturbation block, an air blast was randomly discharged from the stylus in either in the direction of (10 of 60 trials), or opposite to (10 of sixty trials), the movement. A post-test block of 10 unperturbed trials was then performed. This blast was initiated 80 ms following movement initiation and discharged for 100 ms. Throughout the course of the experiment participants wore liquid crystal goggles and were notified that following the onset of movement, vision would be available for 500 ms, after which time the goggles would occlude. They were instructed to use this time to complete their aims as accurately as possible.

During experimental trials, surface EMG (sEMG) activity was recorded from 6 muscles of the right arm, using a multi-channel Delsys System (Delsys Systems, model Bagnoli-8EMG System, Boston, MA). Surface electrodes (3 x 2 cm; 2 contacts of 1 x 0.1 cm and spacing of 1 cm) were placed over the muscle bellies of Extensor Carpi Radialis (wrist agonist), Flexor Carpi Radialis (wrist antagonist), Triceps Brachii (elbow agonist), Biceps Brachii (elbow antagonist), Anterior Deltoid (shoulder agonist) and Posterior Deltoid (shoulder antagonist). A reference electrode was placed over the elbow's lateral epycondile. Prior to electrode placement, the skin surface over the muscle belly was shaved, cleaned with alcohol, and allowed to dry. EMG signals were processed by the Delsys System's main amplifier unit with a selected gain of 1000. Data were digitized and sampled at a rate of 2000 Hz/s through custom LabVIEW™ software (National Instruments, version 7.0, Austin, TX). EMG was recorded for 2 seconds in parallel with optoelectric data. A static trial was collected at the beginning and at the end of the experimental trials to collect EMG activity at the "home" position and at the target position. Raw EMG data were then processed using DIAdem™ software (National Instruments, version 10, Ireland). The raw EMG was filtered through a second degree Butterworth band-pass with cutoff frequencies of 20 to 500 Hz. The resulting data were marked using the kinematic events used to identify the beginning and the end of the movement.

For each trial, just prior to the auditory tone, both the Delsys, and Optotrak-3020 systems were triggered. The spatial position data collected by the Optotrak-3020 system were subjected to the same data collection, reduction, and cleaning procedures as was described in the above methods sections.

Root mean square (RMS) values were obtained to quantify the amount of muscle activity in each condition and during different time periods throughout the movement. These time periods corresponded to movement initiation to 80 ms (pre-blast), from 80 ms to 180 ms (blast) and from 180 ms to the end of the movement (post-blast). Amplitude values from the static home position were subtracted from the trial RMS values and further normalized to obtain a fold increase from home position (the amount of activity elicited during the movement). These normalized RMS (nRMS) values were then used to analyze the relationship between agonist and antagonist muscles during the movement compared to their static state at the home position. For each participant, for each condition within each block, Pearson correlations were run on the nRMS measures. These coefficients were then converted to z-scores and were run in a series of analyses to determine differences in the relative activations of agonist-antagonist muscle pairs.

The significant results of any of these analyses are discussed in terms of differences in co-contraction. However, it should be noted that the term co-contraction, for our purposes, refers only to the relative and coordinated activations between the two muscles and does not indicate that a particular threshold of mutual muscular activation was achieved. For example, it may be the case that in one condition an agonist was contracted while its antagonist exhibited a lack of activation, and in another condition the agonist contracted with some minimal contraction from the antagonist. While neither situation may be conventionally deemed as "co-contractive", if the difference in coordinated action between the two conditions was significant, we reported that for this muscle pairing the latter trial showed more co-contraction than the former.

Results

Within Block Analyses: Analysis of the unperturbed block

Each performer's mean nRMS data and standard deviation nRMS data were determined for the pre-blast, blast, and post-blast movement portions for each muscle for the pre-test and post-test experimental blocks. Separate t-tests yielded no differences between the pre-test and post-test for any of the muscles or movement time periods. As such these trials were combined to form a single unperturbed block of trials. To determine the patterns of muscular activity throughout a typical movement, the RMS values for each muscle and the normalized correlation coefficients of agonist-antagonist muscle pairs gleaned from the unperturbed trials performed during the pre-test and the post-test were analyzed in a 3 time (pre-blast, blast, post-blast) repeated measures analysis of variance.

The analysis of muscle activity revealed that agonist muscle activity at the shoulder was greater during the post-blast movement portions (65.8 +/- 13 mV) than during the pre-blast (24.8 +/- 4.5 mV) or blast movement (38.8 +/- 8.3 mV) portions, F (2, 6) = 19.9; p < .01. The shoulder antagonists showed no differential activation at any time throughout the movements (grand mean = 19.3 +/- 3.5 mV). At the elbow, agonist activity was greater during the post-blast period (15.5 +/- 2.2 mV) than the pre-blast (9.7 +/- 2.5 mV) or blast periods (10.3 +/- 2.7 mV), F (2, 6) = 8.62; p < .05. Activity from the elbow antagonist was greater during the post-blast (40.0 +/- 11.8 mV) period than during the pre-blast (24.0 +/- 8.7 mV) period, F (2, 6) = 6.39; p < .05. Agonist activity at the wrist was larger during the post-blast (45.1 +/- 9.1 mV) period than during the pre-blast (28.7 +/- 4.2 mV) period, F (2, 6) = 7.25; p < .05. No differences in the wrist antagonist activity were noted at anytime during the movements (grand mean = 15.2 +/- 6.5 mV).

Co-contraction analysis at each of the joints provided no indication that any of the muscle groups differentially co-contracted at any point in the movement.

The mean reaction time was 314ms, the mean movement time was 663 ms, and the mean constant error was -1.35 mm.

Within Block Analyses: Analysis of the predictable forward blast block

A 2 perturbation (forward blast, unperturbed) by 3 time (pre-blast, blast, post-blast) ANOVA was conducted on the RMS values for each muscle and the normalized correlation coefficients of nRMS values of agonist-antagonist muscle pairs gleaned from the trials performed during the predictable forward blast block. Differences in reaction time, movement time and constant error were determined via a 2 perturbation (forward blast, unperturbed) repeated measures analysis of variance.

Agonist activity at the shoulder was greater during the post-blast (52.3 +/- 9.4 mV) portions of the movement as compared to the pre-blast (19.4 +/- 5.1 mV) and blast (27.2 +/- 8.8 mV) portions, F (2, 4) = 20.3; p < .01. No shoulder antagonist differences were revealed at any time for either perturbation condition (grand mean = 20.9 +/- 3.1 mV). Elbow agonist (12.6 +/- 2.8 mV) and antagonists (37.3 +/- 13.7 mV) exhibited no differential activity throughout the movement. Movements that were forward blasted (42..2 +/- 8.9 mV) resulted in larger wrist agonist activity than those that were unperturbed (40.1 +/- 8.2 mV), F (1, 2) = 21.3; p < .05. No differences were noted for the wrist antagonists (grand mean = 20.7 +/- 8.7 mV).

The investigation into agonist-antagonist co-contraction revealed no significant differences at either the elbow or wrist joints. However, the shoulder muscles exhibited less co-contraction during the blast portions of the movements, F (2, 4) = 16.02; $p < .05$, than during the pre-blast portions. Additionally perturbed movements generated significantly less co-contraction at the shoulder than unperturbed movements, F (1, 2) = 22.98; $p<.05$. Examination of the relative muscle activity indicated that, in each case, during this portion of the movement as the shoulder antagonist increased activity the agonist decreased. No differences in co-contraction were yielded from the analyses at the wrist and elbow.

No reaction time (344 ms), movement time (685 ms), or constant error (- 2.43 ms) differences were yielded between perturbation conditions.

Within Block Analyses: Analysis of the predictable backward blast block

A 2 perturbation (backward blast, unperturbed) by 3 time (pre-blast, blast, post-blast) ANOVA was conducted on the RMS values for each muscle and the normalized correlation coefficients of nRMS values of agonist-antagonist muscle pairs gleaned from the trials performed during the predictable backward blast block. Differences in reaction time, movement time and constant error were determined via a 2 perturbation (backward blast, unperturbed) repeated measures analysis of variance.

Shoulder agonists show greater activity during the post-blast (68.0 +/- 13.6 mV) portion of the movements than during the pre-blast (26.0 +/- 6.8 mV) period, F (2, 6) = 7.69; $p < .05$, while no differences were evidenced from the shoulder antagonist analysis (grand mean = 21.9 +/- 3.8 mV). Elbow agonists were more active post-blast (18.5 +/- 3.2 mV) than during the blast (11.1 +/- 1.1 mV) or pre-blast (10.1 +/- 1.1 mV), F (2, 6) = 16.79; $p < .05$ and elbow antagonists were more active during the blast (65.2 +/- 19.2 mV) than pre-blast (15.8 +/- 5.0 mV), F (2, 6) = 6.03, p < .05, regardless of the presence of a blast. In addition to a significant main effect, F (2, 6) = 7.72; p < .05, the agonist wrist analysis also produced a significant interaction F (2, 6) = 11.14; p < .01, in which agonist muscle activity reached higher levels during the post-blast movement portions when the limb was perturbed (66.0 +/- 12.2 mV) as compared to when it was unperturbed (53.7 +/- 9.0 mV) (pre-blast mean = 35.9 +/- 5.7 mV; blast mean = 47.6 +/- 9.7 mV). The analysis of wrist antagonist activity yielded a similar interaction, F (2, 6) = 6.86; p < .05, in which the antagonist activity of perturbed movements (27.4 +/- 6.7 mV) was greater than unperturbed movements (15.8 +/- 2.4 mV) during the post-blast period (pre-blast mean = 17.2 +/- 6.2 mV; blast mean = 14.6 +/- 6.5 mV).

While no co-contraction differences were noted at the shoulder or the elbow for perturbed or unperturbed movements at anytime, the analysis indicated greater co-contraction at the wrist during the post-blast period, F (2, 6) = 5.19; p < .05, regardless of perturbation.

There were no reaction time (302 ms), movement time (647 ms), or constant error (-2.76 mm) differences between perturbation conditions.

Within Block Analyses: Analysis of the unpredictable blast block

A 3 perturbation (forward blast, backward blast, unperturbed) by 3 time (pre-blast, blast, post-blast) ANOVA was conducted on the RMS values for each muscle and the normalized correlation coefficients of nRMS values of agonist-antagonist muscle pairs gleaned from the trials performed during the unpredictable blast block. Differences in reaction time, movement time and constant error were determined via a 3 perturbation (forward blast, backward blast, unperturbed) repeated measures analysis of variance.

Shoulder agonists exhibited more activity during the post-blast (64.6 +/- 10.0 mV) movement portion than during the pre-blast (24.1 +/- 5.4 mV) or blast (40.3 +/- 7.6 mV) portions, F (2, 6) = 17.54; p < .01, while no differences were gleaned from the analysis of shoulder antagonists (grand mean =22.5 +/- 4.5 mV). Elbow agonists exhibited greater activity during the post-blast (20.1 +/- 3.9 mV) portions of the movement than during the pre-blast (10.9 +/- 1.7 mV) or blast (11.6 +/- 1.7 mV) portions, F (2, 6) = 12.98; p < .01. In addition, these elbow agonists were more active during this post-balst period when perturbed forward (22.5 +/- 4.0 mV) or backward (21.0 +/- 4.8 mV) than when unperturbed (16.9 +/- 3.3 mV), F (4, 12) = 5.89; p < .01. Analysis of the elbow antagonists revealed no significant differences in the muscle group's activation (grand mean = 42.0 +/- 13.5 mV). Similar to the elbow, the wrist agonists showed increased activity during the post-blast (57.1 +/- 6.9 mV) portions of the movement as compared to the pre-blast (32.3 +/- 4.0 mV) or blast (40.6 +/- 5.6 mV) portions, F (2, 6) =16.36; p < .01. This activation was greater during this period in the event of either a forward (60.2 +/- 5.8 mV) or backward (61.7 +/- 7.7 mV) blast, F (4, 12) = 11.17; p < .001, than when unperturbed (49.5 +/- 7. 1 mV). The analysis of wrist antagonists also showed greater activation during the post-blast (26.5 +/- 6.3 mV) period as compared to the pre-blast (16.8 +/- 5.4 mV) or blast (15.7 +/- 5.9 mV) periods, F (2, 6) = 8.27; p < .05. A significant main effect also revealed that post-blast wrist antagonist activity was greater when the limb was forward blasted (33.8 +/- 6.8 mV) than when it was blasted backwards (27.1 +/- 6.3 mV) and greater when the limb was blasted backward than when it was unperturbed (18.6 +/- 4.4 mV).

The analysis of co-contraction revealed no temporal or conditional differences in shoulder or elbow muscle co-activation. Conversely, at the wrist greater co-contraction was noted during the post-blast portion of the movement regardless of the perturbation, F (2, 6) = 7.74; $p < .05$.

The reaction time (313 ms) and movement time (618 ms) analyses revealed no significant differences; however, the constant error analysis indicated that unperturbed movements missed the target by more (-1.99 mm) than those that were blasted backwards (0.75 mm), F (2, 6) = 6.44, $p < .05$. Forward blasted movements were performed with intermediate but not significantly different constant error (-1.32 mm).

Summary of within-block analyses results

The unperturbed block data highlights the increase in agonist muscle activation as an unperturbed movement progresses. It should be noted that the post-blast portion of the movement represents a greater portion of the movement than the combined pre-blast and blast portions. The increase in post-blast elbow antagonist activity indicates that the deceleration associated with late-trajectory control is managed via this joint.

The predictable forward blast block data highlights that performers plan for forward blasted movements by increasing the relative shoulder antagonist-to-agonist activation during the blast portion of the movement. That this occurs regardless of the presence of a blast suggests that it is action residual to the movement pre-programming. In the event of a blast this coordinated muscle activity involves additional antagonist activation. In all, the results reflect a movement strategy in which performers opt for proximal stability against the potential forward blast while leaving the distal musculature to manage the remaining perturbation impact.

The predictable backward blast block data indicates that performers plan for the backward blasts by increasing the wrist stability during the post-blast portions of the movement.

Also, the increased agonist and antagonist activations during the post-blast portion of perturbed movements suggests that the impact of the perturbation is somewhat controlled for at this joint. As previously, the post-blast elbow antagonist activity represents the operation of late-trajectory limb deceleration. Interestingly, it seems that when the performers are faced with the potential of a backward air blast they opt to first absorb the perturbation at the wrist and then stabilize the distal musculature while the proximal groups are left to manage the remaining perturbation impact.

The analysis of the unpredictable blast block data indicates that performers plan for the unpredictable blasts by increasing wrist stability during the post-blast portion of the movements. Interestingly, the increase in post-blast agonist activation at the elbow and wrist highlights an undiscriminating response that deals with either perturbation. Also, the increased post-blast antagonist activity at the wrist for the forward blasted movements as compared to the backward blasted movements, and for the backward blasted movements as compared to the unperturbed movements, further evidences non-specific control. Though the differences between wrist antagonist activity for forward and backward blasted movements suggests some specificity of response, it should be noted that this response is unidirectional (antagonist activation only; without co-contraction) and differs only in its necessary magnitude. These findings point to a mode of control that stabilizes distal musculature while allowing the proximal groups freedom to manage/integrate the perturbation impact. Importantly, this non-specific form of control resembles that designed to deal with the backward blast and suggests that the system plans its movements and perturbation responses a priori with a bias to overcome the more task-hindering backward blast.

Between Block Analyses: Analysis of the unperturbed movements

A 4 block (predictable forward blast, predictable backward blast, unpredictable blast, and unperturbed) by 3 time (pre-blast, blast, post-blast) ANOVA was conducted on the RMS values for each muscle and the normalized correlation coefficients of nRMS values of agonist-antagonist muscle pairs gleaned from the unperturbed trials performed during each of the aforementioned blocks. Differences in reaction time, movement time and constant error were determined via a 4 predictability (predictable forward blast, predictable backward blast, unpredictable blast, predictably unperturbed) repeated measures analysis of variance.

The analysis of shoulder agonist activity indicated greater activation post-blast (53.0 +/- 10.9 mV) than pre-blast (21.5 +/- 5.0 mV), F (2, 4) = 16. 05; p < .05, for all unperturbed movements. The shoulder antagonist analysis yielded no significant differences (grand mean = 20.4 +/- 3.4 mV). While no elbow agonist activity differences were apparent between unperturbed movements (grand mean = 12.3 +/- 2.3 mV), during the blast period elbow antagonist activity was greater for unperturbed movements made in the backward blast block (63.8 +/- 19.7 mV) than those made in the forward blast (39.1 +/- 14.4 mV), unpredictable (46.5 +/- 14.7 mV), or unperturbed blocks (41.2 +/- 13.0 mV), F (6, 12) = 3.52; p < .05. The analysis of wrist agonist activity revealed no conditional or time period differences (grand mean = 40.9 +/- 7.4 mV). However, during the blast period wrist antagonists were more active in unperturbed movements made in the forward block (19.8 +/- 12.3 mV) than those made in the unperturbed (16.7 +/- 8.0 mV) or backward blast (14.2 +/- 5.5 mV) blocks, and were more active in unperturbed movements made in the unpredictable blast (18.2 +/- 7.4 mV) block than those made in the backward blast block, F (6, 12) = 3.29; p < .05. Furthermore, in the unpredictable block (18.6 +/- 4.4 mV), unperturbed movements showed higher wrist antagonist activity during the post-blast period than they did in the forward blasted (15.5 +/- 6.7 mV) or unperturbed (14.3 +/- 4.2 mV) blocks.

There were no co-contraction differences manifested at the shoulder or the elbow for unperturbed movements. However, co-contraction was significantly less at the wrist during the blast than pre-blast or post-blast, F (2, 4) = 19.24; p < .01.

No reaction time (322 ms), movement time (669 ms), or constant error (-1.87 mm) differences were found between unperturbed movements performed under different predictability conditions.

Between Block Analyses: Analysis of the movements perturbed by the forward compressed air blast

A 2 predictability (predictable, unpredictable) by 3 time (pre-blast, blast, post-blast) ANOVA was conducted on the RMS values for each muscle and the normalized correlation coefficients of nRMS values of agonist-antagonist muscle pairs gleaned from the forward blasted trials performed during the predictable forward blast and the unpredictable blast blocks. Differences in reaction time, movement time and constant error were determined via a 2 predictability (predictable forward blast, unpredictable blast) repeated measures analysis of variance.

The analysis of forward blasted movements indicated that shoulder agonists increased in activity post-blast (63.8 +/- 9.9 mV) relative to their pre-blast (29.0 +/- 14.2 mV) and blast (35.5 +/- 7.7 mV) period levels, F (2, 6) = 23.61; p < .01. No differences were noted in the shoulder antagonists (grand mean = 22.5 +/- 3.9 mV). The elbow agonists were shown to be more active post-blast (21.4 +/- 3.7 mV) as compared to the pre-blast (10.2 +/- 1.4 mV) and blast (11.7 +/-

1.9 mV) periods, F (2, 6) = 13.02; p < .01. Though no differences were apparent from the analysis of elbow antagonist action (grand mean = 39.8 +/- 13.8 mV), the difference between the activity of the elbow antagonist during the predictable forward blast and its unpredictable counterpart approached conventional levels of significance (p = .06). Both the post-blast (58.5 +/- 7.8 mV) wrist agonist activity, F (2, 6) = 15.20; p < .01, and the post-blast (33.0 +/- 6.3 mV) wrist antagonist activity, F (2, 6) = 7.06; p < .05, were greater than their respective activations during the pre-blast (agonist = 30.3 +/- 3.3 mV; antagonist = 16.1 +/- 6.4 mV) or blast (agonist = 39.0 +/- 5.7 mV; antagonist = 16.1 +/- 7.3 mV) portions of the movements.

No co-contraction differences were noted at any of the joints for any forward blasted movements.

No reaction time (325 ms) or constant error (-1.97 mm) differences were found for forward blasted movements performed under different conditions of predictability. Forward blasted movements that were predictable took longer to complete (652 ms) than those that were unpredictably blasted forward (592 ms), F (1, 3) = 13.2, p < .05.

Between Block Analyses: Analysis of the movements perturbed by the backward compressed air blast

A 2 predictability (predictable, unpredictable) by 3 time (pre-blast, blast, post-blast) ANOVA was conducted on the RMS values for each muscle and the normalized correlation coefficients of nRMS values of agonist-antagonist muscle pairs gleaned from the backward blasted trials performed during the predictable backward blast and the unpredictable blast blocks. Differences in reaction time, movement time and constant error were determined via a 2 predictability (predictable backward blast, unpredictable blast) repeated measures analysis of variance.

The analysis of backward blasted movements revealed that shoulder agonist activity was greater post-blast (68.1 +/- 6.9 mV) than pre-blast (25.4 +/- 6.9 mV), F (2, 6) = 14.68; p< .01, and that shoulder antagonists showed no conditional or time period activity differences (grand mean = 22.8 +/- 4.7 mV). The analysis of elbow agonists showed that post-blast activity (20.5 +/- 3.9 mV) was greater that pre-blast (10.4 +/- 1.6 mV) or blast (11.2 +/- 1.4 mV) period activity, F (2, 6) = 11.02; p < .01. No differences were yielded from the analysis of elbow antagonist action (grand mean = 44.5 +/- 16.7 mV). At the wrist, post-blast agonist activity (63.9 +/- 9.5 mV) was greater than pre-blast agonist activity (33.2 +/- 5.3 mV), F (2, 6) = 16.34; p < .01, and post-blast antagonist activity (27.2 +/- 6.0 mV) was greater than pre-blast (17.3 +/- 5.6 mV) or blast (15.1 +/- 6.0 mV) period antagonist activity, F (2, 6) = 8.43; p < .05.

During backward blasted movements, post-blast co-contraction was greater at the wrist regardless of the perturbation predictability than either the pre-blast or blast periods, F (2, 6) = 5.08; p < .05.

No reaction time (301 ms) or movement time (628 ms) differences were noted for backward blasted movements that were predictable as compared to those that were unpredictable. The analysis of constant error indicated that movements that were predictably backward blasted were performed with greater undershooting error (-3.47 mm) than those that were unpredictable (0.75 mm), F (1, 3) = 11.1, p < .05.

Summary of the between block analyses results

The analysis of the unperturbed movement data highlights that performers use a priori knowledge to differentially prepare movements. For example, in the predictable backward blast condition the performers increase elbow antagonism during the blast period while in the predictable forward blast and unpredictable blast conditions the movements are characterized by increases in wrist antagonist activity. Interestingly, a decrease in wrist activation for all conditions during the blast portions of the movements highlights a mechanism that uses this joint to dampen the perturbation's impact on the whole limb.

The analysis of forward blasted movements shows that when predictable, performers trend to account for the blast by reducing the elbow antagonist activity; a motor response that allows for the blast to be integrated into the reach. Conversely, the analysis of backward blasted movements indicated that when predictable, performers increase the amount of elbow antagonism. The similarity of elbow antagonist activity in the unperturbed backward blasted condition to that in the predictably backward blasted movements further highlights the influence of a priori knowledge on movement preparation.

