

Goal-Directed Reaching

The Multiple Process Model of Goal-Directed Reaching Revisited

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Abstract

Recently our group forwarded a model of speed-accuracy relations in goal-directed reaching. A fundamental feature of our multiple process model was the distinction between two types of online regulation: impulse control and limb-target control. Impulse control begins during the initial stages of the movement trajectory and involves a comparison of actual limb velocity and direction to an internal representation of expectations about the limb trajectory. Limb-target control involves discrete error-reduction based on the relative positions of the limb and the target late in the movement. Our model also considers the role of eye movements, practice, energy optimization and strategic behavior in limb control. Here, we review recent work conducted to test specific aspects of our model. As well, we consider research not fully incorporated into our earlier contribution. We conclude that a slightly modified and expanded version of our model, that includes crosstalk between the two forms of online regulation, does an excellent job of explaining speed, accuracy, and energy optimization in goal-directed reaching.

Keywords: speed-accuracy, aiming/reaching, visual feedback, movement planning, limb trajectories

1. Introduction

Since the classic work of Woodworth (1899), a fundamental challenge in the area of perception and motor control has been to identify the sensory-motor and cognitive processes associated with rapid and accurate goal-directed upper limb movements. Woodworth held that most aiming/reaching movements were made up of two components. There was a ballistic component (i.e., an initial adjustment) designed to get the limb to the target area and then a feedback-based or homing phase to the movement (i.e., current control) that was responsible for correcting any error associated with the initial adjustment (Woodworth, 1899). This feedback-based phase was responsible for bringing the limb onto the target. The homing or corrective phase of the movement was thought to rely heavily on visual feedback about the position of the hand relative to the target. Although not stated explicitly, the planning of the ballistic phase of the movement also depends on visual information about the position of the target relative to the hand's starting point.

Over the next century, there were a number of important models of speed-accuracy relations in goal-directed aiming (e.g., Beggs and Horwarth, 1972; Carlton, 1981; Crossman and Goodeve, 1963/1983; Elliott et al., 2001; Keele, 1968; Meyer et al., 1988; Vince, 1948). Fundamental to most of these models (cf. Schmidt et al., 1979) was the distinction between Woodworth's ballistic and feedback-based components. During the last 15 years however, many empirical studies have made it clear that the ballistic component of a typical aiming movement is not as ballistic as was previously thought (see Cluff et al., 2015 and Smeets et al., 2016 for recent reviews).

Several years ago, our group published a paper in which we presented a new model of speed-accuracy relations in goal-directed aiming (Elliott et al., 2010). Our Multiple Process Model of Goal-Directed Reaching builds on Woodworth's two-component explanation of speed-accuracy relations, but also argues for a different type of online control associated with the initial distance-covering phase of the aiming movement. This type of early control involves graded adjustments to the initial movement trajectory based on visual information about limb velocity and direction. Like Woodworth, our model includes a discrete corrective phase, late in the movement, that is based on the relative positions of the limb and the target. We have termed these two distinct corrective processes impulse control and limb-target control respectively.

Figure 1 provides an overview of the main features of our model and the time-course of the sensory-motor processes associated with limb regulation over the trajectory of a single aiming movement. Briefly, any goal-directed aiming movement involves an initial planning (Event 1) and specification process (Event 2) that take into consideration the stochastic properties of neural-motor noise and force specification error, as well as the associated spatial error, over multiple attempts to perform the same type of movement. Aiming movements are organized to optimize not only movement speed and endpoint error, but also energy expenditure over many trials. The force-time specification process also includes the formation of an internal model of the planned movement that comprises information about both expected efference and the expected sensory consequences of the movement, including expected limb direction and velocity. Almost immediately after movement initiation, limb efference and afference regarding movement direction and velocity are compared to expectancies associated with the internal model/representation

(Events 3 and 4), and graded adjustments are made to the primary acceleration and deceleration portions of the movement trajectory. This type of limb regulation can occur very rapidly (i.e., 70-85 ms; Bard et al., 1985; Zelaznik et al., 1983). Our model refers to this corrective process as impulse control. In parallel, afferent visual and proprioceptive information about limb position is compared to visual information about the spatial position of the target (Event 5). This information provides the basis for any late adjustment(s) to the limb trajectory that might be necessary to hit the target. We call this discrete corrective process limb-target control (Event 6). Limb-target regulation involves greater top-down control and therefore requires more time. Although most estimates for visual processing time in limb-target regulation are consistent with the time required for a visual reaction time (i.e., 180-200 ms; see Elliott et al., 2010 for a review), there are estimates as low as 100 ms for at least the beginning of a discrete corrective response (Paulignan et al., 1991).

As we will explain later, because it is usually strategically sound to undershoot the target with the primary movement, limb-target regulation often involves a second limb acceleration-deceleration to reach the target. At the completion of the aiming movement, terminal visual and proprioceptive feedback are processed and subsequently used to refine strategic behavior and the internal model associated with planning future movements (Event 7).

In this paper, we review the empirical and theoretical background associated with our 2010 multiple process model, and in particular impulse and limb-target control. We then evaluate and update our model based on work published both by our group and others over the last several years. Our update and evaluation includes the examination of

some work published prior to 2010 that was not incorporated in our 2010 paper (Elliott et al., 2010). We also provide an expanded explanation for the role of specific types of ocular information play in limb control. Where appropriate, we acknowledge the similarities and differences between our model and other explanations of speed-accuracy relations in goal-directed aiming.

2. The Multiple Process Model: Limb-Target Control

Although the iterative correction model (Crossman and Goodeve, 1963/1983; Keele, 1968) and the single correction model (Beggs and Howarth, 1972; Carlton, 1981) were both timely and important variations of Woodworth's explanation of speed-accuracy relations, the most influential model of limb control has been Meyer et al.'s optimized submovement model. Like Woodworth, Meyer et al. (1988) held that an initial distance covering movement is planned and executed to bring the limb into the vicinity of the target. The planning of the movement however, takes into consideration stochastic principles associated with the specification and generation of the muscular forces required to move the limb (see also Schmidt et al., 1979). Specifically, multiple attempts to produce a similar aiming movement result in a normal distribution of movement endpoints centered on the middle of the target. The degree of variability associated with any set of similar movements depends on the magnitude of the muscular forces recruited to accelerate and decelerate the limb. Greater muscular forces get the limb to the target area more quickly but, on any given trial, the limb is less likely to hit the target. This outcome occurs because the distribution of primary movement endpoints is larger. A larger distribution occurs because force variability, and thus spatial variability, increase with the absolute magnitude of the forces specified to move the limb. If the limb falls

outside the target area, a corrective submovement is required. Corrective submovements take time to complete. Thus, the optimal strategy is to produce movements that get the limb to the target area quickly, but not so quickly that a time-consuming corrective submovement is required on the majority of trials. As the name of the model suggests, the performer plans and executes movements that optimize movement velocity (and movement time) so that the need for corrective submovements is minimized.

Although the optimized submovement model provides an excellent mathematical explanation of speed-accuracy relations, including Fitts' Law (Fitts, 1954; Fitts and Peterson, 1964), the hypothesized nature of primary movements and corrective submovements is not consistent with the spatial-temporal characteristics of the trajectories seen in most three-dimensional aiming movements.¹ Specifically, the endpoint of the primary, distance-covering, phase of the movement is not centered at the middle of the target. Rather primary movement endpoints typically fall short of the target (see Elliott et al., 2004, Engelbrecht et al., 2003 and Worringham, 1991 for information about frequencies). This endpoint bias is consistent with a strategic approach to manual aiming because target overshoots are more costly in terms of both time and energy than target undershoots. Specifically, an overshoot requires the limb to cover a greater overall distance and overcome the inertia of a zero velocity situation at the point of reversal. Thus, while the performer takes into consideration the stochastic characteristics of endpoint aiming distributions (Meyer et al., 1988), these distributions are generally centered short of the target to reduce the probability of target overshooting on any given trial (Elliott et al., 2001, 2010).

The degree of primary movement undershooting in any given target context depends on the trial-to-trial variability associated with the primary movement endpoints. That is, the amplitude of the primary movement is inversely related to the spatial variability (Elliott et al., 2004; Worringham, 1991), because the strategic goal of the performer is to keep the far tail of the endpoint distribution as close to the far boundary of the target as possible. Thus, rapid-large amplitude movements that are characterized by greater spatial variability than slow small amplitude movements are also associated with greater undershooting. When a performer is able to reduce primary movement endpoint variability, via extended practice, undershooting also becomes less pronounced. This means that more aiming attempts hit the target area without a corrective submovement. However, the low proportion of target overshoots remains unchanged (e.g., approximately .05; Elliott et al., 2004).

Our model predicts that if one increases the temporal and energy costs of a target overshoot, undershooting with the primary movement becomes even more pronounced. For example, participants undershoot to a greater extent when aiming downward than either upward or horizontally (Lyons et al., 2006). This outcome occurs because target overshoots, when moving downward, entail a corrective submovement against gravity, thus requiring more time and energy than corrections made to upward or horizontal movements. A strategy of undershooting downward movements to a greater extent than other movements appears to be even more pronounced in older adults (Bennett et al., 2012). This exaggerated ‘play-it-safe’ strategy in older adults is consistent with other findings in the literature which show that older adults often sacrifice movement speed to reduce final endpoint error and minimize energy expenditure (Ketcham et al., 2002;

Poletti et al., 2015; Pratt et al., 1994; Van Halewyck et al., 2014, 2015a, 2015b; Welsh et al., 2007).