General Discussion

Through the development and testing of a novel perturbation device, the present study sought to investigate the impact of actual velocity perturbations to the early portions of goal directed reaches and the control processes employed to reduce their impact on movement speed and accuracy. The results show that the compressed air successfully impacted the portions of goal directed reaches associated with the limb's peak acceleration. This was evidenced most saliently in the case of the forward blast, operating to alter the peak velocity achieved by the limb. That the effects can be attributed to the additional application of force in the direction of, or the opposite to, the moving limb at peak acceleration, rather than any auditory stimulus associated with the discharge of air is shown through the lack of any early trajectory differences attributable to the bi-directional blast. In all, the air compressor was demonstrated to be a useful tool for introducing an early perturbation to the limb.

Furthermore, the present results indicated that performers had the ability to accurately rectify the unexpected modifications to the trajectory created by the perturbations. In fact, movements made against perturbations were completed with greater accuracy than their unperturbed counterparts. Surprisingly, similar control processes were applied to rectify the impacts of the forward blast and the backward blasts. That is, at peak acceleration, when the compressed air was discharged, participants adopted an undiscriminating strategy to limit the hindering nature of potential backward air blasts. With a minimal time lag, this response successfully maintained movement acceleration while alleviating any spatial discrepancy generated by the backward blast. This strategy did not fully limit the forward blast from advancing the limb. However, because the forward blast advanced the limb in the intended direction of movement, participants were able to integrate the impact of the perturbation into the unfolding action. This integrated perturbation impact was rectified later in the trajectory. The kinematic analyses indicated that individuals modified their movements via a response designed to limit the negative outcomes of the worse case perturbation scenario. That is, early trajectory control worked to advance the limb to offset the movement hindering backward blast perturbation while leaving later control processes to prevent movement advancing perturbations from over-extending the limb (i.e., in the absence of visual confirmation of limb position and velocity, relatively high peak decelerations were noted for the forward and bi-directionally blasted movements). This type of control seems to be consistent with energy optimization principles of limb control (Elliott, Mendoza, Hansen, & Tremblay, 2004) and to operate through control of the dynamic properties of the limb movement.

The results of the small supplementary study, which measured the muscle activation magnitudes and patterns in response to the air compressor, further substantiate the idea that the control initiated in response to the perturbation is non-specific with a bias to offsetting the most detrimental of possible perturbations. When performing under a condition of a possible forward blast the individual initiated increased stability at the shoulder joint, while reducing co-contraction at the elbow to allow the potential movement advancement to be integrated into the planned trajectory. Conversely, the individual offered distal joint stability, at the elbow and wrist, when performing against a potential backward blast. However, when the individual was faced with either a potential forward or backward blast the control executed was congruent with the mode initiated in response to the predictable backward blast. In this way, the EMG data confirm the prepared mode of control favours alleviating the impact of the more hindering perturbations.

The current study differs from the majority of previous research on the processes of early online control of rapid goal-directed aiming movements in that participants in this study were required to perform actions against a physical perturbation rather than an illusory manipulation. This was done with the hope of alleviating some discrepancy concerning the mechanisms that operate when movements are made over a moving background. While some (Grierson & Elliott, under review; Proteau & Masson, 1997) have suggested that a moving background affects forward model control processes through a misperception of limb dynamics, Whitney, Westwood, and Goodale (2003) reported that the influence of background motion on reaching was not due to the visual representation of the hand speed or location. The results of the present study lend some support to both notions. The presence of non-specific counter-measures to the compressed air perturbation under full vision and no vision conditions suggest that visual information of the hand velocity and location is not necessary for early trajectory control. However, a lack of spatial differences in acquiring peak velocity in the presence of visual afference indicates that this information does attenuate these early control processes. It is not unreasonable to suppose that the early perturbation response acts to rapidly bring the limb under the supervision foveal vision, regardless of perturbation type. Presumably, following the acquisition of the limb by central vision, the sensorimotor system is better equipped for implementing the type of late, discrete adjustments associated with two-component models of limb control (Meyer et al, 1988; Woodworth, 1899). However, the ability of the individuals to rectify all spatial differences by the acquisition of peak deceleration regardless of the presence of visual information suggests that this afference is redundant to effective early control processes. The evident redundancy inherent to visual and proprioceptive information in guiding the early portion of reaches to a consistent location (maximum deceleration by the latest) maintains that "propriomotor" control is based on the attainment of a particular end posture. Seemingly, these findings provide the grounds to explore an amalgamation of equilibrium point and impulse-variability explanations of online movement control.

It was assumed in the introduction that moving background perturbations affected early anticipatory control through impacting the model's comparisons of expected sensory afference to actual afference; a comparison whose resultant is used to adjust the gain associated with modulating the expected reafference via efferent copies. However, the present findings suggest that responses to early movement perturbations do not require the full processing of response produced feedback in order to take effect. Rather, the results suggest that early control only requires that the sensorimotor system recognizes an expected-to-actual mismatch.

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Chapter 4

KINEMATIC ANALYSIS OF GOAL-DIRECTED AIMS MADE AGAINST EARLY AND LATE PERTURBATIONS: AN INVESTIGATION OF THE RELATIVE INFLUENCE OF TWO ONLINE CONTROL PROCESSES

Editorial Note: This manuscript has been submitted to the Human Movement Science and approval is pending.

Running Head: TWO ONLINE CONTROL PROCESSES

Kinematic analysis of goal-directed aims made against early and late perturbations: An investigation of the relative influence of two online control processes

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Abstract

Examination of goal directed movements has evidenced two processes of visually regulated online control: early trajectory control that operates to make movement adjustments on the basis of limb velocity comparisons to internally generated models of the expected limb velocity, and late trajectory control that uses allocentric information about the limb and target positions to make corrections in the latter movement portions. The results of experiments using illusory perturbations has indicated that the efforts exerted by the two systems have an additive influence on movement outcome, and has led to the conclusion that because they depend on different information they are relatively independent of one another. To expand the investigation into the independence of two control processes, 3 experiments were conducted in which actual perturbations to the aiming limb dynamics and the tasks demands were introduced. Compressed air expulsed through a stylus, in the direction of, or opposite to, that of the movement has been used to impact limb velocity and elicit evidence of early control, and manipulating target location has been effective in gleaning evidence of the discrete control associated with late trajectory evaluations of target and limb position. To investigate the relative influence of these two types of on-line control, following movement initiation, perturbations to the performer's limb, the environment or both were introduced while kinematic analyses of the performer's aiming movements were conducted. The results of the compressed air-only and moving target-only conditions replicated the previous evidence of early and late control, respectively. Interestingly, movement accuracy measures yielded an interactive effect of the two perturbations when presented in tandem. It was concluded that the perturbations prompted parallel operation of the two control processes.

PsycINFO classification: 2330

Keywords: movement; feedback; speed-accuracy; motor control

Article Outline

1. Introduction

Classic research on the accuracy of voluntary movement uncovered that speeded movements to targets are composed of at least two distinct components (Woodworth, 1899). The first component acts to transport the limb to the vicinity of the target while the second component, given the movement is made within the temporal constraints associated with visuomotor processing, uses visual information to bring the effector to rest on the target. These two components have been labeled the initial impulse and current control phase, respectively. Current versions of the two component model (e.g., Elliott, Hansen, Mendoza, & Tremblay, 2004; Meyer, Abrams, Kornblum, Wright & Smith, 1988) hold that, as the required distance or speed of a movement increases, the impulses necessary to produce the movement also increase (Schmidt, Zelaznik, Hawkins, Frank & Quinn, 1979). With this increase, greater noise in the neuromuscular system is generated such that the end-point variability associated with the initial impulse portion of the movement increases. Visual feedback from the limb is then utilized during the late trajectory to correct any errors associated with this variability. As such when the accuracy demands of the movement are high, movement trajectories are characterized by either an extended deceleration phase or second accelerations in the kinematic profile late in the movement. These late departures from acceleration-deceleration symmetry represent online adjustments designed to bring the limb onto the target. Presumably these corrections are based on visual feedback about the position of the limb relative to the target (Elliott, Helsen, & Chua, 2001; Woodworth, 1899).

Historically, feedback-driven control processes have been thought to operate late in goal-directed aiming movements while the initial impulse portion of the movement results from a preset and ballistic motor plan. However, recent examinations into the central tendency and trial-to-trial spatial variability at important kinematic events (peak acceleration, peak velocity, and peak deceleration) under various conditions of practice (Hansen, Tremblay, & Elliott, 2005) and feedback (Hansen, Elliott, & Tremblay, 2007; Khan, Franks, Elliott, Lawrence, Chua, Bernier, Hansen, & Weeks, 2006; Saunders & Knill, 2003) have indicated that the initial impulse may not be as stereotyped as once believed. Specifically, performers are able to use information regarding effector velocity (Grierson & Elliott, under review; Proteau & Masson, 1997) and direction (Hansen et al., 2007) to make very early corrections to movement trajectories.

While substantial evidence shows that discrete control is subserved by visual information concerning relative target and limb location late in the movement (see Elliott et al., 2001 for a review), the modifications associated with early trajectory control can be ascribed to comparisons made via an internally generated forward or predictive model of the movement. Forward models are produced through the integration of an efferent copy of the executed motor command with information regarding the current state of the performer. This model allows the processing system to generate a prediction of the sensory consequences of the movement such that errors in the forthcoming movement may be rapidly identified and corrected. Though the use of a forward model provides a basis for corrections that may be made in the absence of direct sensory afference, in order for the processing system to maintain confidence in its predictions it must compare its modeled estimations of sensory feedback against actual sensory feedback. Any expected-to-actual discrepancy that is determined from this comparison is then used to modulate an inverse model, which amends the movement based on the expected next state and the desired final state of the performer (Davidson & Wolpert, 2005; Desmurget & Grafton, 2000; Miall & Wolpert, 1996; see also von Holst, 1954). Thus, afferent manipulations that influence the perceived velocity or direction of the limb purportedly create a mismatch between the expected and actual sensory feedback and, as such, perturb the operation of the forward model online control process.

To determine to what extent the control of early and late portions of goal-directed movement is interactive, Grierson and Elliott (under review) had performers make reaches in which perturbations designed to influence the perceived position of the target and the perceived velocity of the moving effector were introduced. In the first of these experiments, the perceived position of the target that performers moved to was altered through the use of tails-in and tails-out Müller-Lyer figures (Elliott & Lee, 1995; Mendoza, Hansen, Glazebrook, Keetch & Elliott, 2005; Mendoza, Elliott, Meegan, Lyons & Welsh, 2006). In the cases in which the target structure was altered to a tails-in configuration, consistent with the perception that the to-be-attained position was closer, performers ended their movements after significantly less distance traveled than in those instances in which the target location was perturbed to a Müller-Lyer tails-out configuration. Although an early conditional difference was noted in the magnitude of peak acceleration (i.e., lower peak accelerations were achieved in the perturbed conditions compared to the control condition) that was subsequently realized at each kinematic event, the lack of any difference in the spatial locus of each kinematic event suggests that the illusion had its primary influence following peak deceleration. In the second experiment, as performers reached towards the target, the textural elements of the aiming surface were either translated in the direction of, or the direction opposite to, that of the movement. This moving background illusion has been effective in creating the perception that the effector is traveling at a lesser or greater velocity, respectively, than it actually is (Proteau & Masson, 1997). As such, performers produced greater undershooting error when moving against a background that moved in the opposite direction.

This finding is consistent with the idea that the individual prematurely slows the limb to counteract an over-evaluation of perceived limb velocity. Furthermore, movements made under these conditions were already affected by the perturbation at peak deceleration. While perturbing the background in the same direction as the movement did not produce endpoints of significantly greater amplitude, the trajectories of these movements were marked with a significant decrease in trial-to-trial spatial variability as early as peak velocity. In each case, the trajectory analysis of movements made against the translating backgrounds indicated that control began operating during the early portions of the reaches.

Grierson and Elliott's third experiment tested the relative influence of perturbations that elicit early and late control processes by introducing the Müller-Lyer and moving background perturbations in tandem. Interestingly, the analysis of constant error from this combined perturbation experiment yielded significant main effects for each of the perturbations, which replicated their independent influence. As well, no significant interaction between the two perturbations was evident. Based on Sternberg's (1969) additive factor logic, it was concluded that the perturbations affected two separate modes of online control.

Through the use of illusory perturbations, Grierson and Elliott (under review) were able to highlight the presence of two independently operating on-line control processes. Their results indicated that the impact of perturbing performer's perception of limb velocity affected the portion of trajectories preceding peak deceleration while the perturbations of target position affected the portion following peak deceleration. Of note is that the perturbations introduced in the aforementioned research were solely illusory in nature. That is, neither the target position nor the velocity of the limb was actually altered. Though evidently salient enough to affect the perceptual side of visuomotor processing, these perturbations should not be expected to have as large an impact on online control as would environmental perturbations that required actual motor recourse. In the three studies reported here actual perturbations to the effector velocity (Grierson & Elliott, under review) and the spatial location of the target (Heath, Hodges, Chua & Elliott, 1998) were introduced during goal-directed aiming movements. This was done in order to expand the investigation into the independence of early forward-modulated control and late-trajectory, feedback-driven control.

In Experiment 1, the perturbation was designed to create a mismatch between the expected and actual limb velocity. Although previous research has used moving background techniques to visually induce the perception of an unintended velocity (Grierson & Elliott, under review; Proteau & Masson, 1997), the effects of this illusion are confounded by the potential influence of veridically-processed proprioceptive information concerning limb velocity. In this experiment, individuals performed aiming movements while holding a custom engineered stylus. This stylus was designed to discharge a 3.45N blast of compressed air during the early portions of the movement (at peak acceleration) either in the direction of the movement, the direction opposite the movement, simultaneously in both directions, or not at all. This compressed air perturbation has been shown effective in altering the magnitude of movement velocities and has been used to elicit evidence of early sensorimotor control processes operating to rectify these spatial and temporal disruptions (Grierson & Elliott, under review). Experiment 2 was designed to affect the late trajectory control associated with error reduction based on a comparison of relative effector and target position (e.g., Woodworth, 1899). Performers made reach-and-point movements away from the body (25 cm) to a target represented by the intersection of two lines arranged in a T-shape. Following movement initiation, the length of the target shaft was either extended such that the intersection was further away (27 cm), reduced such that the intersection was closer (23 cm), or remained unperturbed. The hypothesis was that target relocation would manifest discrete corrections late in the movement trajectory (Heath et al., 1998). Through a combination of the perturbations presented in Experiment 1 and Experiment 2, Experiment 3 examined the relative influence of the two proposed forms of online control on movement trajectories and accuracy outcomes. This was done in order to highlight any interaction or co-variation that exists between the proposed control processes. Based on the results of the combined Müller-Lyer illusion and moving-background perturbation studies, we expected the two perturbations to have independent and additive effects on movement accuracy.

2. General Apparatus and Procedure

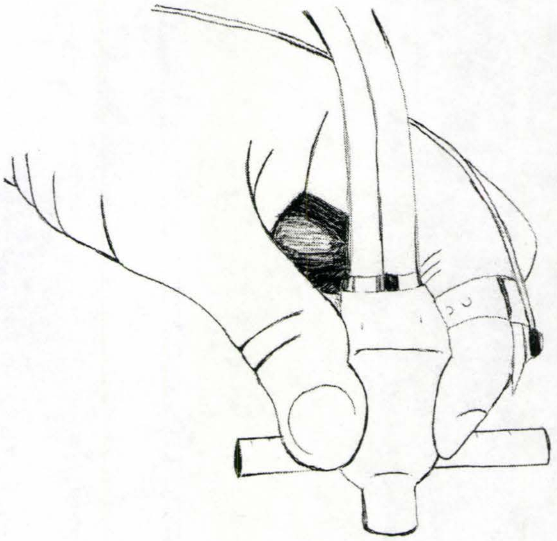

Figure 1. Depiction of the compressed air stylus.

For each of the three current experiments performers sat comfortably at a table on which rested a flat display screen. This display screen served as the aiming surface and was mounted with a "home position" microswitch that performers were instructed to orient at the midline of their body. The beginning of each trial began with the performers depressing this microswitch with a handheld custom stylus (Fig. 1). The display screen presented an intersection of two lines; a long (25 cm) shaft line, which began at the location where the microswitch lay flush with the display screen and extended away from the performer's body, and a smaller (10 cm) line. The smaller line was bisected by the shaft line at a right angle such that the two formed a T-shaped configuration (Fig. 2). The performers were instructed to make an accurate as possible movement from the home position to the intersection of the two lines. Following a short (1000ms) delay, the performers were cued to initiate their planned movements by an 800 Hz auditory tone. Upon releasing the microswitch at movement initiation, the target aiming environment or the progress of the movement could be perturbed according to the procedures outlined in the individual experimental methods sections. In all cases, the performers were notified of the potential for perturbation and were instructed to complete their movements as accurately as possible, regardless of any perturbation.

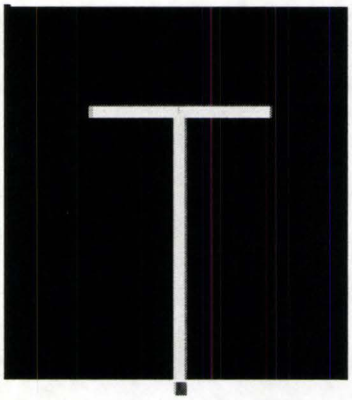

Figure 2. Depiction of control target figure in Experiments 1-3. The small square represents the microswitch home position.

Throughout the course of all experiments the performers wore liquid crystal goggles (Translucent Technologies; see Milgram, 1987). In order to ensure that outcome accuracy differences could not be attributed to speed-accuracy trade-offs, these goggles served to occlude the performers' vision 500 ms following movement initiation. Performers were notified of this imminent occlusion and were instructed to complete their movements while vision was available (see Mendoza et al., 2006). Upon completing the movement, participants kept their pointing finger on their acquired target until the display screen cleared and the goggles returned vision. They then replaced their finger on the home position and prepared for the next trial.

Performers wore an infrared light emitting diode (IRED) on the index finger of their aiming hand. For each trial, just prior to the sounding of the auditory tone, an Optotrak-3020 digital recording camera was triggered. The camera recorded the spatial location of the IRED for 2 seconds at 500 Hz. The spatial position data collected by the Optotrak-3020 system were filtered with an 8 Hz dual-pass Butterworth filter and run through custom software which calculated the displacement of the limb in the primary direction of movement. In addition to differentiating and double differentiating the displacement to acquire velocity and acceleration, this software also discerned the magnitude of the peak acceleration (PA), peak velocity (PV), and peak deceleration (PD) for each reaching movement as well as the spatial location of these kinematic events and the end position (END) of the movement. The Optotrak frames in which the limb velocity rose above or fell below 30mm/s, and remained as such for 70 ms identified the start and the end of the movement. Values for any dependent variable that fell more than 2.5 standard deviation units from the mean were considered outliers and were removed from the data sets prior to analysis.

The microswitch, display screen, stylus, liquid crystal goggles, Optotrak-3020 trigger, speakers, and the randomization of experimental trials were all controlled by a computer that operated E-Prime software. The Optotrak-3020 operation and kinematic data acquisition was performed by a second, independent computer.

The dependent measures for all experiments were reaction time (RT), movement time (MT), constant error (CE), variable error (VE), peak acceleration (PA), peak velocity (PV), peak deceleration (PD), time to peak acceleration (ttPA), time to peak velocity (ttPV), and time to peak deceleration (ttPD), as well as the amplitude displacement and within subject trial-to-trial spatial variability at PA, PV, and PD. The analysis of amplitude displacement and spatial variability at kinematic landmarks serves to indicate the effectiveness of the early movement perturbations and highlights the control processes offered to offset these perturbations early in the movement trajectory (Khan & Franks, 2003; Khan, Franks, Elliott, Lawrence, Chua, Bernier, Hansen, & Weeks, 2006).

3. Experiment 1

3.1 Method

Participants. The participants were 20 (10 female; 10 male) right-handed members of the McMaster University community. They had normal or corrected-to-normal vision and were naïve to the purpose of the study. Prior to participating, all individuals gave informed consent according to the guidelines of the McMaster University President's Committee on Ethical Consideration in Human Experimentation.

Procedure. Participants performed a series of 90 trials in which they were instructed to make rapid, accurate pointing movements from the home position microswitch to a resting target position. All reaches were performed while holding a handheld stylus. This stylus was mounted to an air compressor (Campbell Hausfeld, DK755100A5 0605, South Pasadena, California) and engineered with two small polyethylene tubes for the systematic expulsion of air blasts in both the direction of movement and the direction opposite to the movement (Fig. 1). Eighty milliseconds following movement initiation the stylus either discharged an air blast opposite the direction of the reach (forward blast), discharged an air blast in the same direction as the reach (backward blast), simultaneously discharged air blasts in both directions (bidirectional blast), or discharged no air blast (unperturbed). The blast was timed such that it occurred at the approximate time of the movement's peak acceleration in the primary direction of movement. The air was released from the compressor at 100 psi and represented a 3.45 N perturbation to the movements. The order of the compressed air perturbations was randomized with the majority of the movements remaining unperturbed (forward blast = .11, backward blast = .11, bidirectional blast = .11, unperturbed = .67).

With the index finger of their right hand participants depressed a small microswitch that was mounted to the stylus throughout the course of the study. This microswitch served to fix the handgrip used by participants across trials as well as provide a safeguard deactivation mechanism for the immediate cancellation of air expulsion.

Analysis. Each of the primary performance and kinematic variables was subjected to a one-way repeated measures analysis of variance (ANOVA) to determine if any trajectory or accuracy differences could be attributed to the impact of the compressed air perturbation and/or processes related to the perception of altered limb velocity. In order to determine how movement bias and variability changes as the movement unfolds mean movement amplitude and spatial variability were examined via a 4 condition (forward blast, backward blast, bidirectional blast, unperturbed) by 4 kinematic marker (PA, PV, PD, END) two factor repeated measures analysis of variance. The nature of any significant difference was determined via Tukey's HSD post hoc comparisons ($p < .05$).

3.2 Results and Discussion

Performance Outcomes. The results of the CE analysis revealed that end point accuracy was biased by the compressed air perturbation, F (3, 57) = 5.50, $p < .01$. Post hoc analysis revealed significantly greater negative constant error for the unperturbed trials as compared to the forward blasted, backward blasted and bi-directionally blasted trials (Fig. 3). The latter three conditions did not differ. No significant variable error differences were noted between any of the conditions.

No significant differences were noted in reaction time (grand mean = 454 ms) between any of the conditions. The movement time analysis yielded a significant difference, F (3, 57) = 22.62, $p < .0001$. Movements made against the backward blast (670ms) took longer than those that were forward blasted (609ms), bidirectionally blasted (609ms), or unperturbed (608ms). There was no difference between the later three conditions. This movement time effect is consistent with the notion that the backward blast hindered forward progress.

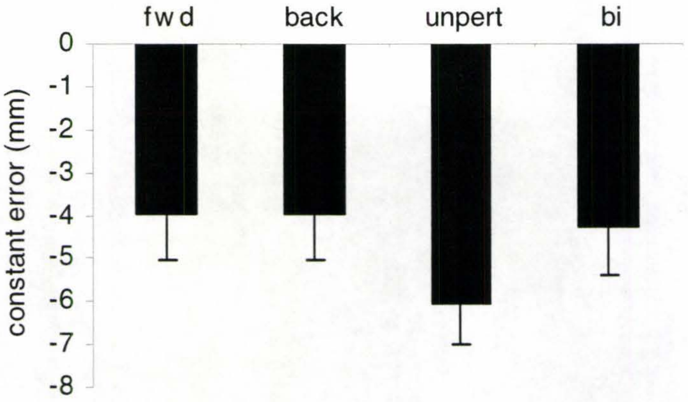

Figure 3. Constant Error (mm) plotted as a function of the compressed air condition, forward blast (fwd), backward blast (back), unperturbed (unpert), and bidirectionally blasted (bi) (Experiment 1).

Magnitude of the Kinematic Events. Analysis of the magnitudes of kinematic events elicited significant differences between conditions. Performers reached higher PA in the forward blast condition relative to the backward blast, bidirectional blast, and unperturbed conditions, F (3, 57) = 14.06, p < .0001 (Fig. 4), which did not differ from one another. In a similar manner, forward blasted movements yielded significantly higher PVs, F (3, 57) = 33.50, p < .0001 (means: forward blast = 2.34 m/s, backward blast = 1.93 m/s, bidirectional blasts = 1.96 m/s, unperturbed = 1.92 m/s), and PDs, F (3, 57) = 15.76, p < .0001, than the other three conditions (Fig. 5). The increases in peak movement acceleration, velocity, and deceleration may be attributed to the extra impulse associated with the compressed air. That no differences were noted for the hindering backward blast suggests that online control processes offset the impact of the perturbation. Post hoc analysis of the magnitude of peak deceleration effect revealed greater deceleration for the backward blast condition relative to the unperturbed condition Investigations into the spatial location and temporal onset of peak acceleration, velocity, and deceleration serves to further clarify the nature of this process. Importantly, it seems the air perturbation device is effective in influencing the velocity of the moving limb.

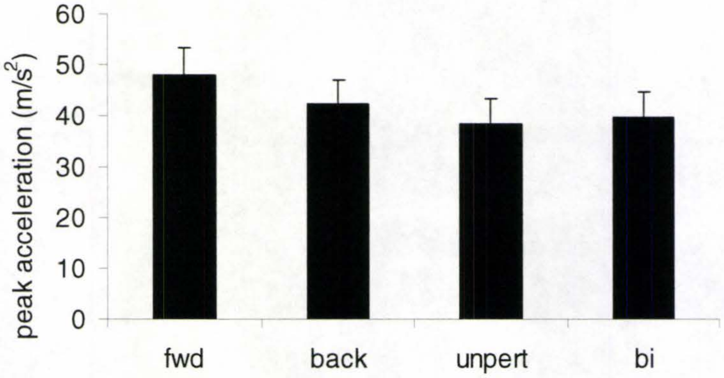

Figure 4. Peak Acceleration (m/s^2) plotted as a function of the compressed air condition, forward blast (fwd), backward blast (back), unperturbed (unpert), and bidirectionally blasted (bi) (Experiment 1).

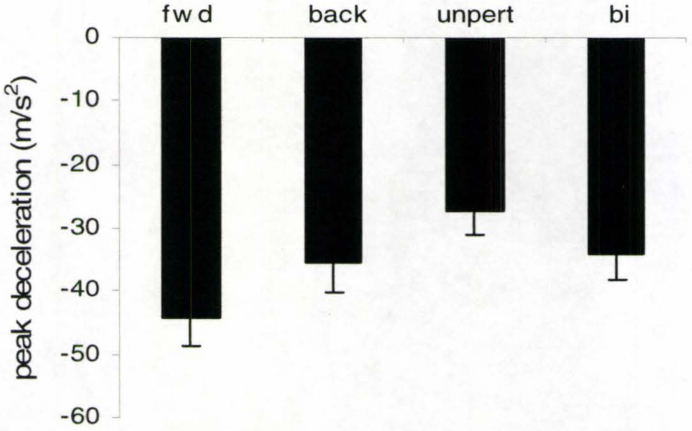

Figure 5. Peak Deceleration (m/s^2) plotted as a function of the compressed air condition, forward blast (fwd), backward blast (back), unperturbed (unpert), and bidirectionally blasted (bi) (Experiment 1).

Timing of Kinematic Events. A significant difference between conditions was noted in the time to peak acceleration (ttPA), F(3, 57) = 8.09, p , .001, in which forward and backward blasted movements took longer to reach PA than bidirectionally blasted and unperturbed movements

(Fig. 6). The investigation into ttPV also revealed a significant difference, F (3, 57) = 8.04, p < .001 (means: forward blast = 245 ms, backward blast = 302 ms, bidirectional blasts = 275 ms, unperturbed = 255 ms). Movements made against backward blasts took longer to reach peak velocity than forward blasted or unperturbed movements. Bidirectionally blasted movements were intermediate and not different from the other three conditions. The forward blasted movements reached PD after significantly less time than the backward blasted, bidirectionally blasted, or unperturbed movements, F (3, 57) = 8.55, p < .0001 (means: forward blast = 395 ms, backward blast = 469 ms, bidirectional blasts = 471 ms, unperturbed = 473 ms).

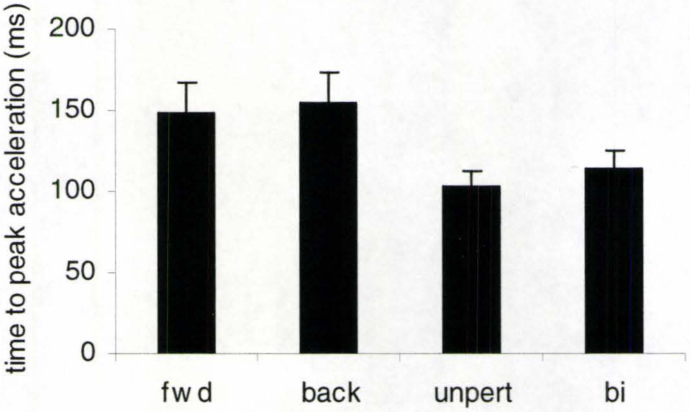

Figure 6. Time to Peak Acceleration (ms) plotted as a function of the compressed air condition, forward blast (fwd), backward blast (back), unperturbed (unpert), and bidirectionally blasted (bi) (Experiment 1).

Mean Displacement of the Kinematic Events. A significant main effect was seen for the displacement of the kinematic landmarks, F (3, 57) = 1438.5, p < .01. The amplitude displacement at PA (grand mean = 18.8 mm) was significantly less than the amplitude displacement at PV (grand mean= 108 mm), which was less than that at PD (grand mean = 213 mm), which was less than that of the end position of the movement (grand mean = 250 mm).

This is a typical effect indicative of a movement that progresses from the home position to the location of the target with no reversals of direction. The amplitude displacement analysis also revealed a significant interaction between kinematic event and perturbation condition, F (9, 171) = 225.5, p < .0001 (Fig. 7). In light of the aforementioned main effect, the nature of the differences inherent to the interaction is best described through examination of the spatial displacements at each of the kinematic events. Post hoc analysis of the limb's amplitude displacement showed that while forward and backward blasted movements reached peak acceleration after significantly more distance traveled (means: forward blast = 27.6 mm, backward blast = 25.8 mm, bidirectional blasts = 12.2, unperturbed = 9.5 mm) and peak deceleration after significantly less distance traveled (means: forward blast = 205 mm, backward blast = 203 mm, bidirectional blasts = 224 mm, unperturbed = 220 mm) than the bidirectionally blasted and unperturbed movements, no differences were present between any of the conditions in the spatial displacement of the limb at peak velocity.

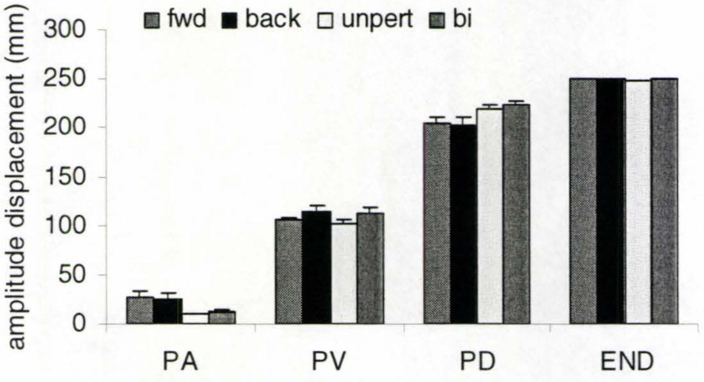

Figure 7. Mean displacement (mm) of peak acceleration (PA), peak velocity (PV), peak deceleration (PD), and the end position of the movement (END) in the primary direction of movement by compressed air condition, forward blast (fwd), backward blast (back), unperturbed (unpert), and bidirectionally blasted (bi) (Experiment 1).

Spatial Variability of the Kinematic Events. Analysis of the spatial variability at each kinematic landmark also produced a significant main effects for kinematic event, F (3, 57) = 31.53, p < .0001, with the variability increasing significantly from PA to PD before dropping to its lowest level at the end position of the movement, and for perturbation condition, F (3,57) = 9.49, p < .0001, which displayed increased spatial variability in movements made against the backward blast perturbation. These main effects were superseded by a kinematic event by perturbation condition interaction, F (9, 171) = 2.44, p < .05. Post hoc analysis of this interaction indicates that while unperturbed movements significantly increase in variability from PA to PV to PD, forward and backward blasted movements did not significantly increase in variability between PA and PV before increasing to PD, and bidirectionally blasted movements did not show any differences in variability from PA to PV to PD (Fig. 8). For all conditions following PD spatial variability of the movements decreased significantly as the limb approached the end of the movement (this finding indicates that the participants exercised online control when the limb had reached the vicinity of the target).

In all these results substantiate the idea that early trajectory control is executed in response to alterations to the limb's dynamic characteristics. This control may be subserved by visual and/or proprioceptive information in combination with information about the expected sensory consequences.

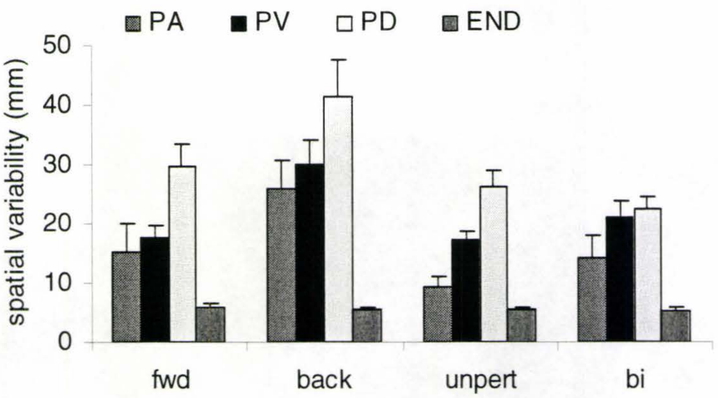

Figure 8. Mean spatial variability (mm) of peak acceleration (PA), peak velocity (PV), peak deceleration (PD), and the end position of the movement (END) in the primary direction of movement by compressed air condition, forward blast (fwd), backward blast (back), unperturbed (unpert), and bidirectionally blasted (bi) (Experiment 1).

Overall. In Experiment 1, the time to peak acceleration means for the unperturbed (103 ms) and bi-directionally (114 ms) blasted movements were temporally located within the period of time in which air was released from the compressor (100 ms air burst at 80 ms following movement initiation). Movements that were exposed to a forward blast during this time reached a greater magnitude of peak acceleration than the other three conditions. Furthermore, no significant differences were elicited between the bi-directionally blasted and the unperturbed movements indicating that effects found in the uni-directional perturbation conditions cannot be attributable to the sound of the air expulsion. In summary, the air compressor perturbation was effective in impacting the peak acceleratory portions of the movement trajectories.

The results of the experiment provide evidence of early online control. If there is no early trajectory online control process concerned with mediating the limb through evaluation of velocity it is expected that the full impact of the perturbation would be integrated into the limb's trajectory characteristics; at least until it is decelerating under the supervision of feedback-mediated control. While the magnitude increase in peak acceleration when the forward blast operates on the limb suggests that the additional force serves to advance the limb, that there are no differences in the amplitude displacement of, or time to, peak velocity suggests that the magnitude increase of this kinematic event is residual to the full impact of the forward blast. That is, in the time following peak acceleration and preceding peak velocity, some manner of control begins to offset the forward blast impact. Otherwise, a limb fully obliged to the effects of increased velocity would be expected to cover a greater amplitude by its peak or to do so in less total time. The increased magnitude of peak deceleration and the reduced time to, and amplitude displacement at peak deceleration highlight the efforts of late trajectory control processes, operating to rectify the effects of the perturbation impact and the distance remaining between the limb and target location.

Moreover, trajectories of movements made against the backward blast show that these movements reached a typical magnitude of peak acceleration but took longer to do so and did so after greater amplitude displacement. Though this indicates that the perturbation has a hindering influence on the early limb trajectory, only the increased time to peak velocity effect manifests the presence of this impact by the onset of the kinematic event. Rather than exhibit a reduction in peak velocity or distance traveled at this event, the velocity of these movements is achieved after the same displacement as all other movements and peak velocity is only less than forward blasted movements. Perhaps because the backward blast operates against the inertial properties of the moving limb it is less effective than its forward blast counterpart in influencing limb dynamics. However, the aforementioned temporal and spatial effects at peak acceleration cast doubt on this explanation. In contrast, this finding suggests an early control process operates to accelerate the limb such that it can overcome the backward blast and maintain course. As a consequence of this additional force output, the limb manifests no reduction in peak velocity.

Furthermore, that the backward blast condition exhibited greater deceleration relative to the unperturbed condition substantiates that the limb requires greater impulse to overcome the backward blast to maintain course and, as such, requires greater deceleration as the limb nears the target.

Furthermore, all perturbed movements (forward, backward, and bidirectionally blasted) exhibited significantly lower constant error values. While in the case of the forward blast an unsupervised movement may show reduced undershooting error as the result of the perturbation, attributing the movement outcomes solely to the impact of the air compressor would do little to account for the constant error reductions seen for movements made against backward or bidirectional blasts. This finding replicates previous work from our laboratory (Grierson & Elliott; under review) and strongly supports feedback based descriptions of the control of voluntary movement

Two aspects of the aforementioned results are particularly noteworthy. First, the motor response to both the forward and backward perturbations represents an increase in limb velocity. Though the forward blasted movements seem to temper some of this increase, the higher peak decelerations suggest that the majority of the speed increase is managed via feedback-based control following peak velocity. Secondly, regardless of perturbation direction, the control processes are successful in maintaining a constant location for the achievement of peak velocity. This finding, which is presented as part of the results of Experiment 1 and Experiment 3 in this paper, was also revealed in a preliminary study investigating the validity of the compressed air device as a perturbation tool (Grierson & Elliott, under review). Taken together these findings evidence a control process that operates against either type of air blast with the primary concern of moving the limb to a pre-set location for the initiation of limb deceleration.

4. Experiment 2

4.1 Method

Participants. The participants were the same 20 (10 female; 10 male) right-handed members of the McMaster University community tested in Experiment 1. Participants performed Experiment 1 and Experiment 2 in a counterbalanced fashion. They had normal or corrected-to-normal vision and were naïve to the purpose of the study. Prior to participating, all individuals gave informed consent according to the guidelines of the McMaster University President's Committee on Ethical Consideration in Human Experimentation.

Procedure. Participants performed a series of 90 trials in which they were instructed to make rapid, accurate pointing movements from a home position to a target position. The apparatus and recording techniques for Experiment 2 were identical to those of Experiment 1. At the beginning of each trial, the target that the participants moved to was presented on the display screen (Fig. 2). Participants prepared an accurate-as-possible movement to this target position and, following a go signal, executed this movement. Immediately, upon the initiation of the movement the target translated closer to the participants (23 cm shaft length), translated further away from the performer (27 cm shaft length) or remained unperturbed (25 cm shaft length). Performers were notified that the target location may or may not change and were instructed to complete their movement as accurately as possible regardless of any perturbation. The order of the perturbations was randomized with the majority of the trials remaining unperturbed (short = .17, long = .17, unperturbed = .66).

Analysis. Each of the primary performance and kinematic variables was subjected to a one-way repeated measures analysis of variance (ANOVA) to determine if any trajectory or accuracy differences can be attributed to the impact of the moving target perturbation. In order to determine how movement bias and variability changes as the movement unfolds mean movement amplitude and spatial variability were examined via a 3 condition (short, unperturbed, long) by 4 kinematic marker (PA, PV, PD, END) two factor repeated measures analysis of variance. The nature of any significant difference was determined via Tukey's HSD post hoc comparisons ($p < .05$).

4.2 Results and Discussion

Performance Outcomes. The CE analysis revealed significantly greater undershooting when the target structure became longer, $F(2, 38) = 7.21$, $p < .01$, than when it became shorter or remained unperturbed (Fig. 9). The moving target perturbation is designed to impact control processes associated with the evaluation of the relative limb and target position late in the movement trajectory; however, in light of any constant error deviation when the target becomes shorter it is necessary to examine the kinematic magnitudes, and the spatial characteristics of the early movement trajectories in order to appropriately localize the influence of the perturbation within the trajectory. The variable error analysis yielded no significant differences.

The analysis of the temporal measures showed a significant difference between the conditions for MT, F (2, 28) = 37.87, $p < .001$, with movements made to the long target (646 ms) taking significantly longer than those made to the unperturbed target (612 ms) which took significantly longer than those made to the short target (586 ms). This MT difference can be accounted for by the respective increase and decrease in movement distance created by the long and short target perturbations. No RT differences were noted between conditions (grand mean = 310 ms).

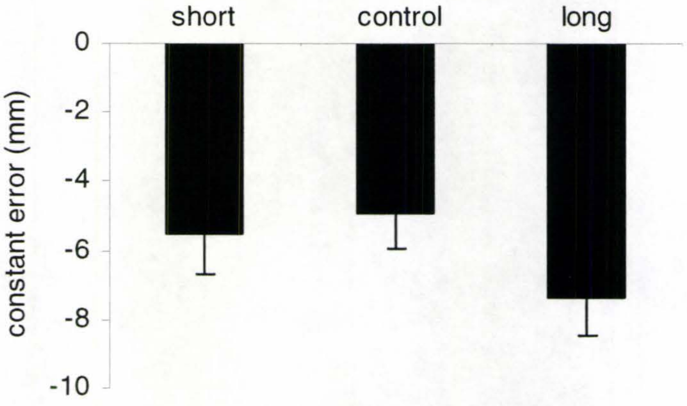

Figure 9. Constant Error (mm) plotted as a function of the moving target condition (Experiment 2).

Magnitude of the Kinematic Events. No significant differences between conditions were revealed in the magnitudes of PA (grand mean = 45 m/s^2), PV (grand mean = 1.99 m/s), or PD (grand mean = -29 m/s^2).

Timing of Kinematic Events. Although the analysis of ttPA (grand mean = 107 ms) and ttPV (grand mean = 254 ms) revealed no significant differences, it indicated that the movements made to the short target reached peak deceleration earlier than movements made to the long target, F

(2, 38) = 8.57, p< .001, with movements to the unperturbed target reaching PD at an intermediate, but not significantly different, time (Fig. 10).

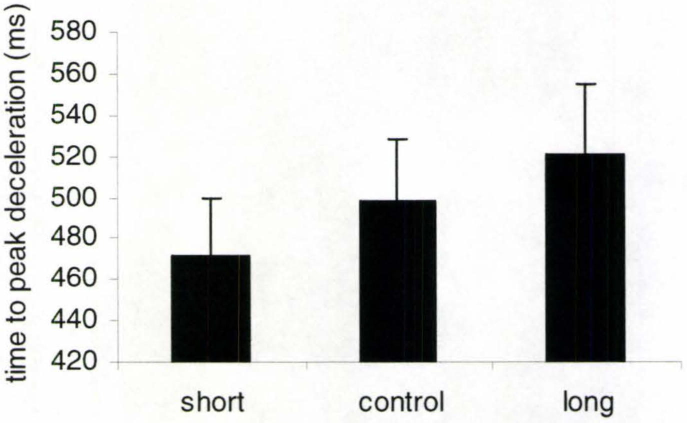

Figure 10. Time to Peak Deceleration (ms) plotted as a function of the moving target condition (Experiment 2).

Mean Displacement of the Kinematic Events. Analysis of the amplitude displacement of the limb at PA, PV, PD, and the End of the movement revealed main effects for kinematic marker, F (3, 57) = 1712.57, p < .01, and target condition, F (2, 38) = 98.51, p < .001, as well as a kinematic marker by target condition interaction, F (6, 114) = 42.49, p < .001. Post hoc analysis of the interaction revealed that PD is achieved after less distance traveled when the movement is made to a short target than when its made to an unperturbed target, and that movements made to an unperturbed target reach PD after less distance traveled than when they are made to the long target (Fig. 11). This finding, coupled with the results of the magnitude of kinematic events and the timing of kinematic events analyses suggests that, rather than depending on late trajectory (i.e. following peak deceleration) information concerning the relative limb and target positions, the operating control process begins to attenuate the movement following peak velocity.

However, it is likely that both the target and limb are foveated as early as PV, such that the early movement modification may still be attributed to allocentrically-derived control. Furthermore, it should be noted that the post hoc analysis indicated that the amplitude displacement at the end of the movement was greater for the long target (268 mm) than the unperturbed target (250 mm) that was greater than the short target (229 mm). Importantly, this indicates that movements were executed differently despite the lack of constant error differences between the short target and unperturbed conditions.

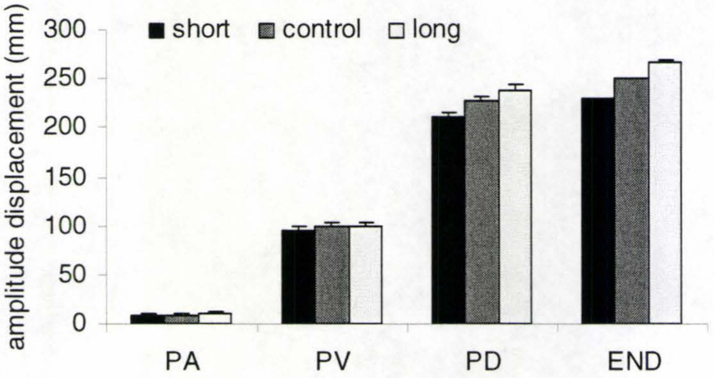

Figure 11. Mean displacement (mm) of peak acceleration (PA), peak velocity (PV), peak deceleration (PD), and the end position of the movement (END) in the primary direction of movement by moving target condition (Experiment 2).

Spatial Variability of the Kinematic Events. The analysis of trial-to-trial within subject spatial variability revealed a main effect for kinematic marker, F (3, 57) = 24.68, p < .001, a main effect for target perturbation condition, F (2, 38) = 6.26, p < .01, as well as a kinematic marker by target perturbation interaction, F (6, 114) = 5.69, p < .001 (Fig. 12). As displayed in Figure 12, the movement variability for the unperturbed and long target conditions increased systematically from PA to PV to PD before significantly decreasing towards the end of the movement. In the short target condition, although spatial variability increased from PA to PV, following PV it did not increase as it progressed to PD. For each condition, there was a significant reduction in variability between PD and the end of the movement.