With respect to vertical aiming, it is instructive that even young adults become more conservative in their strategic aiming behavior when goal-directed limb movements are visually occluded at movement initiation, thus preventing visual online control. Specifically, participants exhibit even more undershooting when aiming downward, and exhibit either no corrective submovements or shorter amplitude corrective submovements than when aiming upward (Elliott et al., 2014). Of equal importance to concurrent visual feedback is the availability of terminal visual feedback about endpoint error. Specifically, when vision is eliminated during the movement and at the termination of the movement (i.e., vision only available for premovement planning) then adult participants exhibit profound undershooting with respect to their primary movement endpoints and final endpoint error (Elliott et al., 2014). This type of outcome might reflect a strategy that minimizes time and energy expenditure, and takes into account safety considerations. That is, target undershoots are less likely to bring the limb into contact with obstacles that may or may not be dangerous (Elliott et al., 2009).

In a recent vertical aiming study (Burkitt et al., in press), we sought to expand our examination of strategic behavior by attaching a short or longer rod to the index finger performing vertical aiming movements to near, middle, and far targets. We expected the extended effector to promote different energy minimizing strategies by engaging the distal joints in the displacement of the end effector (e.g., finger or wrist flexion/extension to move the rod end without displacing the whole arm). Consistent with the predictions of our model, the primary movement undershot far target locations to a greater extent for

downward compared to upward movements. An examination of the joint angles involved in aiming revealed that as rod length increased, shoulder elevation was optimized for far-up targets and elbow flexion was minimized for movements to far down-targets. Overall, although effector kinematics were in agreement with the predictions of our multiple process model, the control of joint angles for energy optimization was less dependent on gravity.

Consistent with the vertical aiming work, we have also demonstrated that increasing the mass of a hand held stylus used for aiming results in greater undershooting with the primary movement (Burkitt et al., 2015). In line with our multiple process model (Elliott et al., 2010), this outcome occurs partly because a greater mass is associated with greater muscular force and therefore increased spatial variability. Moreover, an overshoot in a large mass situation entails more time, and energy-consuming corrections than a target undershoot.

Central to our view of the strategic processes associated with movement planning is the performer's prior knowledge of the visual and other online feedback available for concurrent limb control. Perhaps the first evidence to show the importance of prior knowledge about feedback came from studies in which vision was either provided throughout the movement trajectory or occluded upon movement initiation. Under these conditions, the performer is able to make more effective use of vision if they know, in advance, that it will be available. Thus, an aiming protocol in which the vision-no vision manipulation is blocked, rather than varied randomly from trial-to-trial, allows the performer to make more effective use of vision for rapid online limb control (Elliott and Allard, 1985 and Zelaznik et al., 1983 compared to Keele and Posner, 1968). The idea is

that if the performer knows that vision will be available, they plan the aiming movement in a manner that maximizes the opportunity for visual online control. When there is uncertainty, the performer generally prepares for the “worst-case” or “no vision” scenario.

Analysis of movement kinematics indicates that prior knowledge about the availability of vision affects a number of characteristics of the movement trajectory. For example, Hansen et al. (2006) reported that prior knowledge about the availability of visual feedback influenced the symmetry of the velocity profile. Specifically, when the performer was able to plan the movement with the expectation that vision would be available, the strategy was to move to the target area quickly so that a greater portion of the overall movement time was available for late online control. In terms of kinematics, this meant that participants achieved higher peak velocities earlier in the movement and spent a greater proportion of the overall movement time after peak velocity. When vision was not available, or there was uncertainty about its availability, the aiming trajectories were more symmetric indicating less online control based on vision. When participants know vision will be available they also spend less time preparing their movements (i.e., shorter reaction times; Burkitt et al., 2013; Hansen et al., 2006; Khan et al., 2002).

Presumably, precise planning is not as necessary because they know they will have vision available throughout the trajectory for online regulation. As well, there is sometimes greater spatial variability early in the movement trajectory when aiming with full vision than when vision is eliminated upon movement initiation. However, with vision there is a greater reduction in spatial variability between peak deceleration and the end of the movement, reflecting the robust nature of the limb-target corrective process (Khan et al.,

2002; see also Khan et al., 2003). The overall strategic approach taken by participants under different sensory and/or uncertainty conditions reflects a top-down and perhaps conscious contribution to the optimization of movement time, movement accuracy and energy expenditure.

Recently, we attempted to extend our performance findings associated with prior knowledge to motor learning (Burkitt et al., 2013). The experiment was based on the idea that motor learning, in part, depends on the development of an internal model or representation of the skill being practiced, including information about the intensity and timing of the muscular forces and expectancies about the sensory consequences. In our multiple process model of limb control, the specifics of the movement plan depend partly on strategic, and sometimes conscious, considerations such as the temporal and energy costs of different types of error, while expectancies about feedback are important for the rapid online corrective processes associated with impulse control. Again, our notion was that under conditions of uncertainty about feedback, performers plan for the worst-case scenario. That is, if the probability is 50% (i.e., non-predictive) that vision will be available for online control, adult participants generally prepare themselves to perform goal-directed aiming without vision. The prediction follows that if an individual practices aiming under conditions of feedback uncertainty, they should develop an internal model more similar to those practicing under strictly no vision conditions than those practicing under full vision conditions (Elliott et al., 1995; Proteau et al., 1987). This is exactly what we found, with performers exhibiting similar effects of prior knowledge during acquisition. However, they quickly adapted their aiming strategy to make full use of the sensory information available in retention and transfer (Burkitt et al.,

2013). It would appear, then, that adult performers are extremely flexible in adopting a strategic approach to goal-directed aiming that makes optimal use of the information available for online control. Thus, at least with respect to sensory conditions, the internal model is more adaptable than our model originally held. Specifically, it would appear that a simple aiming model can be adjusted after only a few trials in another sensory condition. In future work, it would be useful to manipulate other aspects of the acquisition and retention/transfer experience. For example, by changing the mass of the effector (e.g., adding or removing weights), we have the potential to gain insights into how internal models of reaching change in the short-term when a performer is required to move objects from one location to another. This type of work may also help us understand how children adjust their internal models for reaching as the mass of their effectors increase. It would also compliment research involving older adults who appear to be quite adept at adjusting their motor behaviors to accommodate a less robust sensory-motor system (e.g., Bennett et al., 2012; Van Halewyck et al., 2015a).

One of the main features of the multiple process model of limb control is that participants plan their movements to minimize the cost of limb-target corrections late in the movement. We have repeatedly used the term “strategic” to describe this play-it-safe approach to upper limb control (Oliveira et al., 2005). In this context, it is important to note that aiming/reaching strategies developed over a lifetime of interacting with objects in the environment are not always conscious strategies. The most compelling evidence to indicate that limb-target control is often more implicit/unconscious than explicit/conscious comes from studies using various masking procedures designed to prevent conscious processing of visual target information (e.g., Binsted et al., 2007).

Using a modified object substitution-masking protocol developed by Di Lollo et al. (2000), Binsted et al. (2007) had adult participants make manual aiming movements to targets of various sizes at several movement amplitudes. Under normal circumstances, the expectation was that movement times to acquire these targets would conform to Fitts' Law. That is, more time would be taken to reach small targets with longer amplitude movements than large-near targets (Fitts, 1954; Fitts and Peterson, 1964). The added movement time associated with higher index of difficulty target arrangements would be reflected, primarily, in the time after peak velocity when limb-target corrective processes operate (Elliott et al., 2001). Participants made aiming movements from a home position at the midline to one of many possible targets presented in an array. The array was presented for only 13 ms, and the target for a trial was identified by 4 surrounding red cue circles. These circles were visible at the four corners of the target area and were oriented in a square that was independent of target size. In what the authors termed their "conscious" condition, the targets and the 4 circles disappeared together after the 13 ms presentation period. This protocol left participants with a conscious visual representation of the target position and size on which to plan and control their aiming movement (see Elliott and Madalena, 1987 and Heath, 2005). In an "unconscious" condition, the red cue circles remained visible when the actual targets disappeared, thus serving to mask information about the target size. Accordingly, participants were consciously aware of the target position (i.e., via the red circles), but not the target size (i.e., only available for 13 ms and then masked).

In spite of no conscious awareness of target size under object substitution-masking conditions, movement time varied with both movement amplitude and target

size as it did in the conscious/no mask conditions. That is, aiming to “unseen” targets conformed to Fitts’ Law with the target size effect being most pronounced in the time after peak velocity (i.e., during limb-target regulation). Binsted et al. (2007) liken this type of unconscious limb control to blindsight seen in patients with damage to primary visual cortex. Some of these patients can regulate limb movements to targets in their blind field without having any explicit (verbal) pattern recognition ability (Weiskrantz, 1996). This type of finding has also been used to support the distinction between vision for perception and vision for action (Milner and Goodale, 1995; see also earlier work on midbrain visual-motor systems: Schneider, 1969; Trevarthen, 1968).

A more traditional method for examining implicit/unconscious target-based corrective processes has been to shift the target position slightly at, or shortly after, movement initiation. In an early study, Pélisson et al. (1986) had participants move their hand, which was masked from view, to small targets that on some trials shifted position slightly (i.e., 2 to 4 degrees) after movement initiation during the time that the participant was making a saccadic eye movement. Under these conditions, participants adjusted their movements toward the new target position without being aware that the target had moved. This adjustment was made at no cost to movement time. Because participants were not able to see their hand, these data suggest that limb-target regulation can occur without concurrent visual information about the position of the limb. Instead, in the case of the Pélisson et al. (1986) study, limb position was likely provided via either proprioception or efference.²

Interestingly, Paulignan et al. (1991) reported a similar result using a grasping experiment in which the position of a dowel was shifted to the right or the left at

movement initiation. Kinematic data revealed that movement was modified based on processing of visual information about the new dowel position. Although it took approximately 250-290 ms to complete a corrective submovement to the new target position, the perturbations of target position added only 100 ms to the overall movement time. Examination of the limb trajectories indicated that limb adjustments started during the deceleration phase of the primary movement. This is consistent with our ideas about limb-target control in the multiple process model. The authors suggested that the corrective process sometimes began in as little as 100 ms. This is the lowest estimate of visual processing time for limb-target control that we have found in the literature. Although not stated explicitly, it would have been surprising if participants were unaware of the large perturbation in this experiment.