The moving target perturbations were designed to influence the late trajectory control associated with two-component models (e.g., Woodworth, 1899), and the analysis of amplitude displacement and spatial variability at kinematic events within the trajectory indicate that these perturbations begin to elicit differences in control following peak velocity. This finding is in concert with earlier work that used visual illusions to perturb the perceived location of target position (Elliott, Binsted, & Heath, 1999; Grierson & Elliott, under review; Mendoza et al., 2006).

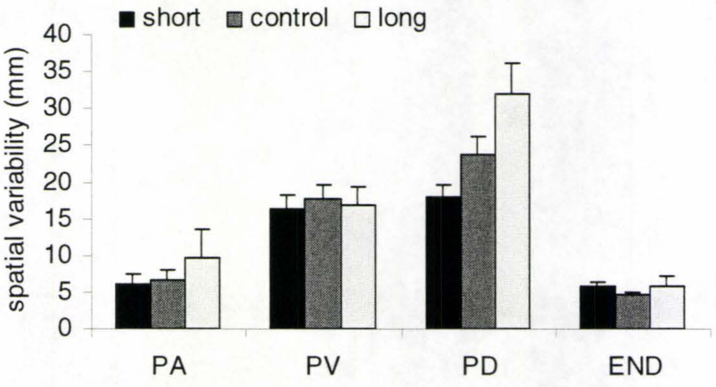

Figure 12. Mean spatial variability (mm) of peak acceleration (PA), peak velocity (PV), peak deceleration (PD), and the end position of the movement (END) in the primary direction of movement by moving target condition (Experiment 2).

Overall. The results of Experiment 2 indicated that the moving target perturbation impacts the late trajectory control associated with classic two-component models of goal-directed aiming (e.g., Woodworth, 1899). Although, the target was perturbed upon movement initiation, no differences were yielded between conditions for any of the amplitude displacement, time to, or magnitude measures at either peak acceleration or peak velocity. Trajectory differences did not become apparent between conditions until peak deceleration. That is, movements made to the short target traveled less distance and took less time to reach peak deceleration than unperturbed movements, while long target movements traveled more distance and took more time to reach peak deceleration than unperturbed movements. Furthermore, the trajectory endpoints also highlighted the reduced and increased spatial displacements of movements made to the short and long targets, respectively. These differences indicate that the altered amplitude demands of the new target positions were appropriately managed by control processes concerned with the visuomotor information garnered late in the trajectory. The increased undershooting for the long target movements indicates that this corrective process was not completely successful.

5. Experiment 3

5.1 Method

Participants. The participants were the same 20 (10 female; 10 male) right-handed members of the McMaster University community tested in Experiment 1 and Experiment 2. They had normal or corrected-to-normal vision and were naïve to the purpose of the study. Prior to participating, all individuals gave informed consent according to the guidelines of the McMaster University President's Committee on Ethical Consideration in Human Experimentation.

Procedure. Participants performed a series of 120 trials in which they were instructed to make rapid, accurate pointing movements from a resting home position to a resting target position. The apparatus and recording techniques for Experiment 3 were identical to those of Experiments 1 and 2. At the beginning of each trial, the T-shaped target that the participants moved to was presented on the display screen (Fig. 2). Participants prepared an accurate-as-possible movement to this target position and following a go signal executed this movement. Upon the initiation of the movement the initial target was translated to a location closer to the performer (23 cm shaft length), translated to location further away from the performer (27 cm shaft length) or remained unperturbed (25 cm shaft length). Concurrently, at eighty milliseconds following movement initiation the compressed air stylus was engineered to discharge an air blast opposite the direction of movement (forward blast), discharge an air blast in the same direction as the movement (backward blast), discharge simultaneous air blasts in both directions (bidirectional blast) or discharge no air (unperturbed). Participants were notified that the target display may change and/or the stylus may discharge air and were instructed to complete their movement as accurately as possible regardless of any perturbation. The order of the perturbations was randomized with equal probability of each potential moving target-air compressor perturbation combination (i.e., 3 target conditions X 4 air blast conditions X 10 trials).

Analysis. Each performance and kinematic variable was subjected to a 3 target condition (short, control, long) X 4 compressed air condition (forward blast, backward blast, bidirectional blast, no blast) repeated measures analysis of variance. As in Experiments 1 and 2, for mean displacement and spatial variability, kinematic marker was also included as a 4-level independent variable (PA, PV, PD, END). Significant differences involving more than two means were examined using Tukey's HSD post hoc comparisons ($p < .05$).

5.2 Results and Discussion

Performance Outcomes. The CE analysis revealed a main effect for the moving target manipulation, F (2, 38) = 19.75, $p < .001$, in which short target movements overshot the target with greater error than unperturbed movements which undershot the target with less error than long target movements (means: short target = 4.62 mm, unperturbed target = -3.39 mm, long target = -9.41). A significant compressed air perturbation by moving target perturbation interaction was also elicited, F (6, 114) = 4.62, $p < .001$. Post hoc analysis of this interaction indicated that unperturbed movements made to the shortened target were made with significantly greater overshooting error than those made against the backward blast, with the forward and bi-directionally blasted movements producing intermediate constant errors. For unperturbed targets, there was no difference between compressed air conditions. The long target was undershot with greater constant error when the movement was unperturbed as compared to when it was blasted in either the forward or backward direction (Fig. 13). The variable error analysis yielded a main effect for target perturbation, F (2, 38) = 4.92, $p < .05$, in which short target movements (7.26 mm) were more variable than movements to unperturbed targets (5.62 mm). Variable error of long target (6.82 mm) movements was intermediate.

The analysis of movement time revealed independent main effects for compressed air condition, F (3, 57) = 25.46, $p < .001$, and target perturbation condition, F (2, 38) = 29.96, $p < .001$. Post hoc analyses of the compressed air effect indicated that backward blasted movements

(708 ms) took longer to complete than forward blasted movements (678 ms), that forward blasted movements took longer than unperturbed movements (658 ms), and that bi-directionally blasted movements (668 ms) took an intermediate but not significantly different length of time to forward blasted and unperturbed movements. Post hoc analysis of the target perturbation effect revealed that long target movements took longer to complete than short target or unperturbed target movements. No reaction time (grand mean = 305 ms) differences were noted between any of the conditions.

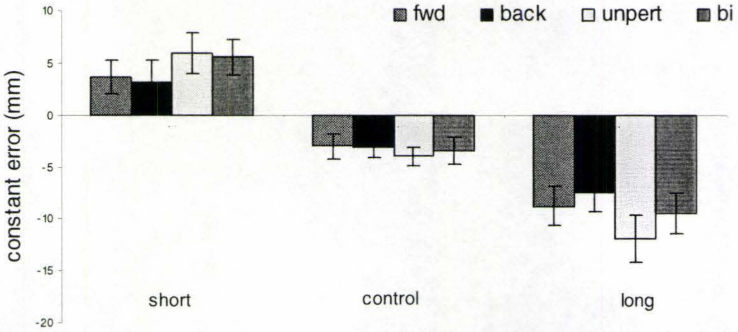

Figure 13. Constant Error (mm) plotted for the compressed air condition, forward blast (fwd), backward blast (back), unperturbed (unpert), and bidirectionally blasted (bi), by the moving target condition (Experiment 3).

Magnitude of the Kinematic Events. Similarly to the results of Experiment 1, analysis of the magnitudes of kinematic events elicited significant differences between conditions. Performers reached higher PA in the forward blast condition relative to the backward blast, bidirectional blast, and unperturbed conditions, F (3, 57) = 11.26, $p < .0001$(means: forward blast = 48 m/s^2, backward blast = 44 m/s^2, bidirectional blasts = 42 m/s^2, unperturbed = 42 m/s^2), which did not differ from one another. In the same manner, forward blasted movements yielded significantly higher PVs, F (3, 57) = 44.50, $p < .0001$ (means: forward blast = 2.26 m/s, backward blast = 1.86

m/s, bidirectional blasts = 1.91 m/s, unperturbed = 1.90 m/s), and PD, F (3, 57) = 12.29, $p < .0001$ (means: forward blast = -39 m/s^2, backward blast = -35 m/s^2, bidirectional blasts = -32 m/s^2, unperturbed = -31 m/s^2). The increases in peak acceleration, velocity, and deceleration for forward blasted movements may be attributed to the advancing effects of the compressed perturbation and the lack of differences for the backward blast suggests that online control processes offset the perturbation's hindering impact. Importantly, the compressed air perturbation successfully influences dynamic properties of the moving limb.

Timing of the Kinematic Events. The analysis of ttPA revealed a significant main effect for compressed air perturbation condition, F (3, 57) = 5.61, $p< .01$, in which forward blasted movements took longer to reach peak acceleration than bidirectionally-blasted or unperturbed movements. Movements that were backward blasted did not differ significantly from those that were forward blasted or unperturbed, but reached peak acceleration after more elapsed time than bi-directionally blasted movements (Fig. 14).

An additional main effect was elicited for target perturbation condition, F (2, 38) = 3.65, $p < .05$. Post hoc analysis of this effect indicated that movements made to the long target took more time to reach peak acceleration than movements made to the unperturbed target. The time to peak acceleration to short targets was intermediate though not significantly different from unperturbed or long target movements.

The analysis of ttPV also revealed a significant main effect for compressed air condition, F (3, 57) = 13.92, $p< .001$. Movements made against the backward blast (319 ms) reached peak velocity after significantly more time than unperturbed (289 ms) or bi-directionally (285 ms) blasted movements. Forward blasted movements (262 ms) reached peak velocity sooner than unperturbed movements, but were not different than movements that were bi-directionally blasted. These differences highlight the respective advancing and hindering impacts of the forward and backward blast perturbations.

A significant compressed air perturbation main effect revealed that movements made against the forward blast also reached ttPD sooner than the other blast conditions, F (3, 57) = 16.25, p < .001 (means: forward blast = 438 ms, backward blast = 520 ms, bidirectional blasts = 533 ms, unperturbed = 529 ms).

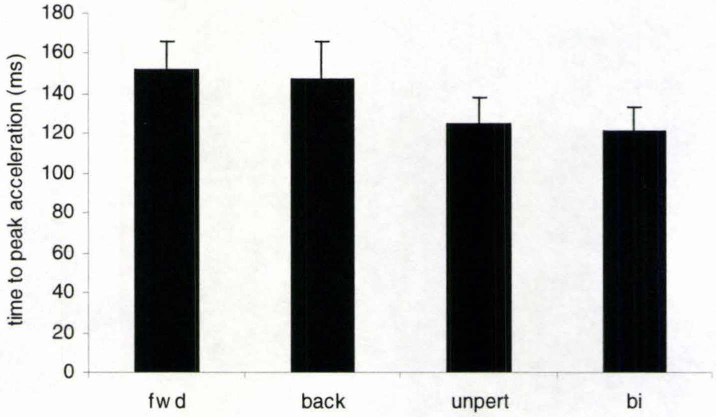

Figure 14. Time to Peak Acceleration (ms) plotted as a function of the compressed air condition, forward blast (fwd), backward blast (back), unperturbed (unpert), and bidirectionally blasted (bi) (Experiment 3).

Mean Displacement of the Kinematic Events. In addition to main effects for kinematic marker, F (3, 57) =1306.03, p < .01, and target perturbation condition, F (2, 38) = 14.92, p < .001, interactions between kinematic marker and compressed air condition, F (9, 171) = 9.43, p < .001, and kinematic marker and target perturbation condition, F (6, 114) = 16.55, p < .001, were revealed.

Post hoc analysis of the kinematic marker by compressed air target perturbation interaction indicates that the forward and backward blasted movements reach peak acceleration after greater amplitude displacement and peak deceleration after less amplitude displacement than the unperturbed and bi-directionally blasted movements (Fig. 15). Interestingly, no differences in the central tendency of peak velocity were apparent between any of the perturbation conditions. In accord with the temporal onset findings this interaction suggests that the forward and backward blasts perturbations are dealt with in a similar manner. That is the movement and its online control are structured, regardless of the specific perturbation, to offset the impacts of the backward blast early in the movement and against the forward blast perturbation late in the trajectory when the individual impacts of these two perturbations are most detrimental to the movement.

Post hoc analysis revealed that the kinematic marker by moving target perturbation interaction was driven by the differences in amplitude displacement at the end of the movement. That is, while there was no perturbation condition differences in the central tendency of PA (grand mean = 15 mm), PV (grand mean = 105 mm), or PD (grand mean = 214 mm), movements finished with less amplitude displacement when made to the short target (238 mm) than when made to the unperturbed target (250 mm), and those movements made to the unperturbed target were made with less amplitude displacement than those made to the long target (263 mm). This indicates that the impacts of these perturbations were rectified via late trajectory control processes.

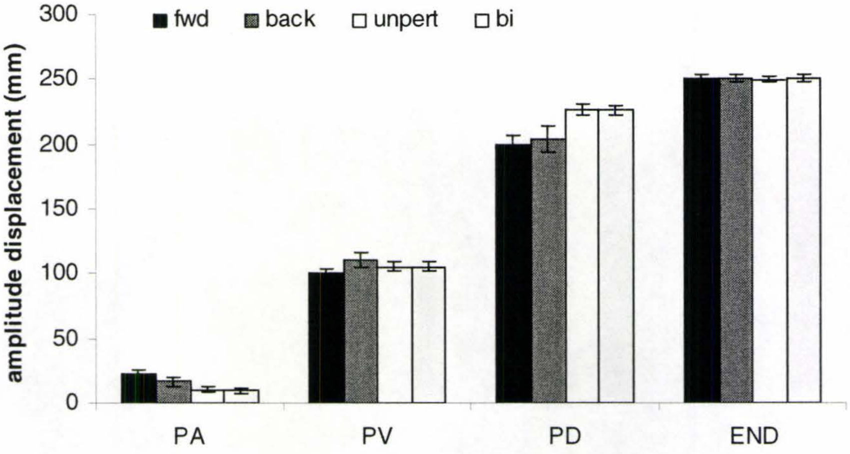

Figure 15. Mean displacement (mm) of peak acceleration (PA), peak velocity (PV), peak deceleration (PD), and the end position of the movement (END) in the primary direction of movement by compressed air condition, forward blast (fwd), backward blast (back), unperturbed (unpert), and bidirectionally blasted (bi) (Experiment 3).

Spatial Variability of the Kinematic Events. The within subject trial-to-trial spatial variability analysis yielded main effects for kinematic marker, F (3, 57) = 50.06, p < .001, compressed air perturbation, F (3, 57) = 14.70, p < .001, and target perturbation condition, F (2, 38) = 8.40, p < .001. Additional kinematic marker by compressed air perturbation, F (9, 171) = 5.88, p < .001, and kinematic marker by target perturbation, F (6, 114) = 6.29, p < .001, interaction effects were also elicited.

Post hoc investigation of the kinematic marker by compressed air perturbation interaction (Fig. 16) highlighted that while unperturbed movements displayed the typical pattern of increasing spatial variability from PA to PV and from PV to PD before significant reduction at the end of the movement, the movements were performed differently within the perturbed conditions. Forward blasted movements exhibited no significant increase in spatial variability between PA and PV before manifesting the typical increase to PD and decrease as the movement terminates. Bi-directionally blasted movements exhibited a significant change in spatial variability from PA to PV, but no increase from PV to PD. Importantly, for both movements made against the forward blast and bi-directional blast it seems that control is executed in order to reduce the increases in spatial variability during the early portions of the movement trajectory. Backward blasted movements, as evidenced by the compressed air main effect, were performed with significantly greater variability; however, these movements exhibited the typical relationship in spatial variability at each of the kinematic markers.

Examination of the kinematic marker by target perturbation interaction revealed that, in all conditions, there was systematic increase in spatial variability from PA to PV to PD before a significant reduction at the end of the movement. However, movements made to the long target were performed with greater variability at PD than were movements to an unperturbed target and movements to an unperturbed target were performed with greater variability at PD than movements made to a short target (Fig. 17). This effect is representative of the increased variability inherent to making movements that cover a greater distance.

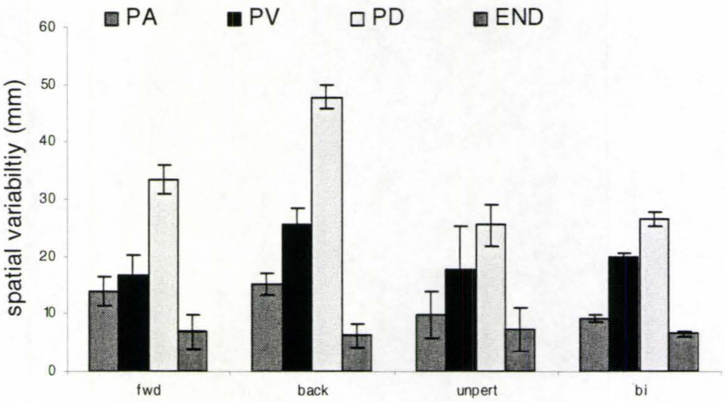

Figure 16. Mean spatial variability (mm) of peak acceleration (PA), peak velocity (PV), peak deceleration (PD), and the end position of the movement (END) in the primary direction of movement by compressed air condition, forward blast (fwd), backward blast (back), unperturbed (unpert), and bidirectionally blasted (bi) (Experiment 3).

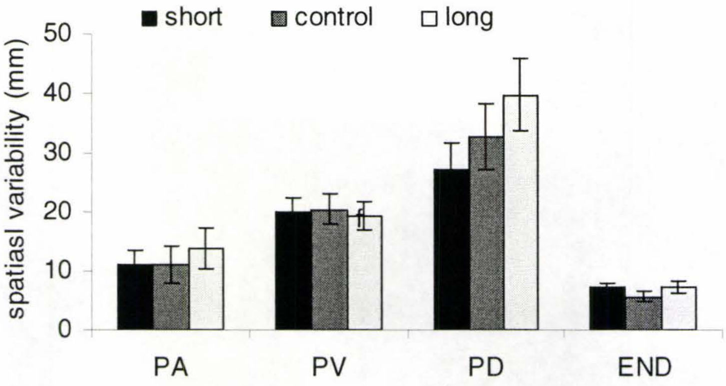

Figure 17. Mean spatial variability (mm) of peak acceleration (PA), peak velocity (PV), peak deceleration (PD), and the end position of the movement (END) in the primary direction of movement by moving target condition (Experiment 3).

Overall. In order to examine the combined influence of the two forms of online control highlighted in Experiments 1 and 2, Experiment 3 investigated the trajectories and outcomes of goal-directed movements under conditions in which the perturbations were presented in tandem. Contrary to Grierson & Elliott's (under review) investigations with illusory perturbations the results of the present work revealed an interactive effect of the two perturbations on movement accuracy. That is, the current set of perturbations, at some point in the movement, prompted parallel operation of these two control processes; insofar, that the operation of the late control process may negate much of, or exacerbate, the control executed earlier in the movement, or vice versa.

In addition to the independent main effects for the compressed air perturbation on the magnitudes of, and the times to, peak acceleration, velocity and deceleration and the moving target on within subject trial-by-trial spatial variability and endpoint amplitude, which serve to highlight the nature of the two elicited control processes, three particular findings shed light on the nature of the control process interaction and its effect on outcome accuracy. First, there is an independent main effect of the moving target perturbation on the ttPA, in which long target movements take significantly more time to reach their acceleratory peak than movements to unperturbed targets. This finding suggests that an early control process operates following the recognition of a change to the target position. Furthermore, the intermediate nature of the ttPA for short target movements suggests the modulation of this control appears to be accomplished via non-specific information regarding the new target position. Similar findings evidencing non-specific responses were gleaned from the PA analysis in Grierson and Elliott's (under review) experiments involving Müller-Lyer target perturbations and the PA and PV analyses of the compressed air perturbations presented in this manuscript. Secondly, the spatial variability analysis indicated that though performers accepted the velocity magnitude increase associated with the forward blast they did temper the blast impact through a reduction in spatial variation. Conversely, the effects of the backward blast were countered with a system-imposed limb advancement whose variability characteristics were representative of a new movement impulse. Consistent with Elliott et al.'s (2004) optimization model of limb control, in each case the early, non-specific modulation of the movement appears to be biased towards accounting for the "worse case" possibility: that target location has moved further away or the limb has received a counter-directional air blast. Thirdly, despite the increased complexity associated with managing the influences of two perturbations presented in tandem, the amplitude displacement at peak velocity analysis yielded no significant differences between any combinations of the perturbations. Peak velocity represents the approximate point in the trajectory when the agonist muscles begin to relax and the antagonist muscle activity begins to brake the movement. The results of Mendoza et al. (2005; 2006), Khan et al. (2006), and Experiment 2 indicate that this location also represents the initiation of a late trajectory control process that mediates movement on the basis of response-produced visual feedback.

6. General Discussion

The experiments presented here were designed to examine the processes that are responsible for the online visual regulation of goal-directed aiming movements. Our primary hypothesis was that there are two types of online regulation. Specifically, early control that makes adjustments to any violations of a comparison of dynamic information about limb velocity and direction to an internal model of the expected dynamic properties of the movement, and late control that, constrained by a fundamental visuomotor processing time, operates when the limb is in the vicinity of the target. This latter type of control is based on a spatial comparison of the relative limb and target positions. The strategy we used to examine this hypothesis was to introduce perturbations to the actual limb movement (Experiment 1), the task demands (Experiment 2) or both (Experiment 3), and to conduct detailed kinematic analyses of these limb trajectories in order to isolate these hypothesized corrective processes. Our second hypothesis was that because these two types of regulation are based on different information, they are relatively independent. By introducing perturbations designed to affect the two processes in tandem (Experiment 3), our goal was to isolate any co-variation between these two types of control.

The results of Experiments 1 and 2 support our primary hypothesis. Specifically, although the forward and backward air blasts in Experiment 1 impacted the acceleration phase of the movement, spatial and temporal differences between conditions were not apparent by peak velocity. This suggests that an early control system contributes to the minimization of the perturbation impact. The operation of early control is further made apparent by differences in early trajectory variability. In Experiment 2, the lack of any spatial or temporal trajectory differences until the later portions of the movement (i.e., following peak velocity) indicates that any rectification does not occur until the limb has reached the target vicinity. Furthermore, when both types of perturbation were introduced in Experiment 3, the compressed air condition main effects at PA and PV and the moving target perturbation main effects on spatial variability and end point amplitude indicated that the 2 perturbations were appropriately managed by the early and late control processes they were designed to impact.

The results associated with our second hypothesis were not as clear. Unlike earlier work using illusions we found that the two perturbations had an interactive effect on movement accuracy. That is, at some point in the movement the perturbations prompted parallel operation of the two proposed modes of control, such that the effect of early executed corrections influenced the effectiveness of later limb control. Furthermore, performer's early trajectories evidenced only a counter of the backward air blasts (i.e. increased time to peak acceleration and velocity with no difference in achieved velocity magnitude from typical) while the impact of the forward air blast was simply incorporated into the trajectory as it unfolded (i.e., increased magnitude of peak acceleration and velocity). The presence of a uni-directional response to the compressed air perturbation was a corollary and unexpected finding.

Based on the model of Paillard (1982), which holds that velocity information is differentially and more efficiently processed in the peripheral visual field, and Binsted and Elliott's (1999) finding that the eye foveated the target prior to the limb arriving in its vicinity, Grierson and Elliott (under review) suggested that the non-interactive effects of the illusory moving background and Müller-Lyer perturbations on outcome accuracy may be a function of the architecture of the eye. That is, peripheral visual receptors, to which early movement portions are available, are responsible for subserving control initiated through internal models concerning limb velocity, and central visual receptors mediate control governed by allocentric referencing of limb and target position late in the movement.

That performers' reaches do not differ in their amplitude displacement at the initiation of their deceleration (peak velocity) supports the notion that error between the limb and the target can not be detected, or rectified, until both occupy the proximity captured by foveal vision. The idea that control based on allocentric visual information (Heath, Hodges, Chua & Elliott, 1998; Khan & Franks, 2003) is not only constrained by a long sensorimotor processing time (e.g. Woodworth, 1899) but also by the spatial locus of the central visual field is further supported by Grierson and Elliott's (under review) demonstration that movements perturbed by the air compressor achieve no consistent amplitude displacement at peak velocity when made in the absence of visual feedback. However, the present results suggest that limiting the process of anticipatory control to the visual periphery is inappropriate. In particular, the moving target perturbation and the Müller-Lyer perturbation used in other work (Grierson & Elliott, under review) both affected the acceleratory characteristics of movements. This indicates that the control of movements based on the evaluation of target position is not constrained to solely late trajectory corrections; but rather, is salient enough to permeate the portion of the movement purportedly under forward-modeled control. Interestingly, these early movement modifications operate on a non-specific platform. The response to an actual target jump involves an increase in time to peak acceleration, while movements made to targets that only appear to move (i.e., Müller-Lyer perturbations) exhibit a decrease in acceleratory magnitude regardless of the new configuration. Additionally, the response to either compressed air perturbation is to maintain forward progress. The undiscriminating nature of these responses suggests that they are executed without full determination of the perturbations' impact, and given that internally modeled expectations may affect movements through the mere recognition that expectations have been violated, these responses are likely controlled through such a system. Thus, control mediated via expected-to-actual comparisons may be performed continuously at all levels of sensory afference: proprioceptive, peripheral visual afference concerning limb dynamics, as well as foveal visual information concerning target location (see also, Abahnini & Proteau, 1999; Bedard & Proteau, 2001; 2004).

The idea is that the performer has internally generated representations of both the movement and the environment. Presumably, these representations assume a certain level of dynamic or environmental stability such that expectations about the movement course and the environment may be formed. Subsequently, when the movement or the target is perturbed and the expectations are violated a response is rapidly imposed to deal with the perturbation. We hold that these responses are constructed with a bias towards adhering to criterion of safety and energy expenditure. As such they may be influenced by a priori knowledge regarding the possible perturbation. However, rather than conceptualizing the concerted operation of two control processes as functions of the early and late portions of the movement, it is more likely that during the final portions of the movement, corrections initiated on the basis of visuo-spatial information overlap with a continuous and multisensory process of predictive control. Importantly, our results indicate that when perturbed the performer tends to shift from this continuous control to more resolute control and does so with consideration for the optimization of energy and the maintenance of movement trajectory as it relates to the attainment of its goal (Elliott et al., 2004). Perhaps examining the characteristics of the corrective courses that augment movements when afferent expectations are not met will offer researchers a new avenue for the study of the strategic nature of motor programming and control.

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Chapter 5

A KINEMATIC INVESTIGATION OF THE STRUCTURE OF EARLY TRAJECTORY AMELIORATIONS TO GOAL DIRECTED MOVEMENTS FOLLOWING EARLY AND LATE PERTURBATIONS

Running Head: AMELIORATIONS TO PERTURBATION

A kinematic investigation of the structure of early trajectory ameliorations to goal-directed movements following early and late perturbations

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Abstract

Kinematic examinations of goal-directed aims have evidenced two visually-regulated processes of on-line movement control. The first form of control operates continuously to make movement adjustments based on comparisons of expected-to-actual sensory afference regarding the velocity of the limb. These corrections are characteristically non-specific but reflect a bias to optimize movement control against the worse case perturbation scenario. The second form of control is a well-documented process, which constrained by visuomotor processing times, is responsible for discrete corrections to movements on the basis of allocentric evaluations of limb and target position late in the movement. Recent work from our lab has revealed that perturbations designed to impact the latter control process also elicit early, non-specific movement amendments. Experiment 1 examined the impact of two perturbations to the perceived velocity of manual aiming movements on early limb control. Experiment 2 was concerned with the impact of two target perturbations designed to affect late control. Kinematic analyses evidenced early, non-specific responses, to both sets of perturbations. In Experiment 1, adjustments to the two perturbations were handled together. In both studies a priori knowledge of the potential perturbations influenced the strategies adopted for minimizing their impact. In general, participants planned their movements to optimize performance in the worse case scenario.

Introduction

For over a century, the evaluation of accuracy measures and the kinematic characteristics of movement trajectories gleaned from aiming studies have been used to highlight the factors that influence the relative contributions of movement planning and online processes to the control of goal-directed action. These studies have been instrumental in identifying that the required speed (Keele & Posner, 1968; Woodworth, 1899) and accuracy demands of the movements (Fitts, 1954; Meyer, Abrams, Kornblum, Wright & Smith, 1988), practice (Proteau, 1992), and a priori knowledge of what sensory information will be available during movement execution (Chua & Elliott, 1993; Elliott, Carson, Goodman & Chua, 1991; Zelaznik, Hawkins & Kisselburgh, 1983) are all important factors in determining the control strategies selected by individuals to optimize their movement performance. For example, when performers are aware that their movements will be made with the benefit of visual feedback, they execute movements with trajectories that are designed to make the best use of vision (Khan, Elliott, Coull, Chua & Lyons, 2002). Specifically, these movements are characterized by asymmetric velocity profiles (i.e., an extended deceleration phase) in which performers, presumably, use the additional time following peak velocity to use vision as an aid in acquiring the target (Chua & Elliott, 1993; Elliott, Carson, Goodman & Chua, 1991). In addition to highlighting the human ability to flexibly employ various movement strategies, the examination of these kinematic profiles has also been used as a medium for addressing the debate surrounding the amount to which movements are amendable online.

While some researchers rely on open-loop explanations of limb control, which hold that movements are programmed entirely in advance and executed without adjustment (Plamondon & Alimi, 1997), two-component models, which amalgamate ballistic impulses with temporally constrained, late movement, feedback-driven corrections (Meyer et al., 1988; Woodworth, 1899; see Elliott, Helsen & Chua, 2001 for a review), have more adequately described the spatial and temporal characteristics of aiming trajectories. For the most part, that movements are amended online has been inferred from the presence of reversals in the movement direction and second accelerations when the initial movement falls short of the target. That the processing of response-produced feedback plays a significant role in making these modifications is highlighted by the increased number of such corrections and more accurate outcomes when performers make these movements in the presence of visual information as compared to when they do so blindly (Chua & Elliott, 1993; Khan, Franks, & Goodman, 1998).

However, it has also been shown that the availability of concurrent visual information can result in greater precision without the increased prevalence of discrete adjustments. For instance, Khan, Franks, and Goodman (1998) showed that the initial portions of goal directed movement were performed less variably in the presence of visual feedback. The underlying assumption in the evaluation of spatial variability early in the movement is that if movements are totally preprogrammed and not altered online, the within subject variability should systematically increase as they progress. The profiles gathered by Khan and colleagues (1998), which deviate from those that describe ballistic action, may also be attributed to the functioning of offline processes that use the visual feedback from a previous movement to improve the programming efficiency of a subsequent movement (Abahnini, Proteau & Temprado, 1997; Khan & Franks, 2003). However, the notion that this feedback information has an online function has been further solidified by the findings of studies introducing visual perturbations to the environmental and target contexts.

The perturbation approach for examining the contributions of online control processes involves the introduction of a visual manipulation either at, or sometime following, movement initiation. The idea is that if the perturbation operates on a portion of the movement that is not rectifiable by visuomotor control the resulting trajectory will reflect the central plan with no evidence of online modification. However, measuring the spatial features and temporal durations of amendments to these perturbations allows researchers to identify the functional locus of sensorimotor control. For example, Proteau and Masson (1997) hypothesized that the perceived velocity of a moving effector influenced the control of initial movement impulses. To test this, performers moved a cursor on a computer screen to a stationary target; however, in order to influence the perceived speed of the moving cursor, on a portion of the trials the background over which it traveled was translated in the direction opposite to that of its movement. On these occasions performers terminated the initial portion of the movement after significantly less distance traveled than when the background remained stationary. In a similar manner, though to a lesser extent, when the background was translated in the same direction as the cursor movement, the aiming trajectories indicated that the initial portion of the movement covered a greater amplitude. These findings are consistent with amendments based on overestimations and underestimations of effector velocity and suggest that velocity information early in the movement trajectory serves to regulate the effector deceleration. Similar evidence of early movement control based on dynamic information comes from studies that show the continuous modification of effector acceleration on the basis of the perceived velocity of a target in motion (Brenner, Smeets, & de Lussanet, 1998; Smeets & Brenner, 1995). Importantly, these findings contradict the century old belief that the initial portions of movements are preprogrammed, ballistic, and not privy to online control (Meyer et al., 1988; Woodworth, 1899). Rather, goal-directed aiming appears to function with contributions from a process concerned with making error corrections manufactured on the basis of allocentrically derived spatial information regarding the relative positions of the hand and target (see Elliott et al., 2001, for a review), as well as a process that regulates limb dynamics through the evaluation of concurrent velocity information. Whether these two processes represent a single mode of control or are distinct entities unto themselves remains a pertinent question.

Recent work from our lab sought to investigate the distinction between these early and late control processes (Grierson & Elliott *a*, under review; Grierson & Elliott *b*, under review). In these studies performers made goal-directed reaches in individual experiments in which they were exposed to perturbations designed to affect late trajectory evaluation of relative limb and target location and early trajectory perception of limb velocity, and also in an experiment in which these perturbations were presented in tandem. The first of these studies (Grierson & Elliott a, under review) used illusory perturbations to impact the early and late portions of the reach trajectory: the Müller-Lyer illusion, which has been shown effective in impacting late trajectory control (Elliott & Lee, 1995; Mendoza, Hansen, Glazebrook, Keetch & Elliott, 2005; Mendoza, Elliott, Meegan, Lyons & Welsh, 2006) and the aforementioned moving background illusion (Proteau & Masson, 1997). In addition to the kinematic evidence that the perturbations indeed affected the intended movement portions, the analysis of movement accuracy indicated that, when presented in tandem, the two perturbations had independent main effects on the reach outcome. Via Sternberg's (1969) additive factors logic, it was deemed that the two processes the perturbations affect are distinct from one another.

Similarly, the second of these studies (Grierson & Elliott b, under review) continued the exploration of two distinct processes of online control; however, rather than illusory perturbations, this set of experiments included manipulations that imposed actual changes to target position and limb velocity. The first of these experiments had the target move either towards or away from the performer upon movement initiation, a perturbation designed to impact late trajectory control (Heath, Hodges, Chua, & Elliott, 1998). As hypothesized, target relocation prompted discrete corrections late in the movement trajectory. In the study's second experiment, performers made their aiming movements while holding a stylus that had been rigged to an air compressor. This stylus was engineered to discharge a 3.45 N blast of compressed air during the peak acceleratory portions of the movements in the direction of, or the direction opposite to, that of the movement. Although previous research used moving background technologies to create the visual illusion of unintended limb velocity, the use of the compressed air device took into consideration that the effects of the illusion may be somewhat offset by the processing of accurate proprioceptive information regarding the dynamic qualities of the moving limb. This compressed air perturbation was effective in both altering the magnitude of movement velocities and eliciting evidence of early sensorimotor control. However, contrary to the findings of the studies employing illusory perturbations, the combined presentation of these actual perturbations yielded an interactive effect on movement outcome, and led to the suggestion that the control processes associated with the two perturbations, at least to some degree, covary. As such, the efforts of early dynamic control may be offset, or exacerbated, by the effects of late, feedback driven control.

A corollary finding that arose from these movement perturbation studies was the presence of modifications to the dynamic quality of early movement trajectories when performers aimed to target locations that changed in either an illusory or actual manner. Interestingly, these responses were not particular to the intended impact of the perturbation. That is, performers achieved lower accelerations when they moved to targets that were altered to either a "tails-in" or a "tails-out" Müller-Lyer figure, and took longer to reach their acceleratory peak when the target moved to a location closer or further away. Importantly, this indicated that some mode of control allows for perturbations designed to impact the late portions of trajectories to render an influence on the movement's earlier portions. Furthermore, exposure to the compressed air condition also yielded trajectories which were characterized by early, non-specific responses. In these instances, the response to any compressed air perturbation, regardless of its direction, was to rapidly move the limb forward until it was in foveal vision; presumably where its deceleration could be more efficiently monitored. Of particular note was that in each case the characteristics of the non-specific responses were in accord with managing the possible perturbation impact that was most detrimental to the movement course: a target that has moved further away from the limb or a hindering air blast. It was proposed that these findings represent the operation of a single mode of online control similar to those associated with a forward model (Davidson & Wolpert, 2005; Desmurget & Grafton, 2000; see also von Holst, 1954) that is distinct from the control mode associated with discrete, late trajectory corrections (Meyer et al., 1988; Woodworth, 1899). We made this proposal for 3 reasons. First, because these responses are executed in the very early portions of the movement and without regard for the direction of the perturbation, they probably reflect recognition of a mismatch between the expected and actual sensory consequences of the movement without the full processing of the specific afferent information available. Secondly, the motor responses initiated via this form of control are influenced by a priori knowledge of the nature of the possible movement perturbations and are prepared accordingly. Our hypothesis is that these responses are preprogrammed with the mandate of optimizing safety, speed, accuracy, and energy expenditure outcomes. Thirdly, this form of control is proposed to evaluate the congruence of expected and actual afferent information on all levels of sensory afference, and to do so continuously such that both continuous and late trajectory modes of control may operate, for a time, in parallel.

Experiment 1

To examine the manner in which performers manage movements made against two simultaneous perturbations of early anticipatory control, Experiment 1 utilized established kinematic methods (Khan et al, 2006) to investigate the movement trajectories of reaches made against a random presentation of all possible combinations of the illusory moving background (illusory perturbation) and the actual compressed air perturbations (physical perturbation). Thus, at the beginning of a trial, the background would either translate in the direction of (perceived velocity decrease), or opposite to (perceived velocity increase), the movement, or remain stationary. Eighty milliseconds following movement initiation the air compressor stylus discharged a blast in the direction of (velocity decrease), or opposite to (velocity increase), the movement, or in both directions (no change in velocity), or not at all.

Considering the role of advance knowledge in the preparation of responses to violations of expected sensory afference, two different sets of hypotheses were proposed. The first predicts the trajectories if the two perturbations are managed independently. The second specifies the expected results if the performer prepares a single response to manage the combined impacts of the two perturbations. In the case of independent control, it was hypothesized that when the background moved, the performer would initiate a non-discriminating movement modification. Particularly, we expected an overall slowing of the movement such that the distance covered by the limb would be minimized until the nature of the perturbation had been fully determined. In this way, the limb would be in a less compromising location should the perturbation demand a substantial motor recourse. However, in the situations in which the limb was blasted at the approximate onset of peak acceleration, a second non-specific response was expected. From our previous work, it was expected the air blast perturbation would prompt the performer to initiate an early deference of the control from forward-modeled expectancies to a course of control that maximizes allocentric referencing. As such, the limb movement would be advanced forward until deceleration could be mediated by central vision. Given the conflicting, slowing-versus-advancing, nature of these two emergent responses, it was expected that the trajectories would represent the combined impact of the compressed air perturbation and the influences of the two responses.

However, the performer may use the a priori knowledge of the possible perturbations to plan early online responses to the two perturbations in a combined manner. That is, the knowledge that a physical perturbation might occur, may alter the nature of control executed in response to the moving background perturbation. Specifically, because of the high outcome relevance of the physical perturbation, the response to the illusory perturbation may be withheld until the performer has determined whether or not there will be an air perturbation (after ~80ms into the movement). Assuming the forward modeled response to the translating background is delayed, it is reasonable to suppose that a single, unique response would be prepared for execution shortly following the potential onset of the air blast. It was hypothesized that this response would be structured with dynamic qualities that reflect recourse to offset the hindering backward blast and defer the limb to the more resolute control associated with allocentric referencing. However, in the event that this blast was applied during an illusory perturbation trial, the increased complexity associated with the additional moving background information may influence the efficiency with which this response is executed. That is, though a response to the background is withheld, when the system uses visual information to respond to the physical perturbation, the illusory perturbation will have an impact.

Methods

Participants. 20 right handed performers (10 male, 10 female) with normal or corrected-to-normal vision from the McMaster University community volunteered to participate in this study. All performers were naïve to the purpose of the study, gave informed consent according to the guidelines set out by the McMaster University President's Committee on Ethical Consideration in Human Experimentation, and were paid $5 (Cdn) for their participation.

Apparatus and Procedure. Individuals sat comfortably in front of a display screen positioned flat on a table top. The screen served as the target-aiming surface. A microswitch was mounted flush to the screen edge closest to the participant and served as the home position.

Each trial of the experiment required participants to make an aiming movement to a target defined by the point of intersection of a 25 cm line and two perpendicular 5 cm lines, which were arranged such that they formed a "T" configuration. The target figure was presented against a background of white dots (1.5 cm diameter) (Fig. 1a). All aims were performed with a custom made, handheld stylus. This stylus was mounted to an air compressor (Campbell Hausfeld, DK755100A5 0605, South Pasadena, California) and engineered with two small polyethylene tubes for the systematic expulsion of air blasts in both the direction of movement and the direction opposite to the movement (Fig. 2). The air was released from the compressor at 100 psi and represented a 3.45 N perturbation to the movements. Mounted to the stylus was a small microswitch that participants were required to depress with their index finger throughout the course of the study. This microswitch served to fix the handgrip used by participants across trials but also provided a safeguard deactivation mechanism for the immediate cancellation of air expulsion. On no occasion did any participant release the microswitch during a trial. Individuals wore an infrared light emitting diode (IRED) on the aiming finger. The spatial location of this IRED was recorded on each trial at 500 Hz for 2 seconds by an Optotrak-3020 digital recording system (Northern Digital, Waterloo, Ontario, Canada). Participants also wore liquid crystal goggles (Translucent Technologies, Toronto, Ontario, Canada) such that their vision could be systematically occluded.

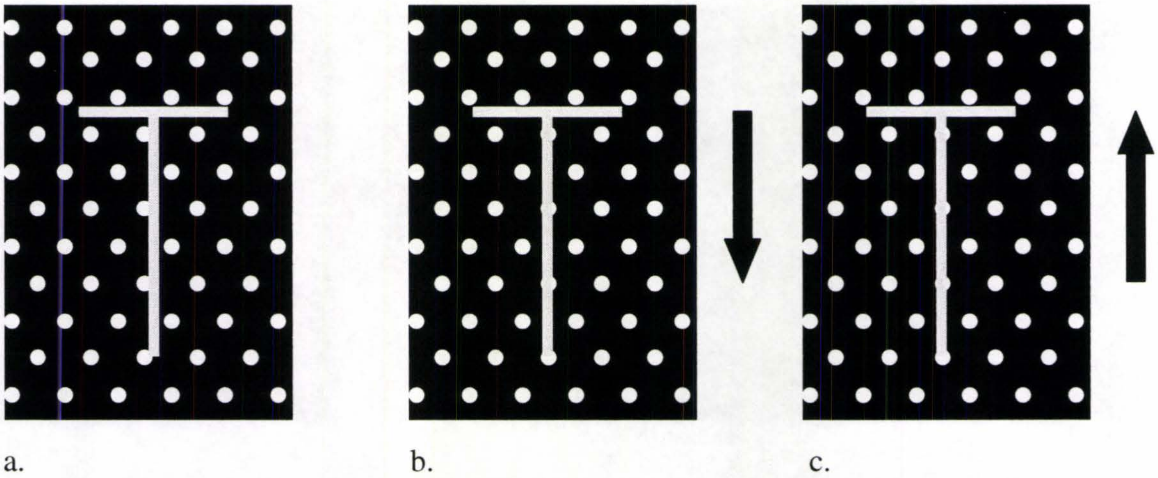

Figure 1. Depiction of the target display for Experiment 1: a) Stationary background b) Oppositely-translating background c) Similarly-translating background.

Performers began each trial sitting comfortably with the stylus depressing the home position. Following a brief '***ready***' image, the tabletop screen changed to display the target image. A variable foreperiod (1000 ms – 1500 ms) ensued after which an 800 Hz beep from computer mounted speakers prompted the participants to initiate their movement. The performers were exposed to a random combination of one of four compressed air perturbation conditions- an air blast opposite the direction of the movement (forward blast), an air blast in the same direction as the movement (backward blast), offsetting and simultaneous blasts (bidirectional blast), or no air dispensed (unblasted), and 3 moving background conditions (opposite direction translation (Fig. 1b), same direction translation (Fig. 1c), stationary background). Based on our previous work, the timing of the blast was such that it occurred at the approximate time of the movement's peak acceleration in the primary direction of movement (80 ms after movement initiation) (Grierson & Elliott *a*, under review). The moving background perturbation began on movement initiation and represented a 0.21 m/s translation of the background dots in the designated direction. Participants were notified that following the onset of movement, vision would be available for 500 ms, after which time the goggles would occlude. They were instructed to use this time to complete their aims as accurately as possible. Upon completing the movement, participants kept the stylus on the target until the display screen cleared and the goggles returned vision. They then replaced their finger on the home position and prepared for the next trial (self-paced). Participants were aware of the possibility of a perturbation and were instructed to complete their movement as accurately-as-possible, regardless of any perturbation. Each participant performed 180 trials (15 trials/condition).

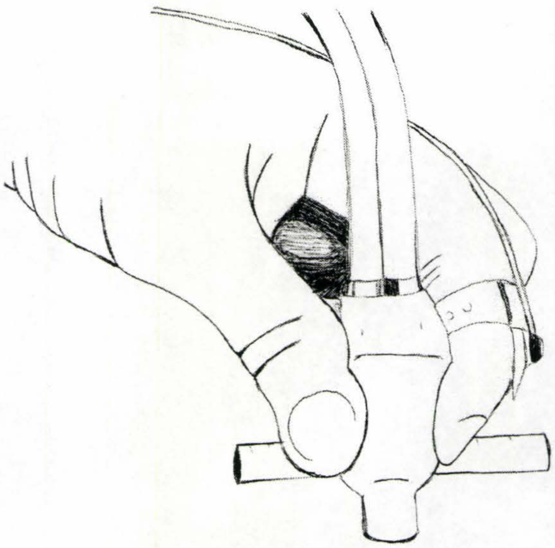

Figure 2. Depiction of the compressed air stylus.

The target display, liquid crystal goggles, computer speakers, Optotrak-3020 digital recording system trigger, and the compressed air expulsion were all controlled via a program developed using E-Prime software (Psychology Software Tools Inc., Pittsburgh, PA, USA).