In our work, we have not attempted to conceal the nature of the perturbation from conscious awareness. For example, when we shifted either the size of the target or the position of the target at movement initiation (e.g., Hansen and Elliott, 2009; Heath et al., 1998), participants were clearly aware of the new target circumstance. Still, with respect to our multiple process model of limb regulation, it is instructive to consider how and when changes to the movement trajectory are realized. Specifically, Heath et al. (1998) had participants make rapid aiming movements to a single target on the midline. On 76% of the trials, the characteristics of the target remained unchanged as the movement was executed. However on 24% of the trials, target size either decreased (12%) or increased (12%) upon movement initiation. Although on these perturbation trials participants changed their aiming to accommodate the new speed-accuracy demands, this change did not occur until the deceleration phase of the movement. Thus, peak velocity and time to

peak velocity reflected the size of the target visible during the planning phase of the movement, while the time after peak velocity was influenced by the new target size (i.e., greater deceleration time for the smaller target and less deceleration time for the larger target).

In a second experiment, Heath et al. (1998) used a similar protocol, but instead of changing target size, the target moved position on movement initiation (i.e., 1.5 cm closer to or further from the home position). Once again, on the perturbation trials, the early characteristics of the movement trajectory reflected the initial target position while the late characteristics of the trajectory and movement outcomes were driven by the new target position. With respect to the multiple process model of limb regulation, this finding is consistent with the notion of the late portion of the movement trajectory being associated with limb-target control (Woodworth, 1899; see also Hansen and Elliott, 2009).

In other work, our group has used an illusory target context to perturb aiming movements that have already been planned. For example, Handlovsky et al. (2004) used the Ebbinghaus illusion (or Titchener circles) to make the size of a central target circle appear bigger or smaller than its actual size. Similar to Heath et al. (1998), participants prepared their movement based on one target configuration, which in some trials was changed on movement initiation. When the target configuration presented at movement initiation made the central target appear bigger (i.e., central target surrounded by much smaller circles), participants completed their movements more quickly than in the other contexts. Moreover, the difference in movement time between conditions was primarily due to the time after peak velocity when limb-target regulation occurs.

Similar illusory biases have been expressed following rapid aiming to the vertices of Müller-Lyer configurations appearing shorter (tails-in) or longer (tails-out) than a control configuration (X or T). Once again, one form of the illusion or a control configuration was visible for movement planning, but was sometimes changed upon movement initiation (Mendoza et al., 2006). Of interest was how biases unfolded over the movement trajectory. Indeed, the figure that was visible during movement planning had an impact on movement amplitude consistent with the illusory context (e.g., shorter amplitude for the perceptually shorter tails-in than the longer tails-out) during the early portions of the movement (i.e., up to peak deceleration). However, the configuration introduced at movement initiation did not have an impact on bias until peak deceleration. It did however have an impact on aiming error between peak deceleration and the end of the movement. Together, these data provide strong evidence for late, limb-target control and how it manifests through both real (e.g., Hansen and Elliott, 2009; Heath et al., 1998) and illusory target changes (Handlovsky et al., 2004; Mendoza et al., 2006). These studies helped provide the foundation of our multiple process model and also the impetus for the work of Grierson and colleagues designed to test our model (also see studies in the impulse control section).

In this theoretical and empirical context, Grierson and Elliott (2009b) conducted a study in which both real and illusory target perturbations were introduced in the same aiming movement. Specifically, participants were required to make rapid 25 cm aiming movements to a control target at the midline (i.e., the vertex of a T). At movement initiation, the figure either remained in the same position, or shifted its real position, illusory position, or both. The real shift was a 2.5 mm displacement either away from or

toward the home position. Once again the illusory shift involved a change from the control target to the tails-in or tails-out version of the Müller-Lyer illusion. Both types of target shifted endpoint error in the expected direction with the effect starting to unfold in the mid to late portion of the movement trajectory (i.e., from peak velocity to the end of the movement). The timing of these trajectory adjustments was consistent with our model. Although the effects of the two types of perturbation were very similar for late limb regulation (i.e., limb-target control), there was also a nonspecific influence of the illusory manipulation on the early movement trajectory. That is, when the target changed from the control figure to either the tails-in or tails-out Müller-Lyer configuration, participants slowed their movements taking more time to reach peak acceleration. This early adjustment to the trajectory may reflect a play-it-safe strategy that allows the performer more time to process the specific nature of the change in task demands. Therefore, consistent with our previous suggestions, it appears the performer attempts to alleviate the temporal and energy costs associated with late error corrections by refining their initial movement.

In recent work, we sought a better understanding of the relation between strategic movement planning processes and limb-target control by examining the impact of the Müller-Lyer illusion in a paradigm that involved vertical aiming (Roberts et al., in press). Specifically, participants aimed at Müller-Lyer targets presented in both the vertical (up and down movements) and horizontal plane (forward and backward movements). Because the illusion impacts perceived target location and strategic target undershooting varies with direction of the movement with respect to gravity, we expected the two manipulations to interact. As anticipated, downward undershooting biases emerged late

in the movement while illusory biases were apparent from peak velocity until movement termination. The illusory effects were greater for downward movements toward the end of the movement suggesting that limb-target control is more susceptible to target biases than impulse control. These findings indicate that our manipulations had relatively independent contributions to aiming trajectories until their combined impact emerged during the final portions of the trajectory (i.e., limb-target control).

Overall, our target perturbation studies indicate that the early portion of the movement trajectory reflects the target conditions presented prior to movement initiation. However, the time spent after peak velocity and the eventual performance outcomes are typically consistent with the new task requirements. In our work with illusions, participants are aware of the changes made to the target configuration. However their failure to adjust their aiming behavior from trial-to-trial suggests that participants were unaware of what impact these changes had on their movement trajectories or movement outcomes. From this work, it would seem that both explicit/conscious and implicit/unconscious processes contribute to limb-target control.

In this theoretical context, some of the most compelling work on conscious versus unconscious corrective processes in limb control comes from studies conducted by Cressman and colleagues. In an initial study, Cressman et al. (2006) had participants aim to targets that could change position either by moving to a new spatial location or by changing color with a second target object. They had participants aiming under “go” and “stop” instructional conditions that required them to make either the necessary correction to the change in target position or to abort the movement. These conditions were introduced to index intentional and automatic limb control respectively. Although under

intentional control (go instructions) participants were able to adapt their movements effectively based on shifts associated with spatial location and color, only shifts in spatial location elicited involuntary/automatic trajectory modifications (stop instructions). Thus, the procedure created dissociation between the neural systems responsible for rapid limb regulation based on spatial position and the color of the target.

In subsequent work, Cressman et al. (2007) used a backward masking procedure (see Binsted et al., 2007) to show that online limb control can be influenced by the “unconscious” processing of shapes (see also Cressman et al., 2013). These unseen shapes provided a directional cue (i.e., a triangle pointing to either the left or right) to the participant that could not be ignored. Assuming that this type of cue-response association is learned, these data suggest that limb-target regulation, while often unconscious, still has rapid access to acquired/learned representations of visual space (e.g., the meaning of an error pointing to the left or right). Recent work by Diamond et al. (2015) indicates that online limb regulation systems also have access to the acquired characteristics of hand-held object dynamics.

In summary, although evidence regarding the importance of limb-target control in rapid goal-directed aiming has a long history (e.g., Woodworth, 1899), in recent years we have been able to identify a number of variables that modulate not only movement outcome, but also the characteristics of the movement trajectory. Specifically, performers plan and execute their movements to not only minimize time and maximize accuracy, but also to minimize energy expenditure. They often plan their movements taking into consideration worst-case outcomes. As well, in order to engage in optimal planning for limb-target control, it is important that the performer knows in advance the

sensory information that will be available for limb-target regulation. Although in one sense the prior planning and online processes associated with limb-target can be thought of as strategic, it is also clear that, in a skilled adult performer, limb-target corrective processes can occur without explicit awareness (see Smeets et al., 2016). Moreover, given that movement planning plays an important role in determining the characteristics of the initial movement trajectory, perturbations to the target position, size and/or the visual context of the target result in trajectory adaptations designed to accommodate the new target circumstance. Consistent with our multiple process model of limb regulation and our ideas about limb-target control, these changes to the limb trajectory occur during the deceleration phase of the movement. This is the portion of the movement typically associated with discrete feedback-based control (Elliott et al., 2001; Woodworth, 1899).

3. The Multiple Process Model: Impulse Control

Since the seminal studies of Woodworth (1899), there has been general agreement about the importance of limb-target control in goal-directed aiming. More controversial is the notion of continuous limb regulation during the distance-covering phase of the movement. In our model (Elliott et al., 2010), we refer to this type of limb regulation as “*impulse control*”. We have suggested that impulse control is used to modulate movement direction and movement velocity. Although based on goal-directed premovement planning, during a single movement, impulse regulation is independent of comparison processes associated with the relative position of the limb and the target. Rather it involves a comparison of the unfolding movement characteristics, specifically limb direction and velocity provided by vision and proprioception, to expectations about this feedback developed prior to movement initiation. That is, corrective processes

associated with impulse control involve a comparison of the actual sensory consequences of the movement to the expected sensory consequences of the movement. The expected sensory consequences are part of an internal model specific to the movement plan developed and executed on any movement attempt (Wolpert and Miall, 1996; for historical context see von Holst, 1954, Sperry, 1950, and Teuber and Mishkin, 1954). The internal model is based on both general and specific prior experience with reaching/aiming movements, and becomes more refined with repeated practice involving the same class of movement (Elliott et al., 1995, 2010; see also Burkitt et al., 2013).