Displacements in the primary direction of the movement were filtered with an 8 Hz dual-pass Butterworth filter and then differentiated and double differentiated to obtain velocity and acceleration. Custom software identified the magnitude of the peak acceleration (PA), peak velocity (PV), and peak deceleration (PD) for each reaching movement, as well as the spatial location of these kinematic events and the end position (END) of the movement. The Optotrak frames in which the limb velocity rose above or fell below 30mm/s, and remained as such for 70 ms identified the start and the end of the movement. Values for any dependent variable that fell more than 2.5 standard deviation units from the mean were considered outliers and were removed from the data sets prior to analysis.

The performance variables examined were reaction time (RT), movement time (MT), constant error (CE), and variable error (VE). We also examined mean peak acceleration (PA), peak velocity (PV), peak deceleration (PD), as well as the time to each of these kinematic events. In order to provide insight into the impact of the perturbations as the movement unfolds, analysis was also conducted on the mean amplitude of the movement at PA, PV and PD, as well as the within-participant standard deviations of these spatial positions.

The primary dependent variables were analyzed using a 4 compressed air perturbation condition by 3 moving background perturbation condition repeated measures analysis of variance. Additionally, the within participant trial-by-trial spatial variability across the entire movement was analyzed via a 4 kinematic marker (PA, PV, PD, End) by 4 compressed air perturbation condition by 3 moving background perturbation condition analysis of variance. All significant effects involving more than two means were decomposed using the Tukey HSD, $p < .05$ procedure.

Results

Effects at Peak Acceleration. The analysis of the amplitude displacement at peak acceleration yielded a significant main effect for the physical perturbation, $F(3, 54) = 4.33$, $p < .01$, in which backward blasted movements (19.4 mm) reached the kinematic event after traveling more distance than the bidirectionally blasted movement (15.9 mm). The unperturbed (16.1 mm) and forward blasted (19.2 mm) movements traveled intermediate distances. There was also a significant interaction of the perturbations on the distance traveled by peak acceleration, $F(6, 108) = 5.97$, $p < .001$. The post hoc analysis of this interaction revealed that when the background translated in the same direction as the movement, forward blasted movements traveled further by peak acceleration as compared to backward blasted or bi-directionally blasted movements. Movements that were unperturbed by the air compressor traveled an intermediate, but not significantly different distance by peak acceleration when made over the similarly translating background. When the background translated in the direction opposite that of the reach, movements that were bi-directionally air blasted traveled further by peak acceleration than those that were forward blasted. The amplitude displacements at peak acceleration for backward blasted and unperturbed movements performed over an oppositely translating background were intermediate and not significantly different. When the background did not translate, backward blasted movements achieved peak acceleration after more amplitude displacement than unperturbed or bi-directionally blasted movements, and forward blasted movements achieved peak acceleration after more amplitude displacement than bi-directionally blasted movements (Fig. 3a).

The analysis of the magnitude of peak acceleration revealed a significant main effect for compressed air condition, F (3, 54) = 22.71, $p < .001$, which indicated that uni-directionally blasted movements (forward blasted = 33.9 m/s^2, backward blasted = 34.0 m/s^2) achieved higher peak accelerations than bi-directionally blasted movements (31.4 m/s^2). Furthermore, bi-directionally blasted movements achieved higher accelerations than those that were not blasted (29.4 m/s^2). The magnitude of peak acceleration analysis also yielded a significant interaction between the physical and illusory perturbations, F (6, 108) = 26.47, $p < .001$. When the background translated in the same direction as the movement, forward blasted movements attained higher peak accelerations than backward blasted, bi-directionally blasted, and unperturbed movements, and unperturbed movements attained higher peak accelerations than backward blasted and bi-directionally blasted movements. When the background translated in the direction opposite the movements, bi-directionally blasted movements attained higher peak accelerations than backward blasted movements, and backward blasted movements attained higher peak accelerations than forward blasted or unblasted movements. When the background did not translate backward blasted movements attained higher peak accelerations than forward blasted movements, and forward blasted movements attained higher peak accelerations than bi-directionally blasted and unperturbed movements (Fig. 3b).

The time to peak acceleration analysis produced a significant main effect for physical perturbation, F (3, 54) = 3.71, p < .05, which indicated that forward (198 ms) and backward (198 ms) blasted movements took longer to reach the kinematic event than those that were bidirectionally blasted (178 ms). Unblasted movements (186 ms) were intermediate to, but not significantly different than, those made against the other compressed air conditions. The analysis also yielded a significant compressed air by illusory perturbation interaction, F (6, 108) = 7.83, p < .001. The post hoc analysis of the interaction revealed that when the background translated in the same direction as the movement, unperturbed reaches took longer to achieve peak acceleration than backward blasted or bi-directionally blasted reaches. Forward blasted reaches took an intermediate, but not significantly different, amount of time. However, when the background shifted in the direction opposite that of the movement, movements that were blasted backwards took longer to obtain peak acceleration than unperturbed or forward blasted movements. Movements that received bi-directional air blasts took an intermediate time to reach peak acceleration. When the background did not translate, forward blasted movements took longer to reach peak acceleration than bi-directionally blasted and unperturbed movements. Reaches that were exposed to backward blasts took an intermediate, but not significantly different, length of time (Fig. 3c).

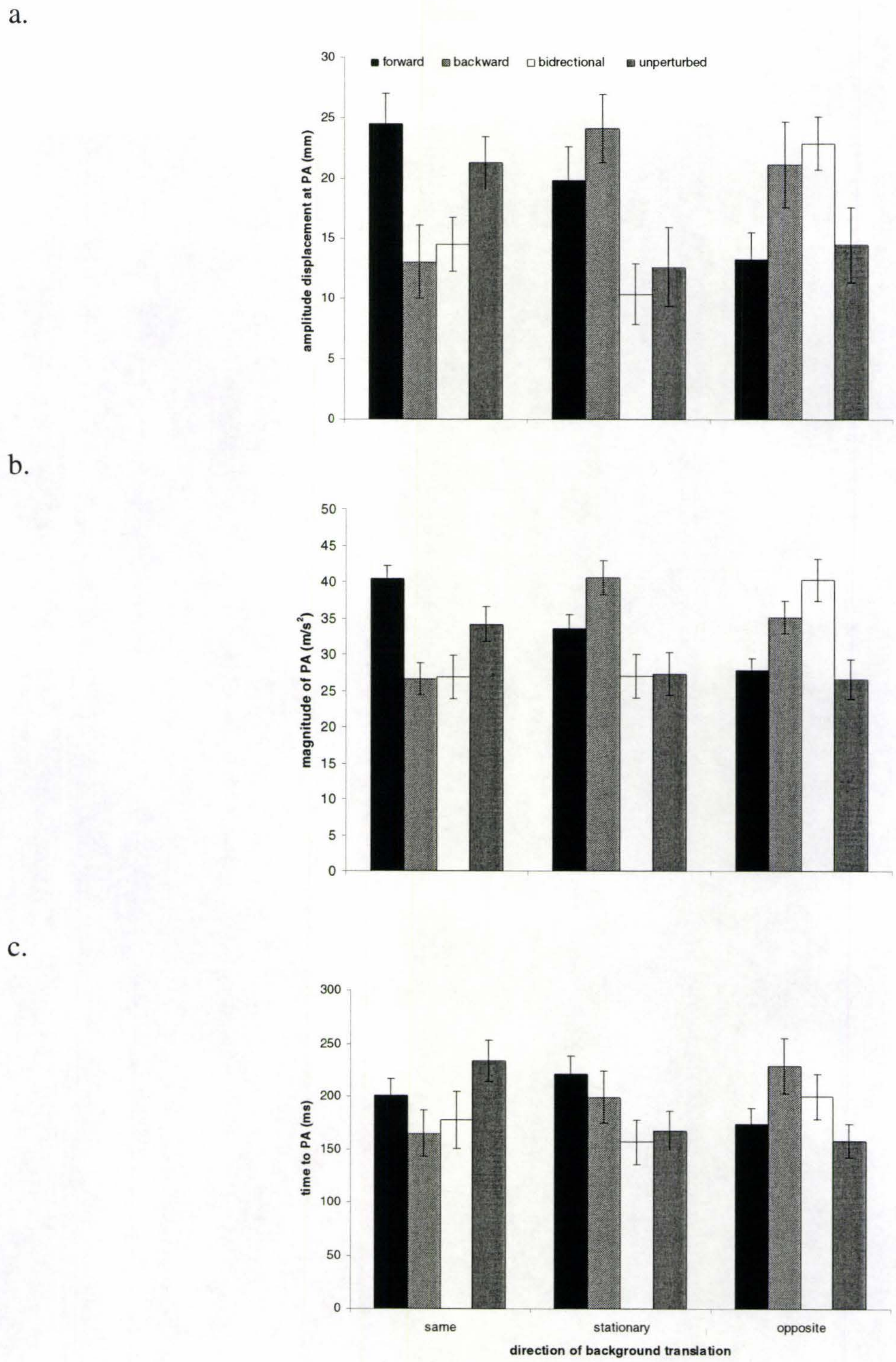

Figure 3. Experiment 1. Mean kinematic effects at peak acceleration (PA) for movements performed over the similarly-translating background (same), stationary background (stationary), and oppositely-translating background (opposite): a) Amplitude displacement at PA (mm) b) magnitude of PA (m/s^2) c) Time to PA (ms).

When taken together, the amplitude displacement at, magnitude of, and time to peak acceleration findings highlight the movement strategy and early control adopted by the performers. Foremost, that main effect differences for each of the dependent measures are only apparent between movements made against the physical perturbations suggests that the illusory perturbation did not have an independent impact on early control. Although it may be that the peak acceleration landmark is too early for the illusory perturbation to be recognized, the presence of a moving background by air compressor interaction for each dependent measure suggests otherwise. These interactions describe the operation of differential control when the performers attempt to rectify the impacts of the physical perturbation over similarly or oppositely translating backgrounds. Importantly, in the absence of any moving background, in response to either a forward or backward blast, the findings reflect a control process which operated to advance the limb. The non-specific characteristics of these responses draw attention to the performers' pre-established bias to offset the more movement hindering backward blasts. However, when the background moved in the same direction as the movement (a perturbation designed to create the perception of reduced limb velocity) the nature of the exercised control changed. Specifically, while forward blasted movements exhibited the typical limb advancement, movements that were backward blasted did not. Likewise, when the background translated opposite the direction of the movement (a perturbation designed to create the perception of increased limb velocity) the nature of the control exercised also changed. In particular, the limb advancement typically seen in response to the air blasts was not seen for forward blasted movements. Additionally, in the oppositely-translating background condition, movements that were exposed to bi-directional air blasts exhibited an increase in the amplitude displacement at, magnitude of, and time to peak acceleration even though this perturbation did not have any impact on velocity. Seemingly, when the physical perturbation and the illusory perturbation operated to influence movement velocity in opposing manners (forward blast and a similarly translating background; backward blast and an oppositely translating background) the integrity of the advancing response to the compressed air was maintained; however, when the two perturbations corroborated with each other (forward blast and an oppositely translating background; backward blast and a similarly translating background) the exhibited response reflected an early slowing of the movement.

Interestingly, the mean time to peak acceleration findings for the forward blast, backward blast and unblasted conditions indicated that performers do not reach their acceleratory peak until after the air blasts had, or would have, ceased to discharge. This finding is contrary to earlier work employing the compressed air device (Grierson & Elliott *b*, under review) and suggests that knowledge of the potential perturbation prompted performers to temper the full impulse of their initial movement in anticipation of a possible air blast.

Effects at Peak Velocity. The analysis of amplitude displacement at peak velocity yielded a significant main effect for compressed air condition, F (3, 54) = 12.75, p < .001, which revealed that forward blasted (101.1 mm), backward blasted (98.6 mm), and bidirectionally blasted (101.3 mm) movements achieved peak velocity after less distance traveled than unblasted movements (109.3 mm). This analysis also produced a significant physical by illusory perturbation interaction, F (6, 108) = 12.82, p < .001. The post hoc analysis of the interaction revealed that when the background moved in the same direction as the movement, forward blasted movements traveled less distance by peak velocity than backward blasted, bi-directionally blasted, or unblasted movements. However, when the background shifted in the direction opposite that of the movement, the displacement of bi-directionally blasted movements at peak velocity was less than it was for forward blasted, backward blasted or unblasted movements. When the background remained stationary, backward blasted movements achieved peak velocity after less amplitude displacement than forward blasted, bi-directionally blasted, and unperturbed movements (Fig 4a).

The magnitude of peak velocity analysis yielded a main effect for physical perturbation, F (3, 54) = 44.3, p < .001 (forward blasted = 1.72 m/s, backward blasted = 1.70 m/s, bidirectionally blasted = 1.68 m/s, unperturbed = 1.55 m/s), which indicated that forward blasted movements reached higher velocities than unperturbed movements. This analysis also revealed a significant interaction between the air compressor and moving background conditions, F (6, 108) = 53.5, p < .001. The post hoc analysis of the interaction indicated that when the background shifted in the same direction as the movement, forward blasted movements attained higher peak velocities than backward blasted, bi-directionally blasted, and unperturbed movements. However, when the background translated in the direction opposite the movement, bi-directionally blasted movements attained higher peak velocities than forward blasted, backward blasted and unperturbed reaches. In the instances that the background did not translate, backward blasted movements attained higher peak velocities than forward blasted, bi-directionally blasted, or unperturbed movements (Fig. 4b).

In addition to a significant compressed air condition main effect in which unperturbed movements took longer to reach peak velocity than perturbed movements, F (3, 54) = 10.0, p < .001 (forward blasted = 349 ms, backward blasted = 345 ms, bidirectionally blasted = 344 ms, unperturbed = 376 ms), the time to peak velocity analysis also yielded a significant interaction between the compressed air and moving background conditions, F (6, 108) = 26.5, p < .001. The post hoc analysis of the interaction revealed that when the background moved in the same direction as the movement, the unperturbed movements took longer to reach peak velocity than backward blasted and forward blasted movements. In order to reach peak velocity, movements that were bi-directionally blasted took an intermediate, but not significantly different, amount of time to the unperturbed and backward blasted movements. When made over a similarly-translating background, bi-directionally blasted and backward blasted movements took more time to reach peak velocity than forward blasted movements. When the background shifted in the direction opposite the movement, bi-directionally blasted movements took less time to reach peak velocity than forward blasted, backward blasted, and unperturbed movements. When the background remained stationary, backward blasted movements took less time to reach peak velocity than forward blasted, bi-directionally blasted, and unperturbed movements (Fig. 4c).

Any kinematic differences found at peak velocity may be interpreted as a function of either the residual impacts of the applied physical perturbation or the ameliorative control employed in response. It is our contention that when the limb is perturbed by either a forward or backward air blast the performer initiates a non-discriminating response to advance the limb forward. As such, we expected the amplitude displacement at, magnitude of, and time to peak velocity findings against the backward blast to represent an increase in velocity that is associated with an increase in applied effort to overcome the blast. Alternatively, though we expected the trajectories of forward blasted to also reflect an increase in velocity, we posit that this increase is attributable to the incorporation of the blast's influence. Congruent with our expectations, examination of the kinematic results revealed that, in the absence of a moving background, when the aims were made against a backward blast, despite its hindering nature, performers achieved

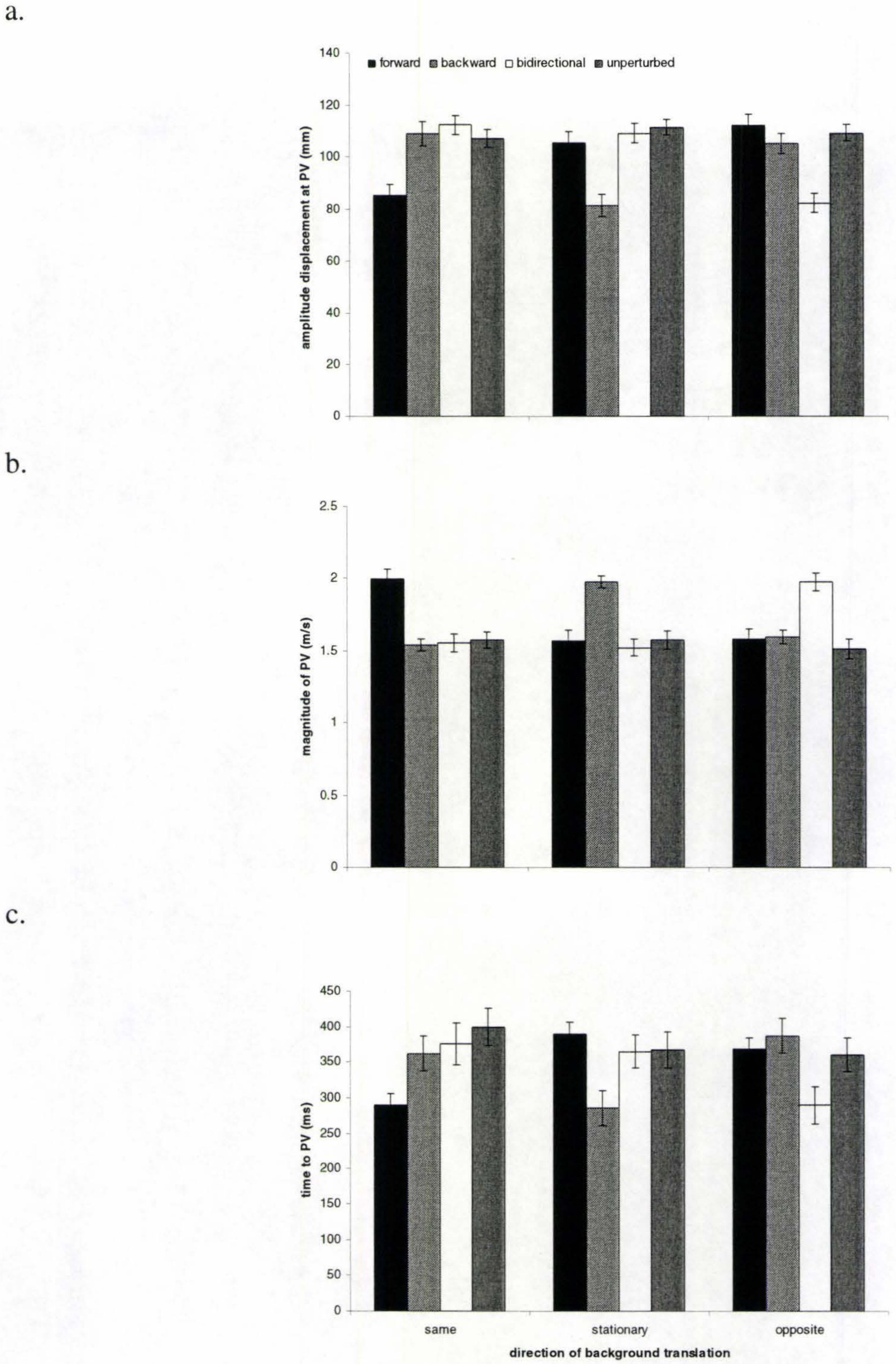

Figure 4. Experiment 1. Mean kinematic effects at peak velocity (PV) for movements performed over the similarly-translating background (same), stationary background (stationary), and oppositely-translating background (opposite): a) Amplitude displacement at PV (mm) b) magnitude of PV (m/s) c) Time to PV (ms).

higher magnitudes of peak velocity and, as such, reached this peak after less time and distance traveled. Furthermore, the overall increased magnitude of peak velocity following a forward air blast indicated that the air blast appropriately affected limb velocity. The lack of an increase in peak velocity magnitude for forward blasted movements made over a stationary background suggests that the impact of the forward blast perturbation is tempered online such that it is not fully realized by this kinematic event. However, the nature of this control changed depending on the presence of any background perturbation. Although, forward blasted aims attained higher velocities and reached their peak after less time and distance when performed over a similarly-translating background, they did not when performed over an opposite translation. Again, the results highlight that when the two perturbations that are designed to promote the perception of increased limb velocity (forward blast and oppositely-translating background) are presented in combination, performers respond by slowing the limb.

It is particularly noteworthy that movements performed against the non-perturbing, simultaneous bi-directional air blasts achieved higher peak velocities when performed over oppositely translating backgrounds. Presumably, the auditory stimulus associated with the air discharge triggered a superfluous response. The advancing influence of the bi-directional air blast may be attributed to the performers' bias to overcome the hindering backward blast. However, that the auditory stimulus only elicited this response when the background shifted counter to the movement's direction complicates this explanation.

In all, the results reflect the control exercised to offset the physical perturbations and the supplementary attenuation that the moving backgrounds have on this control. Interestingly, the lack of any overall effect of the illusory perturbation on any of the peak velocity dependent measures substantiates the notion that no response to the illusory perturbation is initiated unless a response to the physical perturbation has been executed. Presumably, in the absence of an air perturbation, responses to alleviate the impacts of the moving backgrounds are withheld. However, when presented in tandem with the physical perturbations, the moving backgrounds had significant effects on movement control.

Effects at Peak Deceleration. The analysis of amplitude displacement at peak deceleration revealed a main effect for the compressed air condition, F (3, 54) = 14.3, $p < .001$, in which aims made against the forward (188.7 mm) and backward (187.6 mm) blasts traveled significantly less distance by the kinematic event than aims that were either bi-directionally blasted (206.1 mm) or unperturbed (206.3 mm). This main effect was superseded by a significant physical perturbation by illusory perturbation interaction, F (6, 108) = 30.03, $p < .001$. The post hoc analysis of this interaction revealed that, when the background translated in the same direction, backward blasted and bi-directionally blasted movements traveled a greater distance by peak deceleration than forward blasted and unblasted movements. Backward blasted and bi-directionally blasted movements did not differ in their amplitude displacement at peak deceleration; nor did forward blasted and unperturbed movements. By contrast, in the instances that the background shifted in the direction opposite to that of the movement, forward blasted and unperturbed movements traveled a greater distance by peak deceleration than backward blasted or bi-directionally blasted movements. Again forward blasted and unperturbed movements, and backward blasted and bi-directionally blasted did not differ in their peak deceleration amplitude displacement. Consistent with the main effect, when the background remained stationary, the bi-directionally blasted and unperturbed movements traveled further by peak deceleration than forward and backward blasted movements (Fig. 5a).

In addition to a significant physical perturbation main effect, F (3, 54) = 7.28, p < .001, in which forward blasted movements attained a higher peak deceleration than unblasted movements (forward blasted = 27.7 m/s^2, backward blasted = 27.5 m/s^2, bidirectionally blasted = 26.7 m/s^2, unperturbed = 25.8 m/s^2), the analysis of the magnitude of peak deceleration also yielded a significant physical perturbation by illusory perturbation interaction, F (6, 108) = 14.58, p < .001. The post hoc analysis of this interaction indicated that when the background translated in the same direction as the movements the forward blasted and unperturbed movements attained significantly higher peak decelerations than the bi-directionally blasted and backward blasted movements. However, when the background translated in the direction opposite to the movement backward blasted reaches attained higher peak decelerations than forward blasted, bi-directionally blasted, and unperturbed movements. When the background did not translate, the bi-directionally and backward blasted movements achieved higher peak decelerations than the forward blasted and unperturbed aims (Fig. 5b).

The time to peak deceleration analysis yielded a significant physical perturbation main effect, F (3, 54) = 11.57, p < .001, that revealed that forward (537 ms) and backward (532 ms) blasted aims took less time to reach the kinematic landmark than bidirectionally (571 ms) or unblasted (599 ms) aims. In addition to this main effect, the analysis also yielded a significant physical perturbation by illusory perturbation effect, F (6, 108) = 24.46, p < .001. The post hoc analysis of the interaction indicated that when the background moved in the same direction as the movement bi-directionally and backward blasted movements took more time to reach peak deceleration than unperturbed movements, which, in turn, took more time to reach peak

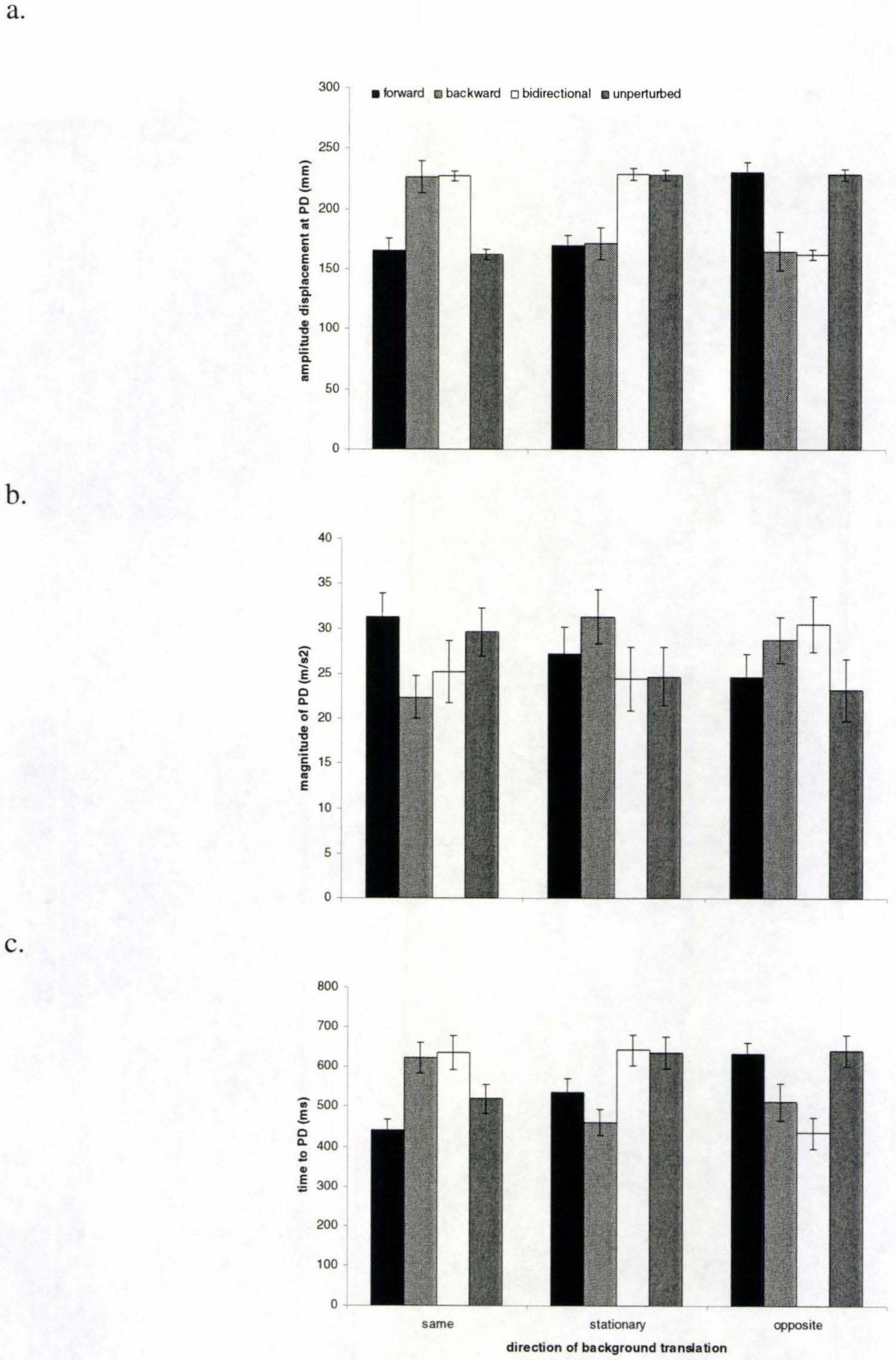

Figure 5. Experiment 1. Mean kinematic effects at peak deceleration (PD) for movements performed over the similarly-translating background (same), stationary background (stationary), and oppositely-translating background (opposite): a) Amplitude displacement at PD (mm) b) magnitude of PD (m/s^2) c) Time to PD (ms).

deceleration than forward blasted movements. However, when the background translated in the direction opposite to the movement forward blasted and unperturbed movements took more time to reach peak deceleration than backward blasted movements, which, in turn, took longer to reach peak deceleration than bi-directionally blasted movements. When the background remained stationary bi-directionally blasted and unperturbed movements took loner to reach peak deceleration than forward blasted movements, which, in turn, took longer than backward blasted movements (Fig. 5c).

The effects gleaned from the analysis of amplitude displacement at, magnitude of, and time to peak deceleration revealed the way in which performers rectified the impacts of the air perturbations and the influence of the early responsive control applied. Overall, the increased magnitude of deceleration for forward blasted movements, which resulted in decreased amplitude displacements and times to this kinematic peak, highlighted the performers' efforts to counter the increased velocities these movements experienced. A similar increased deceleration was revealed for backward blasted aims performed over a stationary background. These findings further highlight the performers' efforts to alleviate the increased velocity that was generated in overcoming the hindering air blast. In a similar fashion, the deceleration effects seen for movements made over the similarly-translating background reflect the efforts to offset the increases in velocity that were seen earlier in the movement. In particular, forward blasted movements achieved higher decelerations. However, although backward blasted movements that were made over an oppositely translating background did not attain a significantly higher peak velocity, these movements did exhibit more deceleration than forward blasted and unperturbed aims.

As was the case for the analyses at peak acceleration and peak velocity, the peak deceleration findings support the notion that the illusory perturbation is ignored and only has an impact on the movement when the performer responds to a physical perturbation. That no independent differences are apparent in the amplitude displacement, magnitude of, or time to peak deceleration for the illusory perturbations suggest that any independent effects of this manipulation on outcome accuracy or movement time are derived from sensorimotor processes occurring during the movement's late trajectory corrective portion.

Performance Outcomes. The analysis of movement time revealed a significant interaction effect between the compressed air and moving background conditions, F (6, 114) = 16.77, $p < .001$. Post hoc analysis indicated that when the background remained stationary, those movements which received a forward air blast (802 ms) took significantly longer than those made against backward air blasts (736 ms), bidirectional air blasts (755 ms), or no air blast (748 ms); however, when the background translated in the same direction as movement, the unblasted movements (798 ms) took significantly longer than the forward (733 ms), backward (745 ms), and bidirectionally blasted (755 s) movements. When the background translated toward the participant, the backward blasted movements required the most time (forward blasted = 750 ms, backward blasted = 791 ms, bidirectionally blasted = 736 ms, unperturbed = 749 ms). There were no reaction time differences between any of the conditions (grand mean = 362 ms).

The analysis of constant error revealed an independent main effect of the air compressor perturbation, F (3, 54) = 9.03, $p < .001$. The post hoc analysis of this effect indicated that unperturbed movements (-5.97 mm) undershot the target location to a greater degree than did bidirectionally (-4.23 mm), forward (-2.94 mm), or backward blasted (-3.8 mm) movements, which did not differ from one another. The illusory perturbation also yielded a main effect, F (2, 36) = 3.95, $p < .05$, in which reaches made over the oppositely translating background (-5.05 mm) terminated with greater undershooting error than those made over same direction translating backgrounds (-3.75 mm) and stationary backgrounds (-3.88 mm). No significant variable error differences were noted between any of the conditions (grand mean = 4.76 mm).

The constant error differences yielded for the moving background condition suggest that sometime following peak deceleration and the movement end point, the translation of the background significantly altered the operation of performers' late trajectory control process (i.e., movements made over the oppositely translating background were performed with greater undershooting error). However, noting that the movement times for all aims exceeded the time for which the goggles remained open indicates that any late trajectory effect of the moving background must be attributed to a memorial representation of the target and limb locations, as well as a representation of the limb's dynamic qualities. Presumably, the presence of an oppositely translating background renders an influence on this memorial representation.

Spatial Variability of Kinematic Events throughout the Entire Movement. Analysis of the within subject trial-to-trial spatial variability at each kinematic event throughout the entire movement yielded a significant kinematic marker main effect, F (3, 54) = 61.79, $p < .001$, a significant compressed air main effect, F (3, 54) = 11.15, $p < .001$, a significant kinematic marker by physical perturbation interaction, F (9, 162) = 9.30, $p < .001$, a significant kinematic marker by moving background interaction, F (6, 108) = 2.25, $p < .05$, and a significant physical perturbation by illusory perturbation interaction, F (6, 108) = 19.92, $p < .001$. These significant effects on spatial variability were superseded by a three-way kinematic marker by physical perturbation by illusory perturbation, F (18, 324) = 13.93, p < .01 (Fig. 6).

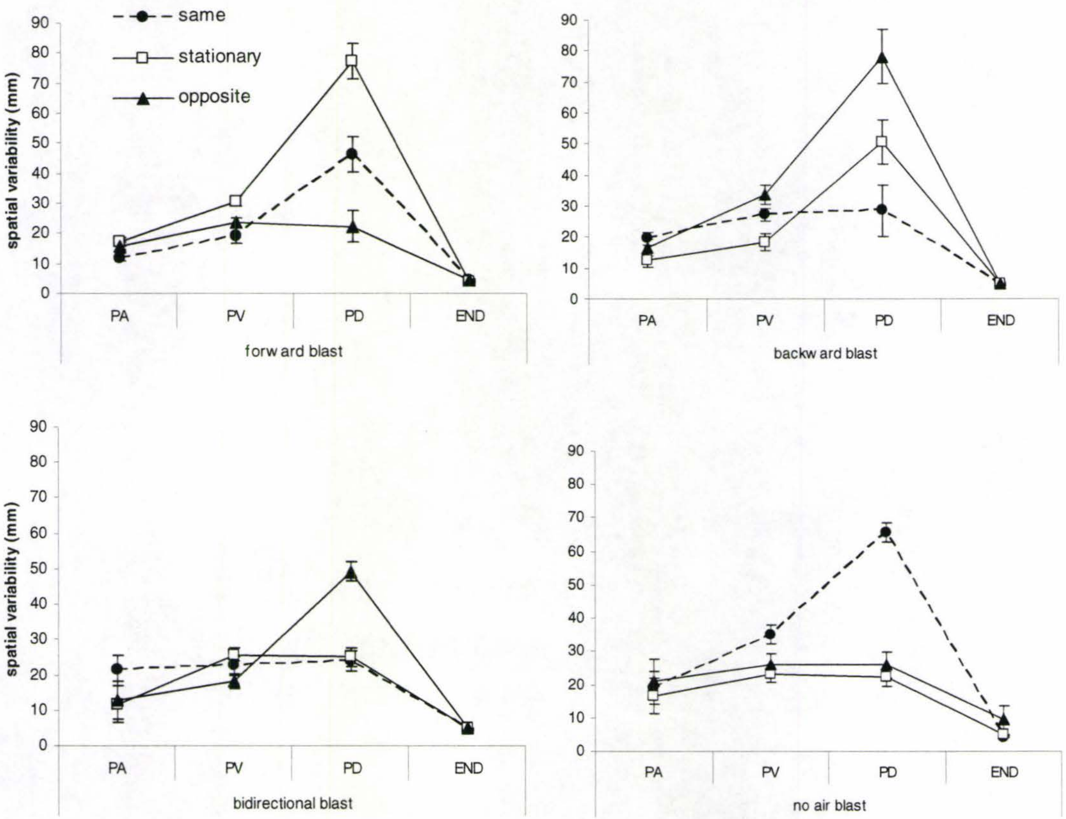

Figure 6. Experiment 1. Mean spatial variability (mm) for each moving background condition (same, stationary, opposite) plotted as a function of kinematic event (peak acceleration (PA), peak velocity (PV), peak deceleration (PD), and movement endpoint (END)) and compressed air blast condition (forward blast, backward blast, bi-directional blast, no air blast).

Movements made against the forward blast exhibited different variability courses depending on what background condition they were completed over. Forward blasted movements performed over a similarly translating background showed significant increases in variability from peak acceleration to peak velocity and from peak velocity to peak deceleration before dropping drastically in variability at the end of the movement. As did forward blasted movements made over a stationary background. However, when made over oppositely translating backgrounds, the analysis at each kinematic event suggested that forward blasted movements significantly increase in spatial variability from peak acceleration to peak velocity, but experienced no systematic increase from peak velocity to peak deceleration before decreasing in variability at the end of the movement. While no differences were present in the amount of spatial variability at peak acceleration or peak velocity for movements made over any of the background conditions, forward blasted movements made over the stationary background achieved higher spatial variability at peak deceleration than those made over the similarly translating background, which in turn achieved higher variability at peak deceleration than those made over an oppositely translating background. No differences in spatial variability were yielded between any of the forward blasted movements at the end of the reach.

Movements made against the backward blasted movements also displayed different variability courses depending on the background translation. That is, when these movements were made over an oppositely translating background they increased in spatial variability from peak acceleration to peak velocity and from peak velocity to peak deceleration before significantly decreasing at the end of the movement. But when backward blasted movements were made over a similarly translating background the spatial variability increased from peak acceleration to peak velocity but not from peak velocity to peak deceleration, and when backward blasted movements were made over a stationary background there was no increase between peak acceleration and peak velocity after which event the variability increased significantly to peak deceleration. In all cases the spatial variability decreased from peak deceleration to the end of the movement. For backward blasted movements there was no difference in the spatial variability at peak acceleration for any of the background conditions; however, post hoc analysis revealed that the spatial variability of movements made over the oppositely translating backward was greater for these movements than when they were made over a stationary background, to which those made over the similarly translating background were intermediately variable. At peak deceleration those backward blasted movements made over the oppositely translating background were more variable than those made over the stationary background, which, in turn, were more variable than those made over the similarly translating background. At the end of the reach there was no difference between those movements made against a backward blast for any of the moving background conditions.

When the movements exposed to bidirectional blasts were performed over a stationary or oppositely translating background the variability at each kinematic marker increased from peak acceleration to peak velocity, and from peak velocity to peak deceleration, before decreasing at the end of the movement. However, bidirectionally blasted movements performed over a similarly translating background manifested no differences in spatial variability at peak acceleration, peak velocity, or peak deceleration. These movements significantly decreased in variability between peak deceleration and the end of the movement. There were no apparent differences in spatial variability for any of the bidirectionally blasted movements at peak acceleration, peak velocity, or the end of the movement. However, at peak deceleration, bidirectionally blasted movements performed over the oppositely translating background were done so with more variability than those performed over a stationary or similarly translating background.

Post hoc analysis of the three-way kinematic marker by physical perturbation by illusory perturbation interaction indicated that only movements that were not blasted and were made over the similarly translating background exhibited a variability course indicative of truly ballistic action. That is, these movements displayed significant increases in spatial variability from peak acceleration to peak velocity and from peak velocity to peak deceleration. Movements that were not blasted that were made over the stationary or oppositely translating backgrounds displayed no significant difference in spatial variability at any of the peak acceleration, velocity, or deceleration landmarks. All unblasted movements showed a significant decrease in variability from peak deceleration to the end of the movement. Furthermore, there were no differences manifested in the spatial variability unblasted movements at peak acceleration, peak velocity, or the end of the movement. This was regardless of the moving background condition. However, at peak deceleration, movements that were not blasted, which were performed over a similarly translating background, were more variable than those performed over a stationary or oppositely translating background.

The spatial variability findings further support the notion that the moving background illusion exacerbated the impacts of the physical perturbation by rendering an influence upon the movement ameliorations made in response to the latter. Importantly, the lack of variability differences from peak acceleration to peak velocity and from peak velocity to peak deceleration, when the physical perturbation does not discharge, indicated that these movements are prepared-in-advance to be of low variability (Khan et al., 2003), and continued to be so regardless of the moving background. Interestingly, the peaks in variability for the conditions in which the two perturbations worked in a collaborative fashion (forward blast and oppositely-translating background; backward blast and similarly-translating background; no blast and 1stationary background) remained fairly constant throughout the entire course of the movement. In these situations the elicited secondary response to the moving background is in concert with the response to the compressed air. As such, the overall complexity associated with the combined perturbations is low and individuals are able to maintain trajectories of decreased variability.

Furthermore, the early trajectory findings indicated that reached were subjected to a general slowing when exposed to like-acting compressed air and illusory perturbations. With this early movement slowing, the overall reduction in spatial variability is expected.

Overall. Foremost, only the air compressor perturbations yielded main effects on the early kinematic measures, and the moving background only influenced the limb in conjunction with the compressed air. Seemingly, responses to the moving background were withheld unless the performer determined the presence of physical perturbation. Although the results confirmed our expectation that responses to the air blasts are non-specific in nature and designed to advance the limb through potential backward blasts, they also indicated that such a response is complicated by the presence of a moving background. One may conceptualize that when the performer responds to the air blast, the visuomotor process that was closed to the moving background, in anticipation of the blast, opens. Interestingly, when the illusory perturbation was designed to affect the movement in a manner contrary to the physical perturbation, the translating background generally continued to be ignored. However, when the moving background affected the reach in a manner congruent with the physical perturbation, performers exhibited a slowing of the movement. In these situations, the visual illusion intensified the perceived impact of the compressed air blast. As such, a visual-proprioceptive incongruence was created and a subsequent, non-specific limb slowing was instigated such that the discrepancy could be rectified.

Unlike previous work (Grierson & Elliott *b,* under review; Grierson & Elliott *c,* under review), the bi-directional air blast yielded several effects throughout the kinematic analyses. Because this particular perturbation does not actually apply any physical or visual effect, the influences of this perturbation must be attributed to the auditory information inherent to the discharge of the compressed air. We propose that the sensorimotor delay process needed to prevent any early response to the illusory perturbation may limit the processing resources that were previously dedicated to preventing responses to the auditory stimulus.

In all, the results support the hypothesis that the performers prepare responses to the moving background and air compressor perturbations such that the impacts of the two are combined and managed as though they were a single perturbation. This overall response is designed to delay responses to the illusory perturbations in favour of planning modifications for the more salient physical perturbations.

Experiment 2

To examine the manner in which performers manage movements made against two simultaneous perturbations of late trajectory discrete control, Experiment 2 utilized similar kinematic methods (Khan et al, 2006) to investigate the movement trajectories of reaches made against random presentations of all possible combinations of the Müller-Lyer illusion and actual target relocation. At the beginning of a movement, the target would either reconfigure to a tails-in structure (perceived amplitude decrease), or tails-out structure (perceived amplitude increase), or remain in its control form. Simultaneously, the target could move towards (amplitude decrease), or away from (amplitude increase), the performer, or remain stationary. Although it is known that these two perturbations both act on control process associated with late trajectory control (Woodworth, 1899), we expected these perturbations to have impacts on the early trajectory. It was expected that these responses would be characteristic of those that account for an increase in target distance. If the two perturbations show differential effects, the possibility that the system of visual forward modeling differentially codes allocentric (i.e., the target relative to its surround) and egocentric (i.e., the target relative to the performer) information should be considered.

Methods

Participants. 20 right handed performers (10 male, 10 female) with normal or corrected-to-normal vision from the McMaster University community volunteered to participate in this study. All performers were naïve to the purpose of the study, gave informed consent according to the guidelines set out by the McMaster University Office of Research Ethics, and were paid $5 (Cdn) for their participation.

Apparatus and Procedure. The apparatus for Experiment 2 was the same as described in Experiment 1. Each trial required participants to make an aiming movement to a target defined by the point of intersection of a 25 cm line and two perpendicular 5 cm lines, which were arranged such that they formed a "T" configuration. The target figure was presented against a black background (Fig. 7a). All aims were performed while holding the same handheld stylus used in Experiment 1. The spatial location of the infrared light emitting diode (IRED) worn on the aiming finger was recorded in an identical manner to Experiment. Participants also wore liquid crystal goggles (Translucent Technologies, (Translucent Technologies, Toronto, Ontario, Canada) such that their vision could be systematically occluded.

The procedure for Experiment 2 was the same as that described for Experiment 1; however, rather than perturbing movements with compressed air and/or a moving background, the performers were exposed to a random combination of one of 3 Müller-Lyer illusions (tails-in (Fig. 7b), tails-out (Fig. 7c), control) and 3 moving target perturbation conditions (shorter, stationary, longer). Based on the results of previous work (Grierson & Elliott *a*, under review; Glazebrook, Dhillon, Keetch, Lyons, Amazeen, Weeks & Elliott, 2005) the target distance was shortened or lengthened in the primary movement direction, a distance consistent with the perceived shift imposed by tails-in and tails-out Müller-Lyer figures. Specifically, the target distance was either reduced to 24.75cm or increased to 25.25cm. Participants were aware of the possibility of a perturbation and were instructed to complete their movement as accurately-as-possible, regardless of any perturbation. Each participant performed 180 trials (20 trials/condition).

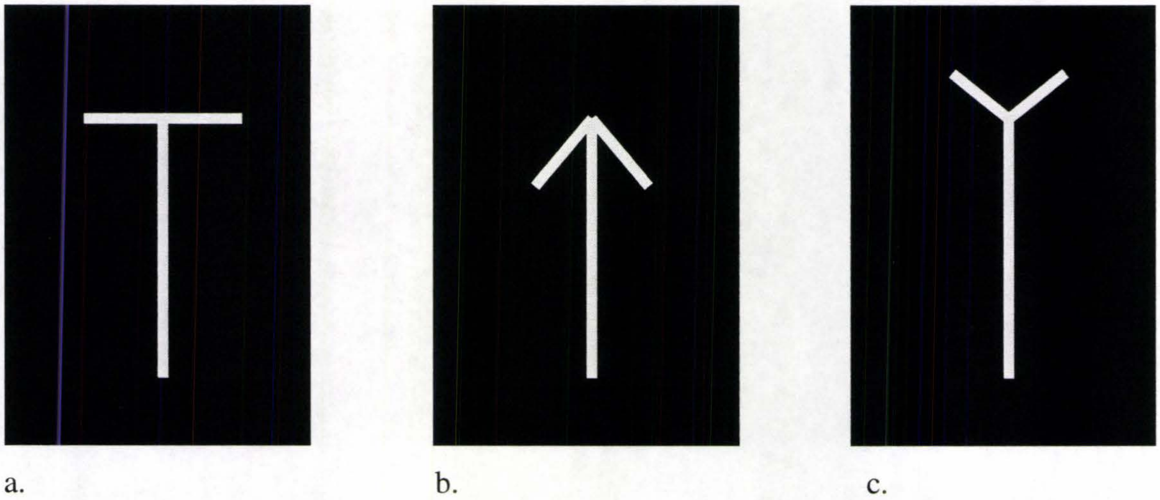

Figure 7. Depiction of the target display for Experiment 2: a) Control target b) Müller-Lyer tails-in target configuration c) Müller-Lyer tails-out configuration.

The collected displacement data were filtered, cleaned, and analyzed in the same manner as described in Experiment 1.