Our first interest in impulse control originated from studies in which we manipulated the availability of visual information for online regulation and measured not only movement outcome but also the spatial-temporal characteristics of the movement trajectory (i.e., the movement kinematics; see Carson et al., 1992; Elliott et al., 1999a; Elliott et al., 1991). In these studies, we often found accuracy advantages associated with the availability of visual information from the limb even though there were no more discrete limb corrections under full vision than under degraded vision conditions. These findings persuaded us to argue for some form of continuous (Elliott et al., 1991) or pseudocontinuous (Carson et al., 1992) control during the distance-covering phase of the movement trajectory. Our findings were also consistent with work in the 1980's on very rapid limb regulation under conditions involving little time for discrete corrective processes to operate (e.g., Bard et al., 1985; Carlton, 1981; Elliott and Allard, 1985; Zelaznik et al., 1983). Specifically, online visual regulation was found to occur in as little as 85 to 100 ms (cf. Keele and Posner, 1968). This type of visual regulation was

deemed too rapid to involve any adjustment to the target goal associated with a new action plan (e.g., Keele, 1968).

Over the years, as digitizing systems became less noisy and kinematic analysis techniques more sophisticated, we became convinced that our failure to find differences in discrete limb corrections between vision and no vision aiming conditions were not methodological. By parsing movement trajectories (Chua and Elliott, 1993; Walker et al., 1997), we were able to examine the distance of the limb from the target at both the end of the primary movement and at movement termination. In this way, we examined the effectiveness of the primary movement, independent of discrete corrective processes, under different sensory and practice conditions (Khan et al., 1998, 2006).³

In two recent aiming experiments, involving the manipulation of both concurrent and terminal visual feedback, Elliott et al. (2014) found that participants were closer to the target at the end of the primary movement under conditions in which vision was available for online control than when it was eliminated upon movement initiation. Because no discrete corrections had been made, this finding provides evidence for impulse control. When a corrective submovement occurred (i.e., a second acceleration or a reversal), error was further reduced, thus showing that limb-target regulation was also effective in reducing aiming error. Although greater endpoint error and variability were exhibited under no vision conditions than full vision conditions, there was evidence of limb-target regulation under both sensory conditions. Presumably, under no vision conditions, limb-target control depends on proprioceptive information about limb position and remembered information about target position (e.g., Elliott, 1988, 1990; Elliott and Madalena, 1987).

Of course there are more subtle ways to study the role of vision on limb regulation than visual occlusion. As an example, Proteau and Masson (1997) provided compelling evidence for impulse control in a study in which they manipulated the visual context in which aiming movements were performed. They used a computer-based aiming task in which participants moved a cursor across a computer screen toward a small target. As well as the cursor and the target, the screen displayed texture elements that, upon movement initiation, would either remain stationary or move in either the same or opposite direction as the aiming/cursor movement. This displacement of the target-aiming context creates an illusion associated with the velocity of the cursor. Specifically, when the background is moving in the same direction as the cursor, participants perceive the cursor to be moving more slowly than it actually is, with the opposite illusory effect in the reverse direction. These illusory effects of limb velocity resulted in participants either extending their primary movement beyond that observed in control conditions (i.e., same direction background) or terminating their movement early (i.e., opposite direction background). The adjustment associated with this misperception of velocity was to the initial impulse/primary movement and did not involve late discrete control. This study provides direct evidence for impulse control based on a mismatch between perceived limb velocity and anticipated limb velocity. Our group has replicated this moving background effect using three-dimensional aiming movements (e.g., Grierson and Elliott, 2009a).⁴

To perturb the position of the target with respect to the limb, we used prism spectacles to offset the actual location of the target while moving (Hansen et al. 2007). Specifically, we introduced or removed 15 degrees of visual displacement perpendicular

to the primary direction of the movement at, or shortly after, movement initiation. Our goal was to create a mismatch between the expected sensory consequences in planning, and the perceived sensory consequences in movement to examine online corrective processes. Under these conditions, participants made rapid adjustments to movement direction to hit, or at least come closer to, the target. These adjustments began prior to peak velocity when the visual perturbation was introduced at movement initiation, and suggest that information provided early in the movement trajectory is important for the regulation of movement direction (see also Bard et al., 1985). Interestingly, with respect to end point error, female participants were more adept than males at this type of directional “impulse control”.⁵ Although females spent significantly longer completing their movements than males when the prism was presented at movement initiation (Experiment 2), compared to control conditions, there was very little movement time cost associated with the operation of this type of corrective process for either gender (i.e., impulse control). This finding is in contrast to limb-target control where discrete corrections take extra time (e.g., Elliott et al., 2004; Meyer et al., 1988).

Just as limb-target regulation has been examined by shifting the position of the target at, or slightly after movement initiation, impulse control has been studied in computer-based aiming by shifting the position of the cursor (effector). For example, Saunders and Knill (2003) shifted the representation of the fingertip perpendicular to the direction of the primary movement at either 25% or 50% of the overall aiming amplitude. Changes to the movement trajectory were evident approximately 160 ms after the perturbation. Thus in the 25% condition the corrective process began somewhere

between peak velocity and peak deceleration. Participants were seemingly unaware that the cursor position had ever shifted (see also Sarlegna et al., 2004).

Proteau and colleagues have used similar methods in a number of experiments. Proteau et al. (2009) found that corrective processes associated with a cursor jump could occur when the cursor was well outside central vision. As well, the corrective process occurred under conditions in which participants were both aware and unaware of the perturbation. Perhaps of greatest theoretical interest was their finding that participants corrected their movement for the cursor jump even when vision of the cursor was removed shortly after the cursor jump. Consistent with our multiple process model of limb regulation, a suitable explanation is that the impulse control system identified a mismatch between the perceived limb direction and the anticipated limb direction and initiated the corrective process immediately.⁶

In other work designed to examine impulse regulation, Veyrat-Masson et al. (2010) manipulated both the size of the target and the size of the cursor jump. The former was varied to determine if corrective processes associated with the cursor jump still occurred when the target was large enough to accommodate the jump without correcting the movement trajectory. Interestingly, participants corrected their limb movements following a cursor jump regardless of whether or not it was necessary (i.e., the size of the target did not impact the corrective process associated with the cursor jump). Once again, this indicates the irrelevance of target information for impulse control. In addition, neither the size of the cursor jump nor the target had any impact on the latency of corrective processes.

Brière and Proteau (2011) have also examined corrective processes involving two cursor jumps. Similar to previous work from Proteau's lab, participants performed a video-aiming task. On a small percentage of trials, the cursor jumped 15 mm laterally shortly after movement initiation. On some of these perturbation trials there was also a second cursor jump of the same size that occurred 100 ms after the first jump. The second jump either doubled or cancelled the initial cursor perturbation. Participants corrected for the second jump with a similar latency to the first jump regardless of its direction. Brière and Proteau reported that under double jump conditions, the two corrective processes "blended seamlessly" (cf. two discrete submovements). Again these findings suggest a continuous mode of control that unfolds rapidly following a mismatch between expected and perceived sensory consequences.

The majority of effector displacement studies have used video-aiming tasks in which it is relatively easy to displace the cursor a known distance at a specific time in the movement trajectory. Although effector displacement is more difficult to accomplish in direct three-dimensional aiming, it is still possible. For example, Grierson et al. (2009) connected an air compressor to an aiming stylus so that they could impede or exaggerate the limb's acceleration in the primary direction of the movement. In this study, participants made rapid aiming movements to a small target directly in front of them, with two-thirds of trials completed without perturbation. On a third of the trials, perturbation involved the compressor producing a brief blast of air from tubes connected to the stylus. The perturbations occurred 80 ms after movement initiation, which was approximate to the moment of peak acceleration. A blast from the posterior tube further propelled the already moving limb in the direction of the target, while a blast from the

anterior tube impeded the progress of the accelerating limb. A control perturbation involved blasts of air from both tubes. In separate blocks of trials, participants either had full visual information available to them or vision was eliminated upon movement initiation. Spatial analyses at early kinematic markers revealed that both the forward and backward perturbations had an impact on the limb trajectory. Although the air blast that impeded limb acceleration had the overall effect of increasing movement time, this negative impact on performance was more apparent under no vision conditions than when visual feedback was available for early limb regulation. Interestingly, participants moved more quickly under no vision conditions when the air blast helped accelerate the limb. Thus, it would appear that visual feedback reduced the impact of both the forward and backward perturbation. Moreover, the impact of vision on the limb trajectory began prior to peak velocity.

In a follow-up study, Grierson et al. (2011) exposed participants to both the moving background illusion and the air compressor perturbation in the same aiming movement. That is, the two perturbations could be introduced alone or in tandem. When paired with a real perturbation to limb velocity, the moving background illusion had little effect on either the movement trajectory or movement outcome. This was regardless of whether the expected effect was congruent with or opposite to the impact of the air blast. However, because vision of the limb was available under all aiming conditions, the corrective processes associated with the air blasts were similar to Grierson et al. (2009). That is, they negated the impact of the perturbation and this corrective process began to operate shortly after the offset of the air blast perturbation (i.e., impulse control).