Results

Effects at Peak Acceleration. No differences were noted in mean displacement at peak acceleration between any of the perturbation conditions (grand mean = 9.84 mm). The time to peak acceleration analysis manifested no significant differences (grand mean = 137 ms).

The analysis of the magnitude of peak acceleration revealed a significant main effect for Müller-Lyer illusion, F (2, 38) = 3.93, $p < .05$. The post hoc analysis indicated that movements made to the control target structure (34.8 m/s^2) achieved higher peak acceleration than movements made to either of the illusory target structures (tails-in = 33.5 m/s^2, tails-out = 33.9 m/s^2), which did not differ from each other.

That this slowing occurs whether the target altered to a tails-in or a tails-out Müller-Lyer figure highlights the non-specific nature of these early responses.

Effects at Peak Velocity. The analysis of peak velocity yielded a moving target main effect, F (2, 38) = 3.41, $p < .05$, and a moving target by Müller-Lyer illusion interaction, F (4, 76) = 3.00, $p < .05$. Movements made to the longer target (104.2 mm) attained peak velocity after more distance traveled than those to the shorter target (101.5 mm). Movements made to the stationary target (102.7 mm) traveled an intermediate, but not statistically different, distance. Post hoc analysis of the interaction effect showed that movements made to the shorter and longer targets attained peak velocity after greater amplitude displacement when the target structure was altered to a tails-out configuration relative to when it was altered to a tails-in configuration. Interestingly, when the target did not relocate, movements achieved their peak velocity after significantly less distance traveled when the structure remained constant as compared to when the structure changed to either Müller-Lyer configuration (Fig. 8).

Movements made to the Müller-Lyer tails-in target structure (1.78 m/s) achieved a lower peak velocity than those movements made to a tails-out (1.81 m/s) or unaltered target structure (1.81 m/s), F (2, 38) = 4.52, p < .05. The time to peak velocity analysis yielded no significant differences between target structure or target distance conditions (grand mean = 294ms).

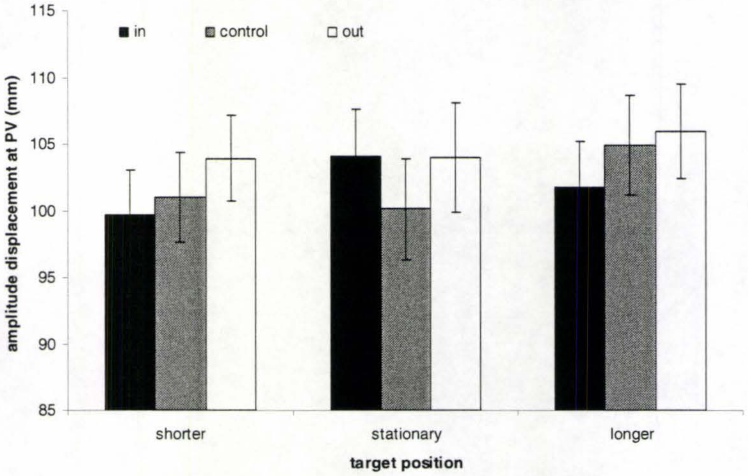

Figure 8. Experiment 2. Mean amplitude displacement at peak velocity (mm) for each moving target condition (shorter, stationary, longer) plotted as a function of Müller-Lyer illusion (tails-in (in), control, tails-out (out).

The findings gleaned from the analysis of the amplitude displacement at, magnitude of, and time to peak velocity revealed the impact of the moving target perturbation on the online control of movements. In particular, performers traveled further to reach peak velocity when the target moved further and they traveled less far when the target moved closer. The discriminating nature of these responses suggests that they are mediated by the full visual processing associated with late trajectory allocentric control. Furthermore, the specific nature of the Müller-Lyer impacts, reflected in the amplitude displacement interaction and the magnitude of peak velocity effects, highlight that by this kinematic event the illusions also were perturbing late trajectory visuomotor control. It is noteworthy, that reaches unperturbed by either a target reconfiguration or relocation began to decelerate after less distance traveled than those that reconfigured to either Müller-Lyer figure.

Effects at Peak Deceleration. The analysis of the mean dispalcement produced significant main effects for moving target perturbation condition, F (2, 38) = 6.97, p < .01, and Müller-Lyer illusion condition, F (2, 38) = 5.89, p < .01. These main effects were superseded by a significant moving target by Müller-Lyer illusion interaction, F (4, 76) = 3.81, p < .01. Post hoc analysis of this interaction indicated that movements made to the longer target traveled more distance by peak deceleration when the figure was altered to a tails-out structure than when it was altered to a tails-in figure. Movements to the longer target that did not reconfigure were at peak deceleration after a distance intermediate to, but not significantly different than, the altered target structures (longer target: tails-out = 231.4 mm, control = 230.6 mm, tails-in = 227.6 mm). When the target relocated to the shorter distance, peak deceleration occurred after less displacement for the unaltered target than for the tails-in target, and after less amplitude displacement for the tails-in target than the tails-out target (shorter target: tails-out = 229.0 mm, control = 223.8 mm, tails-in = 225.8 mm). In the instances that the target did not reposition, the mean displacement occurred after less distance for the unaltered structure as compared to either Müller-Lyer structure (stationary target: tails-out = 229.2 mm, control = 224.2 mm, tails-in = 228.8 mm).

Analysis of the magnitude of peak deceleration revealed a significant Müller-Lyer illusion main effect, F (2, 38) = 5.52, p < .01, in which movements to the tails-out target figure (27.9 m/s^2) generated greater decelerations than did movements to either the control target figure

(26.9 m/s^2) or the tails-in target figure (26.6 m/s^2). The time to peak deceleration analysis yielded no significant differences between perturbation conditions (grand mean = 531 ms).

In all, the amplitude displacement at, magnitude of, and time to peak deceleration results gleaned are in congruence with the well-documented effects of the two perturbations on late trajectory allocentrically driven visuomotor control (Elliott et al., 2001; Woodworth, 1899). However, movements to static targets that did not alter attained peak deceleration after less distance traveled than when those performed to targets that altered to either Müller-Lyer figure. In addition to the similar result found at peak velocity, this finding indicates that when the target experienced no perturbation the participant spent the majority of the distance decelerating towards the target.

Performance Outcomes. The analyses of reaction time (grand mean = 352 ms) and movement time (grand mean = 644 ms) revealed no significant differences for any of the Müller-Lyer or moving target conditions. A significant constant error main effect for the moving target perturbation, F (2, 38) = 18.05, $p < .0001$, indicated that movements made to the long target (-2.77 mm) and the stationary target (-2.34 mm) were performed with greater undershooting error than those made to the short target (-1.56 mm).

A significant constant error main effect was also revealed for the Müller-Lyer illusion, F (2, 38) = 14.66, $p < .0001$. Movements made to the tails-out Müller Lyer figure (-1.32 mm) were performed with less undershooting than those made to the control (-2.63 mm) or tails-in figures (-2.71 mm). Aims made to the control and tails-in figures did not differ. The analysis of movement constant error also revealed a significant interaction between the two perturbation conditions, F (4, 76) = 7.01, $p < .0001$. The post hoc analysis indicated that reaches made to the longer target were performed with greater undershooting error when the structure was altered to a Müller-Lyer tails-in configuration as compared to when it remained as the control structure or was altered to a tails-out structure (longer target: tails-in = -3.65 mm, control = -2.68 mm, tails-out = -1.98 mm). However, when the target shifted to the shorter position, the movements undershot the control structure more than when it altered to the tails-in figure, and the movements to the tails-in figure were performed with greater undershooting error than those to the tails-out figure (shorter target: tails-in = -1.86 mm, control = -2.83 mm, tails-out = -0.002 mm). There were no constant error differences between Müller-Lyer conditions when the target remained stationary (stationary target: tails-in= -2.63 mm, control = -2.39 mm, tails-out = -2.00 mm). The variable error analysis produced no significant differences between any of the movement conditions (grand mean = 4.57 mm).

Spatial Variability of Kinematic Events throughout the Entire Movement.

The 4 kinematic marker (PA, PV, PD, END) by 3 moving target perturbation (shorter, stationary, longer) by Müller-Lyer illusion (tails-in, control, tails-out) analysis of the within subject trial-to-trial spatial variability yielded a significant main effect for kinematic marker, $F(3, 57) = 22.44$, $p < .0001$. Movements in all conditions significantly increased in variability from peak acceleration (9.14 mm) to peak velocity (19.6 mm) and significantly decreased in variability from peak deceleration (19.2 mm) to the end of the movement (5.04 mm). However, no differences were noted in movement spatial variability between peak velocity and peak deceleration indicating that performers exercised a strategy in which rectifications to the movement perturbations were initiated as early as peak velocity (i.e., the onset of limb deceleration).

Overall. The results suggested that the moving target and Müller-Lyer illusion perturbations had relevant impacts on the late-trajectory control that they were designed to impact. Nevertheless, non-specific acceleration differences were evidenced in the early portions of movements made towards either of the illusory Müller-Lyer figures. That this difference was only revealed in the Müller-Lyer illusion conditions suggests that early, forward-modeled control is perturbed by changes to the environmental milieu or target shape characteristics, and not alterations to the perceived target location.

General Discussion

It is our contention that visually-regulated, goal directed action is mediated via two forms of online control. The first of these online processes operates to amalgamate information regarding the current state of the performer and the environment with efferent copies of executed movements, such that acting individuals are able to generate representations, for all streams of sensory afference, of the anticipated sensory consequences of their movements. When these expectations are incongruent with the actual sensory information received, performers modify their movements. Since this form of control functions to influence movements through mere recognition of an expected afference-to-actual afference violation, the amendments that it initiates are able to emerge quicker than possible when full visual processing is required. However, because these responses are generated without full recognition of the nature of the violation, they are not developed in a specific corrective manner. Rather, these alterations exhibit general characteristics to preserve the movements' integrity while giving the performer adequate time to fully re-evaluate the acting “landscapes”. Although basically non-discriminating, it is our position that the characteristics of these responses are pre-selected so that they are the least disruptive (or the most beneficial) to the attainment of the task goals. As such, we reason that a priori knowledge of potential sources of expected afferent violation alters the manner in which these alterations emerge. The second mode occurs later in the movement trajectories when the target and the limb can be simultaneously evaluated by central vision. Through the use of allocentric comparisons of the acting limb and the target, the performer is able to make specific and discrete movement adjustments to rectify any error. Presumably, this latter control form is constrained by the processing time inherent to visuomotor transformations and by the spatial constraints associated with the limits of focal vision. The experiments presented here were designed to investigate the planning and response strategies individuals use when performing visually-regulated goal directed aims against two perturbations to each of the two modes of online control.

The first experiment perturbed the continuous form of online control by exposing participants to all combinations of a physical perturbation (forward air blast, backward air blast, offsetting bi-directional air blasts, and no air blast) and a illusory perturbation (oppositely-translating background, similarly-translating background, stationary background). The compressed air perturbation has been shown effective in altering the early velocity of the moving limb (Grierson & Elliott *b*, under review; Grierson & Elliott *c*, under review) and the moving background illusion has adequately served to elicit movement alterations consistent with misperceptions of limb velocity (Grierson & Elliott *a*, under review; Proteau & Masson, 1997). By exposing movements to combinations of these two perturbations we sought to uncover the way in which performers plan for and respond to tandem early trajectory perturbations. We hypothesized that if advance knowledge of the potential perturbations was pertinent to the formation of rapid, anticipatory responses, the individuals would withhold any amelioration to counter the moving background until they had determined the presence or absence of a physical perturbation. This hypothesis predicted that the resultant trajectories would reflect controlled responses that managed the perturbations' combined impact. Conversely, if the emergent responses were not biased by a priori knowledge of the potential perturbations, we expected independent impacts of the two perturbations to be revealed within the trajectories. The findings support the notion that knowledge of the potential perturbations impacts early movement control. Specifically, the examination of the kinematic characteristics of peak acceleration, velocity, and deceleration, main effects were only uncovered for the physical perturbations, while the illusory perturbations only rendered an influence on the movements when interacting with the physical perturbations. In fact, the illusory perturbations had no apparent effect on goal-directed reaches until the end of the trajectories. As such we propose that responses to the moving background manipulation are withheld by performers for the initial movement portions, even if an air blast was not discharged. However, when an air blast was realized and the performers employed vision to aid with corrections, the visual information associated with the background then affected the implemented control. Interestingly, when the illusory perturbation worked in the same manner as the physical perturbation, the two perturbations intensified the performers' perceptions of limb velocity. As such, the original compressed air response was attenuated with an overall slowing of the limb; a strategy which optimized the performers' use of late, discrete corrective processes while minimizing the costs to movement speed and accuracy.

In order to perturb the late form of online control, the second experiment used a combination of moving target and Müller-Lyer illusion perturbations. By relocating the target on movement initiation, the moving target perturbation has been shown effective in affecting the portion of movements under late trajectory control (Heath et al., 1998). Likewise, Müller-Lyer illusions have been shown to affect late trajectory control by influencing performers' perceptions of target location (Elliott & Lee, 1995; Mendoza et al., 2005; 2006). However, in addition to the well-documented effects of these manipulations on late, discrete control, work form our laboratory also uncovered that these perturbations can have dynamic and non-specific effects on the early portions of reach trajectories. In particular, when performers made movements to target figures that reconfigured into Müller-Lyer structures on movement initiation their trajectories were marked by decreased accelerations and velocities regardless of the direction of the perceived shift (Grierson & Elliott *a*, under review). When the target relocated following the onset of movement, performers increased the amount of time they took to reach their acceleratory peak, regardless of the direction of the relocation (Grierson & Elliott *c*, under review). As such, we reasoned that changes to the target that were designed to impact late trajectory control were salient enough to impart an influence on the early portions of movement trajectories. The non-discriminating nature of these responses suggested that they were derived from violations of forward-modeled comparisons derived from expectations of the target environment. By presenting these two perturbations in tandem we expected, in addition to typical late trajectory differences, to elicit early movement responses. We expected these early responses to be non-specific and therefore to be congruent with changes required to obtain targets that had moved further away, regardless of the nature of the target change. As hypothesized both Müller-Lyer illusions were accompanied by a general decrease in the peak acceleration that performers achieved. However, no such early or non-specific responses were elicited for the moving target manipulations. Seemingly, the forward-modeled control associated with central vision is sensitive to changes to the allocentric relationships between the target and its surround, but not to variations in the egocentric relationship between the actor and the target. Although it must be considered that as the target repositioning was not substantial, the target likely never leaves central vision. As such, the slight target repositioning may not generate a violation of the modeled expected-to-actual comparison. In fact, Desmurget and Grafton (2000) showed that the movement of targets during saccadic eye motion was not recognized by performers despite their ability to appropriately adjust their reaches. Conversely, the relocation of the 5cm tails of the Müller-Lyer figures may breach the limits of focal vision and, as such, reflect a larger discrepancy between what is expected and what is seen, even though the intersection of the lines remains constant.

Importantly, the perturbations to targets, backgrounds and early trajectory dynamics all elicited early control characteristics. Also, in each case, the characteristics of the early responses were non-specific and these non-discriminating responses were congruent with responses to manage the worse case scenario of each of the possible perturbation combinations. Taken together, the results of the present experiments support the notion that forward modeled anticipatory control functions to continuously influence goal-directed aiming on many levels of sensory afference, and highlight how movement trajectories and online responses are differentially formed when individuals have a priori knowledge of potential perturbations.

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Chapter 6

CONCLUSIONS

Conclusions

The four sets of studies presented in this thesis were designed to investigate a theoretical mode of control that operates early and continuously throughout movements (Elliott, Chua & Helsen, 2001), and its relationship to the well-documented late trajectory control associated with discrete, visually regulated corrections (e.g., Woodworth, 1899). Because the modifications associated with this continuous control have been shown to occur quicker than movement-associated visual feedback can be processed, it has been proposed that this process functions by comparing actual incoming afference to internally generated representations of the expected afference (Desmurget & Grafton, 2000). In this way, forward modeled control provides performers with a way of rapidly identifying and rectifying errors of movement selection and execution. However, questions remained concerning whether a mode of anticipatory control is able to make rapid and specific adjustments to unexpected changes to the movement or its environment (e.g, Proteau & Masson, 1997). As such, this thesis examined the kinematic profiles of reaches made against various combinations of actual and illusory, and early trajectory and late trajectory movement perturbations. The purposes of this endeavor were to measure the kinematics of early and continuous movement control, to challenge the forward model explanation of this process, and to investigate the interaction of this control mode with the visually-regulated control that is manifested as the limb nears its target.

The first of these studies examined reaches made in three illusory perturbation experiments. The first experiment perturbed late trajectory control by having performers move to targets that altered to Müller-Lyer figures. The second experiment perturbed the early portion of reaches by translating the background over which performers aimed. The movements made in the third experiment were conducted against all combinations of the Müller-Lyer illusion and moving background perturbations. The results of these experiments replicated the early and late impacts of the perturbations, and also yielded non-interactive effects on endpoint accuracy when the two perturbations were presented in tandem. I interpret these findings as evidence that the two forms of control operate independently. The study also revealed an unexpected reduction in the peak acceleration of movements made to either Müller-Lyer structure. This finding suggests that the early mode of online control may serve a supervisory function that prompts a conservative movement adjustment following non-specific recognition of a change in the environment.

The second study tested the applicability of a novel compressed air perturbation device to alter the velocities of ongoing movements. In addition to examining how movements were modified in response to these air blasts, this study also examined the role of visual information to the process of early online control. The study revealed that the compressed air device effectively impacted limb velocity. Secondly, it showed that early online control works to offset these impacts regardless of the availability of vision; however, the efficiency of this control was attenuated in its presence. Importantly, the results revealed that the response to either forwarding or hindering perturbations was to advance the limb forward. These findings are interpreted as further evidence that early online control operates non-specifically to minimize the impact of the worse case perturbation scenario. Interestingly, when these responses occurred with vision, they each are advanced to a common location for the initiation of limb deceleration. It was suggested that this location represents the point in the trajectory in which both the limb and the target are captured by foveal vision. As such, the management of the perturbation seems to involve a rapid deference from early non-specific control to more resolute visually-regulated control. A small supplementary EMG study, which examined the wrist, elbow and shoulder, agonist and antagonist muscle activations, further supported the notion that performers respond to the compressed air perturbation in a non-specific manner.

The third study used actual perturbations in a similar manner to the illusory perturbations used in the first study. In one experiment early movement trajectories are subjected to perturbations from the compressed air device. In the second experiment the target moved either closer to or further away from the performer. In the third experiment, the performers were exposed to combinations of both perturbations. The findings of the third study showed that the compressed air and moving target perturbations had the intended early and late trajectory impacts. However, contrary to the first study, these perturbations had an interactive effect on movement outcome. It is posited that when the two perturbations are presented in tandem they elicit parallel operation of the two control processes. The third study's findings also highlight an early and undiscriminating response to spend more time accelerating when moving to either relocated target.

The fourth study examined the early, non-specific responses of movements performed against combinations of actual and illusory perturbations to either the early or late portions of the movement. In the first of these experiments performers were subjected to combinations of the moving background and the compressed air perturbations. The results of this experiment revealed that responses to the moving background illusion only influenced early control in the event that the stylus also discharged air. These findings were interpreted as evidence that a priori knowledge influences the way online ameliorations are achieved. That is, when made aware of a potential an air blast the participant withheld non-specific responses to the translating backgrounds. In the second experiment, performers reached to targets that relocated and reconfigured to Müller-Lyer structures. While these perturbations had interactive effects on movement outcome, the findings also highlighted early trajectory modifications that occur in response to target perturbations. The findings of both experiments indicate that early trajectory control is non-specific, but its response characteristics are biased to minimize the impact of the worse case perturbation situation.

When taken together, the findings of these four studies make several noteworthy contributions to models of goal-directed aiming. First, the many differences yielded from the early portions of movements exposed to various perturbations confirm that the initial portion of the movement trajectory is privy to the benefits of online control. However, early movement modifications are seemingly selected on a non-specific basis. As such, the forward model explanation of early movement control can not be dismissed. Presumably, performers generate expectations of the forthcoming sensory consequences to compare against the actual afferent information collected. When a violation between the expected and actual information is noted the system is directed to ameliorate the movement. That these amendments are undiscriminating suggests that the central nervous system does not wait to evaluate the nature of the violation. In this way the modification can be initiated quickly, during the early reach portions, and before full visuomotor processing can take place. Secondly, because this early non-specific regulation occurs in situations in which the target or background is altered, it is posited that performers also make expected-to-actual comparisons concerning the acting environment. Thirdly, these studies highlight that early movement responses are biased towards accounting for the worse case perturbation situation. These worse case biases are manifested in the early limb slowing to targets and backgrounds that move, the forwarding of limbs against potentially hindering backward blasts, and the execution of singular responses when the early limb movement is impacted by two perturbations.

The present findings also confirm the presence of a feedback-regulated form of control that operates to make discrete corrections based on visual information concerning the limb and the target. Importantly, the results of the first study indicated that the two modes of control can operate independently in influencing movement trajectories and outcomes. In the subsequent studies, the increased salience associated with the actual limb velocity perturbation seemingly dictated the parallel operation of the two processes. As such, rather than conceptualizing the forward modeled control as an exclusively early process, it is more likely that it functions continuously with visually regulated control overlapping it later in the trajectory. Furthermore, discrete corrections have been attributed to the late portions of trajectories on the basis of a minimum processing time for visual information. However, this form of control is also subject to the spatial limits associated with simultaneously holding the limb and the target in focal vision. This is particularly evident when performers are faced with a potentially hindering air blast perturbation under full and no vision conditions. In each case, the performers respond by advancing the limb, or allowing it to be advanced. However, in several instances with vision, they attain a common spatial location for the initiation of deceleration. As such, it is posited that when the limb reaches this location it can be simultaneously held in focal vision with the target. In this way, the performer acts to defer movement supervision from a non-specific, anticipatory process to a resolute, allocentric mode of control.

Although Woodworth (1899) put forth the seminal two-component model of voluntary goal-directed movement more than a century ago many of his ideas still resonate today. Arguably the most notable and long-standing aspect of the model is the presence of a visually regulated control process. Despite Woodworth's overestimation of the temporal limits of this process, and the current contention that this process is also encumbered by spatial constraints, his depiction of late trajectory control continues to adequately explain the discrete changes in movements as they approach their target. However, Woodworth's model was not without shortcoming. In particular, over the last one hundred years researchers have questioned and refuted the ballistic nature of the model's initial adjustment component. While Woodworth held that the initial portions of goal-directed reaches were structured completely in advance of movement initiation (see also Keele, 1968), sophisticated technological advances in kinematic analyses techniques have since revealed that these reach portions are amendable online (Elliott et al., 2001; Khan et al., 2006; Proteau & Masson, 1997). This thesis offers evidence that furthers the conceptualization of the control process that operates during the initial portions of movements. Specifically, the control executed early in movements seems to be part of a supervisory process that operates continuously. Its supervisory nature entails that it only initiates adjustments in the instance that what is expected does not happen. As such erroneous movements may, as Woodworth suggested, continue unaltered until late trajectory current control begins operation. However, when the performer's afferent expectations are not met then this continuous control may render an influence on the initial adjustments that begin movements.

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