Interestingly, the air blast perturbation engages early corrective processes that optimize both movement speed and accuracy. For example, an additional adjustment in the primary direction of the movement was evident regardless of whether the air blast was hindering or accelerating. This type of response ensured that the movement overcame the worse-case hindering perturbation. In the event that the perturbation accelerated the limb, the forward response was associated with less time to peak acceleration in conjunction with a greater displacement. However, later in the movement this same perturbation resulted in a higher peak deceleration that was achieved somewhat earlier (Grierson et al., 2009). Thus, it appears the system takes advantage of the positive impact of the forward blast during the initial portion of the movement and then prevents a potential overshoot with a more forceful deceleration near the end of the movement. Furthermore, these effects were even more pronounced when vision was occluded at movement initiation, thus limiting the sensory information available for late limb regulation. Together, these adjustments suggest the system employs a nonspecific response to impulse control perturbations, which protect the movement against the potential worst case possibilities; in this case, the possibility of a movement suppressing backward blast. These corrections may be nonspecific because there is insufficient processing time to determine the nature of the perturbation that early in the movement.

Also consistent with this notion of early online ‘play-it-safe’ processes are the terminal biases shown when exposed to the moving background illusion in isolation (Grierson and Elliott, 2009a; Proteau and Masson, 1997; cf. Grierson et al., 2011). Although the performer typically exhibits illusory biases for both types of background movement, undershoot biases, following background movement opposite to the direction

of the limb (i.e., the limb appears to be moving faster than it really is), are more robust than biases associated with background movement in the same direction as the moving limb (Grierson and Elliott, 2009a). This asymmetry in constant error, in favor of undershooting the final target position with the primary movement, reflects a “play-it-safe” approach to movement planning. In this case, that approach extends not only to the characteristics of the primary movement, but also the strategic nature of early velocity regulation associated with impulse control (Grierson and Elliott, 2009a). That is, impulse control is more evident when response-produced velocity feedback indicates a potential overshoot error as opposed to a potential undershoot error.

As well as perturbing the real or illusory velocity of the limb, impulse control can be examined by creating a situation in which the planned movement no longer meets the requirements for target-goal acquisition at movement initiation. In two experiments Elliott et al. (1999b) used a metal stylus and an electromagnetic home position to unexpectedly vary the amount of force required to break contact with the home position and subsequently achieve the correct aiming amplitude. Peak velocities were higher for aiming movements when the inertial forces increased as compared to the control condition or when they were decreased. This finding suggests that participants adjusted to the need for greater force production at movement initiation or before movement initiation. In terms of movement time cost, participants were more adept at adjusting to the force perturbation when vision was available than when it was eliminated upon movement initiation. As well as the early rapid adjustments to the force perturbation, participants exhibited late discrete corrections when necessary. When full vision was available these corrections occurred on 60 % of the trials. Consistent with our ideas

about limb-target control, almost all of these discrete corrections were secondary accelerations to correct an initial target undershoot.

More recently, our group conducted a study in which we created uncertainty about the force demands of an aiming movement by manipulating the weight of the stylus. Specifically, Burkitt et al. (2015) had participants aim to a small target with either a light or heavy stylus. On some trials, the performer knew in advance the weight of the stylus, while on other trials stylus weight could not be determined until movement initiation. As mentioned in the previous section, participants undershot the target position with their primary movement to a greater extent under heavy stylus conditions. Of greater relevance for impulse control is that stylus weight had very little overall impact on the temporal characteristics of the movement trajectory (e.g., time to peak acceleration and velocity) and movement outcome. Presumably participants rapidly adjusted their initial limb trajectory to accommodate stylus weight. Although advance knowledge of stylus weight had little effect on movement execution, some temporal advantages in aiming were evident when $N + 1$ trials were identical to N trials (i.e., two light trials in a row or two heavy trials in a row). Specifically, in heavy stylus movements, these temporal advantages were prevalent at the kinematic landmarks typically associated with impulse control (i.e., times to peak acceleration and peak velocity). Presumably the first trial experience (trial N) had an impact on movement planning and the associated internal model of the second aiming attempt (trial $N + 1$). Thus, while the internal model appears to be extremely flexible (see Burkitt et al., 2013), there is at least temporary adaptation associated with consecutive trials.

Our multiple process model (Elliott et al., 2010) has also been successful in explaining improvements in goal-directed aiming with practice. During early practice when aiming to a high index of difficulty target (i.e., 6 bits; see Fitts 1954), Elliott et al. (2004) found that adult performers undershot and hit the target equally often. They only overshoot the target with their primary movement on 5% of trials. Once again, this fits with the idea that when a performer makes a series of rapid movements to the same target (i.e., specific target width and movement amplitude), the mean of the primary movement endpoint distribution will often be outside of, or very close to, the near target boundary in order to avoid time and energy costly overshoot errors. After 4 days of practice with the same target setup, movement times were reduced, which was at least partly explained by a reduction in variability of primary movement endpoints. Although they continued to overshoot the target on 5% of trials, the percentage of undershoots was reduced to 25% with the primary movement ending on the target on 70% of trials.

Improvements in performance (i.e., initial target hits and movement time) can thus be linked to a reduction in variability in the primary movement endpoints. This reduction in variability (Elliott et al., 2004) allows the performer to “sneak up” on the target with their primary movement (i.e., shift the center of the distribution from near or outside the near target boundary toward the center of the target). Thus, corrective submovements are not needed on a large percentage of trials and, when necessary, they are of shorter amplitude. In our multiple process model (Elliott et al., 2010), reduction in variability can be achieved in one of two ways. Following Schmidt et al. (1979), adult performers may become more precise at specifying the muscular forces required to accelerate and decelerate the limb in the direction of the movement. In addition, at least

some of the variability in the primary movement trajectory, due to either neural noise or muscle specification error, will be reduced via impulse control. Both types of improvement depend on the development of a more refined internal model/representation of the intended movement.

In summary, the primary movement trajectory (Meyer et al., 1988) or initial adjustment (Woodworth, 1899) does not appear to be as ballistic as previously thought (Elliott et al., 2010). Specifically, even under conditions associated with very rapid manual aiming, adult performers can adjust the direction and/or velocity of their aiming movement to accommodate not only normal aiming errors, but also real and perceived perturbations to the movement trajectory. These adjustments are realized during the distance-covering phase of the aiming movement (i.e., they occur prior to the end of the primary movement) and are not reflected in discrete discontinuities to the movement trajectory. This type of impulse control can be based on either an evaluation of efference at the time of movement initiation, or a comparison of expected to perceived sensory outcome shortly after movement initiation (and throughout the entire primary movement). In either case, the corrective process depends on the viability of an internal representation or model of the motor and sensory consequences against which the unfolding movement can be evaluated. This type of limb regulation can occur in the absence of visual feedback, but it is more effective in reducing error when vision contributes to both the movement expectancies (i.e., the internal model) and the movement outcome (i.e., feedback). If error still remains at the end of the primary movement then impulse control can be supplemented by limb-target control. As

described previously, the limb-target regulation involves a comparison of the limb and target positions at the termination of the primary movement.

4. Examining the Independence of Impulse Control and Limb-Target Control

The kinematic data supporting the presence of these two forms of online limb control gave rise to new research studies that set out to determine the extent to which these two modes of online control interact or covary to influence movement accuracy (Grierson and Elliott, 2008, 2009a). These studies were in part based on additive factor logic first introduced by Sternberg (1969). Specifically, we used experimental manipulations designed to impact both impulse control and limb-target control in the same goal-directed aiming protocol. Each manipulation was expected to affect goal-directed aiming in a manner similar to previous studies. That is, we anticipated similar main effects to those shown in single independent variable experiments. Following the additive factor logic (Sternberg, 1969), main effect findings for each of the two perturbations without an interaction would suggest impulse control and limb-target control are associated with independent feedback processing systems and have additive contributions to the control of goal-directed reaching. However, an interaction between the variables designed to influence impulse control and limb-target control would suggest at least some overlap in information processing associated with the two modes of control.

In our initial study (Grierson and Elliott, 2009a), we manipulated the perceived position of the target and the perceived velocity of the limb during movements while measuring performance. As in previous research, we used the Müller-Lyer illusion to manipulate the perceived position of the target. Participants planned movements to a small target defined by the intersection of three lines, which were arranged such that they

formed a T configuration. Upon movement initiation, the target was changed to a tails-in configuration or a tails-out configuration or remained unperturbed. This perturbation is designed to affect the discrete type of control associated with the limb and the target (i.e., limb-target control). To manipulate the perceived velocity of the limb, we relied on the moving background perturbation introduced by Proteau and Masson (1997). This illusion creates a mismatch between the expected and perceived dynamics of early limb movement (i.e., affects impulse control). Movement accuracy measures (i.e., constant error) yielded non-interactive main effects of the two perturbations, suggesting that the two forms of control operate independently.

In another study, we used the previously mentioned compressed air-stylus manipulation and a moving target manipulation to extend the tandem perturbation paradigm to an examination of the relationship between control processes when actual perturbations to the aiming limb dynamics and the tasks demands are introduced (Grierson and Elliott, 2008). The results of the compressed air-only and moving target-only conditions were consistent with previous evidence for early and late control, respectively. Interestingly, in this case, movement accuracy measures yielded an interactive effect of the tandem presentation of the two perturbations. This finding suggests that at some point during the movement, the perturbations prompted the two proposed modes of control to operate in parallel. That is, the early corrections associated with impulse control mediated the impact of limb-target control. Perhaps this is not surprising given the more robust nature of a real vs illusory disruption to limb control.

When comparing the results of the illusory and actual perturbation studies, it became clear that it was hasty to conceptualize the concerted operation of two control

processes as functions of the early and late portions of the movement. Rather, it is more likely that the corrections initiated on the basis of limb-target information during the final portions of the movement overlap with a process of predictive feedforward control that is active throughout the entire movement. Moreover, any changes in the movement trajectory associated with impulse control have the effect of either increasing or decreasing the need for limb-target control (see Elliott et al., 2014).

Notably, it is perhaps the two types of online control that can explain the different movement outcomes that have been reported when participants are reaching or aiming to illusory target positions (see Westwood, 2010 for a review). In this theoretical context, we conducted a study in which participants performed 500 ms aiming movements to a control target and the tails-in and tails-out Müller-Lyer configurations (Roberts et al., 2013). On the majority of trials, participants had full visual information available to them. However, on some trials, vision was eliminated upon movement initiation and was only returned at the termination of the movement (i.e., no vision condition). As well, there were trials in which vision was only available for either the first 200 ms of the movement or the last 200 ms of the movement (i.e., early vision and late vision conditions respectively).⁷ We found that illusory biases were expressed during no vision, late vision, and full vision conditions, but not the movement early vision conditions. This finding is consistent with the idea that target context impacts both movement planning and late limb-target control processes (Franz, 2001; Mendoza et al., 2006). Because only impulse control operates early in the movement trajectory, one could argue that this type of dynamic control is not only immune to target context, but that it is also responsible for modulating limb velocity errors associated with biased movement planning. The results

of this study suggest that although movement planning, impulse control, and limb-target control each make a contribution to movement outcome, they interact in a way that, under normal circumstances, would be expected to reduce movement error.

In an attempt to elucidate the relative overlap and the contributions of impulse and limb-target regulation to reducing endpoint error, Tremblay et al. (2013), and more recently Kennedy et al. (2015) occluded or provided vision based on the limb meeting specific velocity criteria. In an initial experiment, Tremblay et al. (2013) provided or occluded vision when the limb velocity went above or fell below 0.8 m/s. Terminal error results were comparable in the full vision and vision at high limb velocity conditions, but at a temporal cost to providing vision after peak velocity. Presumably this temporal cost was associated with the time needed to use this high velocity visual feedback for limb-target regulation. In Experiment 2, multiple velocity criteria were used (0.8, 0.9, 1.0, 1.1, & 1.2 m/s) in order to determine if there was a window of vision that contributed most to impulse or limb-target regulation. Interestingly, vision provided at velocities of 0.8-0.9 m/s early in the movement led to increases in movement accuracy presumably via impulse regulation. In addition, vision provided up to 1.0 m/s helped reduce endpoint variability by improving limb-target regulation. However, as in the first experiment, providing vision at higher velocities resulted in greater time spent after peak velocity. This finding indicates that there was less efficient overall processing when vision was only provided at high limb velocities compared to when vision was available throughout the movement.

In follow-up work, Kennedy et al. (2015) segmented the window over which vision was available into three distinct portions; early (0.8-1.4m/s), middle (above

1.4m/s), and late (1.4-0.8 m/s). The purpose was to observe the influence of shorter visual windows and the influence of removing vision of the limb at the highest velocities on movement execution. Despite the shorter duration of the portions, the early and late windows yielded similar consistency to a full vision condition. However, an additional temporal cost was incurred that was associated with the time after peak velocity for the middle condition. The observed increase in accuracy provided evidence that impulse control occurs early in the trajectory and can be based on very little visual input (i.e., 43 ms in the early condition; Kennedy et al., 2015). Overall, providing vision early in the movement trajectory on the basis of the limb's velocity was found to engage the regulatory processes, but there appeared to be the potential for an optimal velocity window that occurs prior to peak velocity that could efficiently engage impulse and limb-target regulation. Further, optimization of the impulse and limb-target regulation may occur via multiple visual samples while the limb travels at different velocities. Specifically, vision gathered early while the limb travels at moderate velocities may inform processes that employ vision gathered at higher limb velocities that occur later in the movement trajectory. Once again, it would appear that impulse and limb-target control interact in subtle ways.

5. Retinal and Extra-Retinal Contributions to Impulse and Limb-Target Control

Having described our multiple process model of goal-directed aiming/reaching, it is important to consider the retinal and extra-retinal information that is used to ensure the limb achieves the movement goal (e.g., hitting a target, grasping an object). As mentioned several times in the preceding paragraphs, the impact of vision in goal-

directed aiming has been confirmed by comparing kinematic characteristics when vision is available or eliminated at certain times prior to or during the movement (see also Elliott and Allard, 1985). However, while enabling the researcher to determine the overall importance of vision, this type of manipulation does not reveal what retinal/extraretinal information is necessary and sufficient for accurate endpoint control. In this empirical context, it is important to consider the information necessary for impulse and limb-target control in various task contexts. For example, accurate prehension requires information about a target's properties (e.g., shape, orientation, size, material characteristics) and location so that a reach can bring the limb toward a target and a grasp can close the fingers and thumb onto preselected points of the target surface. While aiming/reaching has no requirement to grasp an object, findings from studies that have made actual (Hansen and Elliott, 2009; Heath et al., 1998) and illusory perturbations (Handlovsky et al., 2004; Mendoza et al., 2006) have confirmed the contribution of both target position and size to impulse and limb-target control. Of interest in this section is how we move the eyes relative to the limb in order to provide the retinal/extraretinal information needed for efficient and optimal control of prehensile and aiming movements.

When performing aiming movements as part of a sequence of everyday activities (e.g., tea-making or preparing a sandwich), the eyes saccade between task-relevant objects (e.g., cup and kettle, or knife and jar of peanut butter; for a review see Land and Hayhoe, 2001). This provides the extra-retinal (i.e., efference copy and proprioception) and retinal information, which is transformed in the parietal and frontal cortices, to derive an internal model of the spatial surrounds with respect to the responding limb (i.e., a

body-centered representation; for detailed consideration of the transformations required to coordinate eye and upper limb movement see Crawford et al., 2004). Then, for each action within the sequence, the eyes will typically be located on the object-of-interest prior to the onset of limb movement. Specifically, the eyes are moved toward the object with a primary saccade, followed by one or two small corrective saccades that compensate for normal undershoot. The eyes then remain fixed on the object while the limb movement commences (Helsen et al., 1998, 2004). In time-constrained laboratory settings, the limb movement might even begin prior to completing the primary saccade (Binsted et al., 2001), but importantly, the eyes would be stationary on the target for sufficient time to process extra-retinal and retinal input. The same is true when completing a sequence of aiming movements under externally-imposed time constraints (Deconinck et al., 2011; Neggers and Bekkering, 2000; 2001). As shown in Figure 2 (panel B), the eye and limb movements to the second target in the sequence occur almost simultaneously but still the eyes are located on the target before the limb reaches peak velocity. With such coordination between the eyes and limb, visual information about limb motion is initially provided as it crosses the field of view that corresponds to the peripheral retina (Bédard and Proteau, 2004). This region is specialized for perceiving motion (i.e., direction and velocity), and indeed seeing the limb move as it crosses the peripheral visual field results in more accurate reaching than when only the final target is visible (Bennett and Davids, 1998; Sivak and McKenzie, 1992). In this context, moving the background against which the limb travels leads to a misperception of velocity and associated adjustments during the initial impulse control phase of the movement. This is presumably based on peripheral retinal input from the background and limb given the

eyes would most likely already be located on the target (Grierson and Elliott, 2009a; Proteau and Masson, 1997). Finally, during the latter stage of the aiming movement, the limb progresses across the parafovea and finally into the foveal region of the retina, which is specialized for providing information regarding fine detail, and thus making any necessary corrections associated with limb-target control. Only under the most severe temporal constraints in a sequence of aiming movements (e.g., 200 ms between appearances of successive targets) do the eyes move away from the target before the limb movement is completed (Wilmot et al., 2006).

In many situations, extra-retinal input as the eyes move to the object-of-interest (e.g., a coffee cup) and monocular retinal input (e.g., motion parallax, retinal image size) combine to provide sufficient information to perform goal-directed aiming similar to that exhibited in normal conditions of binocular vision (Jackson et al., 1997; Watt and Bradshaw, 2000). In a series of studies by our group, we have shown that this is particularly true if the object-of-interest is located at a predictable location and the movement is performed under full vision conditions (Coull et al., 2000). The availability of information throughout the movement, combined with tactile feedback upon movement completion, enables the participant to develop an effective internal model and online control over repeated trials. Using this process, participants are able to overcome target mislocalization errors due to phoria (i.e., misalignment between the two eyes when one is covered). However, the finding of no difference between monocular and binocular viewing conditions does not imply that binocular retinal input is not used when available. This has been confirmed in several experiments that have used more subtle manipulations of the available information, combined with detailed analysis of movement kinematics, to

examine the sources of information that would typically contribute to goal-directed aiming.

An example of one such manipulation involves the use of a prism placed in front of one eye that modifies the vergence angle (i.e., retinal or extra-retinal) between the eyes (Tresilian et al. 1999; Mon-Williams and Dijkerman, 1999). This manipulation alters perceived target location in depth, but not perceived target size. Melmoth et al. (2007) reported that when pointing in a binocular viewing condition, where visual information was only permitted prior to or around movement onset (i.e., open-loop), participants overshoot the target endpoint (forward and lateral direction) with a base-in prism placed in front of the left eye. This manipulation required less rightward rotation to achieve fixation and consequently a decrease in vergence compared to a normal (i.e., plano lens) control condition. The opposite effect (i.e., undershoot) on endpoint error was observed with the use of a base-out prism that increased vergence when both eyes were fixated on the target. Moreover, there was no difference in endpoint error when participants pointed with a plano lens (i.e., normal vision) or a plus lens that preserved the normal vergence angle while at the same time magnifying the target image on the left eye and thus making it appear slightly closer. The latter effect would not be expected if participants had relied on fine binocular disparity for perception of object location in depth when planning reach amplitude for impulse control of this open-loop aiming task.

Support for the contribution of vergence to reach planning was also observed in a second experiment on prehension, when movements were performed under closed-loop conditions. Once again, participants exhibited movement kinematics (e.g., peak velocity) consistent with overshooting in the base-in prism condition and undershooting in the

base-out prism condition. Participants also modified the early movement kinematics associated with impulse control when looking through a plus lens, but this was suggested to be a strategic response to perceptual uncertainty caused by defocusing. Importantly, however, there was a lengthening of the limb-target control phase and grip closure time in the plus lens condition, both of which were suggested to be consistent with the disruption of fine disparity that contributes to closure of the fingers and thumb onto pre-selected grip points.

In a series of studies from our group on goal-directed aiming (Hansen et al., 2013) and prehension (Bennett et al., 2003; Hansen et al., 2011), we sought to examine the contribution of binocular retinal input by comparing behavior in conditions that required inter-ocular and/or intra-ocular integration of intermittently presented visual samples (see also Wilson et al., 2008). Borrowing from a protocol first reported by Engel (1970), the logic is that binocular information could be gained by integrating monocular samples provided alternately to each eye (for evidence of binocular fusion from neural imaging see Büchert et al., 2002). Using this manipulation for goal-directed aiming, we found that the movement kinematics were similar in a normal binocular vision condition compared to a condition that presented alternating monocular samples without delay. However, there was a reduction in peak velocity, as well as increases in time-to-peak velocity and movement time, when a 25 ms inter-ocular delay was introduced between alternating monocular samples. A more general intolerance for alternating samples was found when participants performed prehension. Irrespective of whether or not a pre-cue was given regarding the near or far object location, participants increased maximum grip aperture, and lengthened deceleration time and movement time when alternating

monocular samples were presented without an inter-ocular delay. These adaptations to movement kinematics were suggested to be reflective of a conservative response strategy in the face of perturbed retinal input, much like the planning procedures favoring increased usage of visual information late within the movement trajectory (Hansen et al., 2006). Specifically, we suggested processing of fine binocular disparity (available when the point of fixation was coincident the object location) that is needed during limb-target control phase for precise grip closure, was disrupted by alternating monocular samples between the eyes.

A commonality to the goal-directed reaching tasks described above is that they typically require participants to perform a natural limb movement in order to make contact with a physical object (for a description of other object-related actions see Land, 2009). Adult participants are well practiced in these everyday aiming and prehension tasks, and thus have a strong preference in the way they move their eyes in order to provide the necessary information for impulse control and limb-target control (Helsen et al., 2004). Indeed, these authors showed that learning sequential aiming movements was least effective when adult participants were instructed to adopt an atypical eye-hand coordination that required them to initially fixate the final target. Examination of eye-hand coordination in typically developing children, confirms that adult-like responses are present by 7-8 years of age (Wilmot et al., 2006). Moreover, when learning a novel task that requires an unfamiliar spatial transformation between limb movement and the sensory consequences, participants track the cursor with their eyes during the initial exploratory phase but later (i.e., skill refinement) shift gaze to the end target in advance of cursor arrival (Sailer et al., 2005). The implication is that, in general, it is beneficial in

goal-directed reaching to move the eyes (with respect to the hand) in a way that initially provides access to extra-retinal information on the spatial layout of our surrounds prior to movement onset, followed by retinal input from the early and late phases of limb movement as it crosses from the peripheral to foveal visual field. Likely exceptions to the rule include object-related action that demand low end-point accuracy or those that can be completed using tactile feedback (e.g., tying shoe laces), performed in situations where there is an advantage for gaze to be located elsewhere (see Land, 2009).

In future work, it would be instructive to independently manipulate the direction and amplitude of eye and limb movements during goal-directed aiming (e.g., Helsen et al., 2004; Neggers and Bekkering, 2000). Depending on the accuracy and information requirements, dissociations of the eye-limb systems would presumably lead to unique disruptions of impulse and/or limb-target control. Conducting these sorts of studies under various sensory conditions would also allow us to determine the relative contributions of retinal and extra-retinal information to impulse and limb-target control.

6. The Multiple Process Model and Other Models of Limb Control

One challenge for any model of goal-directed reaching/aiming is to explain the well-known relationship between movement speed and endpoint accuracy, including Fitts' Law (Fitts, 1954; Fitts and Peterson, 1964). In this regard, our multiple process model has many similarities to Meyer et al.'s optimized submovement model. Although both models highlight the importance of the stochastic principles associated with endpoint variability in optimizing speed and accuracy, the multiple process model also considers the central tendency of aiming distributions. Specifically, the multiple process model is based on solid empirical evidence that, in most cases, shows the optimal mean

primary movement endpoint falls short of the target's center. Moreover, our model also makes specific predictions about the role of effector mass and gravity in determining strategic undershooting bias (e.g., Burkitt et al., 2015; Elliott et al., 2004; Lyons et al., 2006). In contrast to the optimized submovement model, the multiple process model holds that stochastic variability associated with primary movement endpoints occurs due to both neural-motor noise and force specification error. Although the former source of variability is an inherent characteristic of the motor system, the latter source of variability can be reduced with practice. Reductions in force specification variability then lead to a reduction in primary movement endpoint bias (i.e., “sneaking-up” on the target; Elliott et al., 2004).

Our model is also different from the optimized submovement model with respect to what constitutes optimal aiming performance. Specifically, Meyer et al. (1988) contend that performers plan a specific limb velocity/movement time in order to achieve reasonable accuracy with the maximum allowable speed, whereas our model also takes into consideration energy expenditure in the optimization process. This idea is consistent with work by Lui and Todorov (2007) who have shown that, during the corrective process, performers will sometimes sacrifice endpoint error in order to reduce the energy expenditure of a movement (see also Oliveira et al., 2005).

The most important difference between the optimized submovement model and our multiple process model is the inclusion and role of impulse control in limb regulation. Since our first studies in which we identified something similar to impulse control in the early 1990's (e.g., Carson et al., 1992; Elliott et al., 1992), evidence for early and rapid limb regulation has been overwhelming. In their recent review of perturbation studies,

Cluff et al. (2015) conclude that corrective muscle activity occurs in as little as 100 ms following a visual perturbation and 70 ms following a mechanical perturbation.⁸

Our specific ideas about rapid limb regulation (i.e., impulse control) depend heavily on the concept of an internal model of movement that is selected and refined at the time of movement planning. This model includes information about the force-time characteristics of motor outflow (e.g., efference), as well as predictive information about the expected sensory consequences of the planned movement. These ideas are not new, as notions regarding the evaluation of efference date back to Helmholtz (1868/1925). More complex models of movement representation including the evaluation of response-produced feedback relative to an internal model were forwarded by Von Holst (1954) for limb movements (i.e., the comparison of reafference to efference copy) and Sperry (1950; see also Teuber and Mishkin, 1954) for eye movements (i.e., corollary discharge). In recent years, internal predictive models of limb regulation have been extremely important in explaining both typical and atypical motor control (e.g., Wolpert and Ghahramani, 2000; Wolpert and Miall, 1996).

The multiple process model holds that internal representations, developed at the time of movement planning, provide the basis for impulse control. Our model includes the evaluation of efference, and an early comparison of expected sensory consequences to perceived sensory consequences for the graded control of the initial acceleration and deceleration phase of the aiming/reaching movement. Of particular importance is the expected and perceived limb velocity and limb direction. Although we acknowledge that information about the spatial location of the target, with respect to the body, is important for the planning process and thus a component of the internal model, under normal

circumstances this information does not contribute to impulse control (cf. Desmurget et al., 1999). This is because, with full vision and a stationary target, a representation of target position is not necessary because that information is directly available to the performer throughout the movement. An internal representation of the target position becomes important, however, if direct visual contact with the target is prevented prior to (Elliott and Madelena, 1987), at (Zelaznik et al., 1983), or after movement initiation (Roberts et al., 2013). In these cases, limb-target control will also depend on target representations developed during the planning or preplanning process (see Elliott et al., 1990).

An important aspect of our model is the emphasis we place on prior knowledge about the sensory environment available for online control. With respect to limb-target control, prior knowledge about feedback availability impacts the strategic planning process and thus endpoint bias and discrete corrective processes at the end of the primary movement. For impulse control, the expected sensory consequences logically depend on the knowledge the performer has about the availability of feedback. When there is uncertainty we have shown that the performer prepares for the ‘worse-case’ scenario (e.g., impulse and limb-target control in the absence of reliable feedback). Other researchers have also considered the importance of expectancies in skilled limb control (Kording and Wolpert, 2004). These expectancies are sometimes referred to as “priors” (Cluff et al., 2015). Perhaps unique to our model is that the probability of a particular event or sensory condition does not tell the whole story. Rather, both the probability of events and the temporal, spatial, and energy costs of a particular outcome are considered.

In summary, our multiple process model provides an explanation of speed-accuracy tradeoffs in accuracy constrained movements that is also consistent with the characteristics of the performer's limb trajectories over multiple trials and in different aiming contexts (cf. Meyer et al., 1988). Moreover our model describes how an adult performer's aiming trajectories change with practice. Although our model builds on a number of previous explanations of speed-accuracy relations in goal-directed aiming and reaching, the manner in which various strategies and processes contribute to limb control is unique.

7. Summary and Conclusions

The goal of this paper was to update and extend our multiple process model of goal-directed reaching and aiming (Elliott et al., 2010). Our model relies heavily on the foundations provided by Woodworth's (1899) classic two-component model of limb control and Meyer et al.'s (1988) optimized submovement model. However, unlike earlier explanations of speed-accuracy relations in goal-directed aiming, our model makes a distinction between impulse control and limb-target control. Impulse control entails an early, and continuing, comparison of expected sensory consequences to perceived sensory consequences to regulate limb direction and velocity during the distance-covering phase of the movement. In contrast, limb-target control involves an evaluation of the relative spatial positions of the limb and the target in later portions of the movement. Limb-target control takes into consideration movement planning strategies relative to the mass of the effector and influences of gravity that reduce the need for corrective submovements that are particularly time and energy consuming. Although impulse control and limb-target control depend on different types of efferent,

visual, and proprioceptive information at different points in time, the two types of online control interact (Grierson & Elliott, 2008). Under normal circumstances, impulse control and limb-target control are complementary in that early adjustments to limb velocity and direction can often reduce the need for discrete corrections late in the movement. That said, limb-target control is evident when a discrepancy remains between the position of the limb and the position of the target at the end of the primary movement (e.g., Elliott et al., 2014).

Another feature of our model is the importance of prior knowledge about the sensory feedback that will be available for limb control during any specific reaching/aiming attempt (e.g., Hansen et al., 2006). This knowledge determines the speed, accuracy, and energy optimization strategies adopted during movement planning. It also provides the basis for the sensory expectancies that are critical for optimal impulse control (Burkitt et al., 2015; see also Cheng et al., 2008).

In addition to expanding our coverage of optimal limb control, we have provided a framework for understanding how retinal and extra-retinal information contribute to the optimization for speed, accuracy, and energy expenditure. In this context, the eye movements that adult participants make during rapid aiming/reaching are consistent with our model in that they maximize the pickup and processing of information for movement planning, impulse control and limb-target control. In the future, it will be important to not only measure ocular behavior, but also to systematically eliminate and/or disrupt the typical eye-hand coordination in order to examine the impact of these manipulations on limb biases and spatial variability.

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Footnotes

1. Meyer et al. (1988) based their model on empirical work using wrist rotation movements that moved a cursor across a display screen. Thus, the forces required to complete the movements would be low relative to more traditional three-dimensional aiming movements (e.g., Fitts and Peterson, 1964).
2. In an experiment using a very similar aiming protocol, Desmurget et al. (1999) applied transcranial magnetic stimulation over the posterior parietal cortex contralateral to the aiming hand. Compared to no stimulation control conditions, this magnetic perturbation disrupted the limb-target corrective process.
3. Of course by examining the difference in error at the end of the primary submovement and at the termination of the movement, researchers can also index the effectiveness of discrete corrective processes (see Elliott and Hansen, 2010 and Khan et al., 2006 for a discussion of the index of error correction effectiveness).
4. The majority of the work conducted by members of our research group involves aiming/reach to real 3-dimensional targets. Although slightly more time is usually required for aiming situations with indirect spatial mapping, findings from both direct and indirect aiming protocols have been consistent with our model.
5. At least in this perturbation context, males are slightly more influenced by the visual information available for movement planning, while females more readily make adjustments to the new visual circumstance introduced during movement execution (see also Hansen and Elliott, 2009).

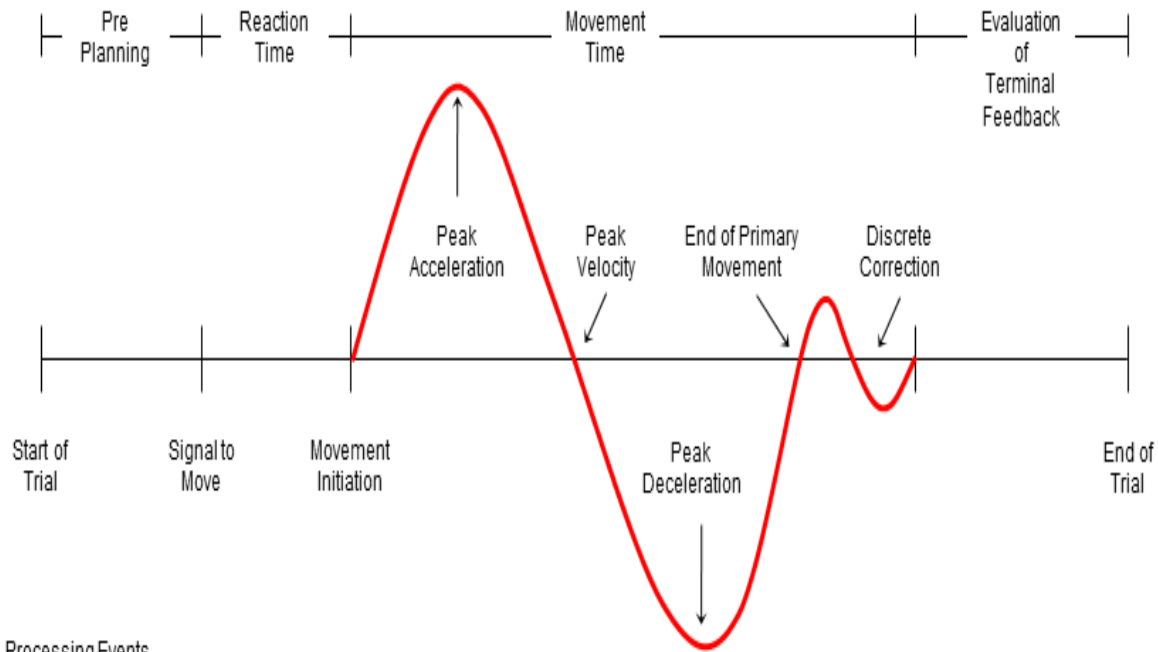
6. In work with spatially-constrained video aiming, Tinjust and Proteau (2009) suggested that there may actually be two types of impulse control. They propose a very early limb modulation designed to stabilize variability associated with the movement planning process. This type of control appears to be independent of the target characteristics and visual feedback, while a second type of impulse control requires visual feedback. In the context of our model, the first type of control could involve the evaluation of efference, while the second type of impulse control involves a comparison of expected to perceived visual consequences.
7. We selected 200 ms based on a very conservative estimate of visual processing time (e.g., Keele and Posner, 1968; cf. Zelaznik et al., 1983).
8. This very rapid response to the latter is consistent with the time necessary for a long-latency muscle stretch response (Ghez and Shinoda, 1978).

Figure Captions

Figure 1. Hypothesized sequence of events during a single rapid aiming movement (Adapted from Elliott et al, 2010, Psych Bull, 136, p 1032. Copyright American Psychological Association; reprinted with permission).

Figure 2. Graphical representation of a 2-target sequence aiming task (panel A) and accompanying eye and finger movements (panel B) with key events identified by dashed vertical lines. In the sequence aiming task, the participant points and fixates at the home target at screen center (yellow dashed circle). The home target then disappears and the first target (filled red circle) in the sequence (i.e., vertical) is presented after 300ms. After a further 300ms, the second target (i.e., horizontal) is presented. In panel B, the eye (solid black line) completes a primary saccade to the vertical target before finger (solid red line) movement begins. Accordingly, peak acceleration and peak velocity of the finger occur with the eye fixated on the target, and thus as the limb moves across the peripheral retina. Then there is a period known as “gaze-anchoring” during which the eye remains stationary in order to ensure foveal information is available to guide target control. Having located the finger accurately on the vertical target, the second eye and finger movement to the horizontal target begin. To try and keep in time with the sequence, the second primary saccade and finger movement occur almost simultaneously, meaning that the eye is not foveating the horizontal target. However, the dynamics of saccades still enable the eye to reach the target close to occurrence of peak acceleration and before peak velocity.

Movement Events

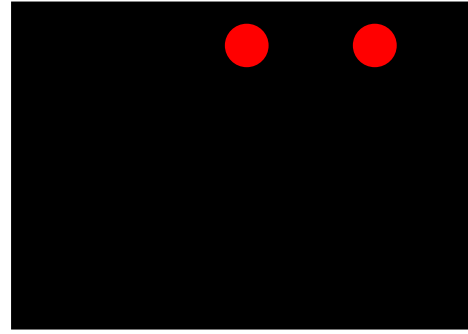
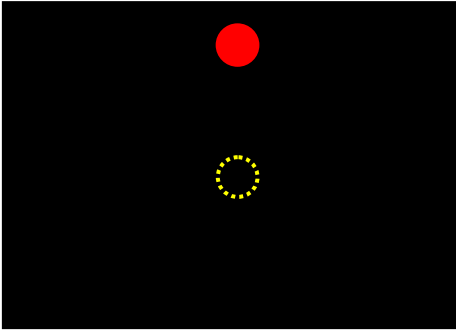


Processing Events

- 1) |—————>|
Preprogramming of movement based on advance information
- 2) |<—————>|
a) Specification of magnitude & timing of muscular forces; b) Formation of internal representation of expected efference; c) Formation of internal representation of expected sensory consequences
- 3) |<—————>|
Comparison of expected efference to produced efference and impulse regulation
- 4) |<—————>|
Comparison of perceived sensory consequences to expected sensory consequences and impulse regulation
- 5) |<—————>|
Pick-up of information about limb (visual and proprioceptive) and target (visual) position
- 6) |<—————>|
Limb-target regulation
- 7) |<—————>|
a) Processing of terminal feedback; b) Refinement of strategy and internal afferent and efferent representations

Goal-Directed Reaching

A



B

