Locomotor Interception of a Moving Target:

On-line or Model-based Control?

By

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Chapter 1. Introduction

Locomotor and manual actions are fundamental to daily human interactions with a complex dynamic environment. The mechanisms underlying the perceptual control of action are of central importance to our understanding of both the function of perception and the organization of action. Two general approaches to visual control have emerged over the last few decades, often referred to as the on-line approach and the model-based approach. The fundamental difference between the two lies in the underlying basis for control. In on-line control, action is controlled by current visual information that is available during the ongoing movement. In contrast, in model-based control, action is controlled by an internal representation such as a world model, an action plan, or both. In this dissertation, I first review the evidence regarding on-line and model-based control drawn from research on locomotion and manual actions. I then describe three experiments that investigate on-line and model-based control in a locomotor interception task, in which a participant walks to intercept a moving target. Finally, I arrive at some conclusions about the plausibility of each approach.

A primary role for current information in the control of action was originally emphasized by Gibson (1958, 1979). According to Gibson, various types of information are available to specify the properties of the environment. Detection of visual information by an attuned perceptual system enables humans to be aware of the specified environmental properties and to control their actions successfully with respect to those properties. As Gibson (1979) asserted, “Locomotion and manipulation … are controlled not by the brain but by information, that is, by seeing oneself in the world. Control lies in the animal-environment system.” Following Gibson’s seminal work, the role of visual information in action control has been increasingly recognized (see Warren, 1998, 2009). A growing number of studies have identified specific optical variables and proposed control laws that couple action to the environment. For example, it has been shown that walking can be steered by using the currently available optic flow, which specifies one’s heading relative to a target (Bruggeman, Zosh, & Warren, 2007; Warren, Kay, Duchon, Zosh, & Sahuc, 2001). The locomotor trajectory and even anticipatory behavior emerges from the actor-environment system as a consequence of lawful regularities governing the coupled system’s behavior (Stepp & Turvey, 2010; Warren, 2006).

The concept of an internal model was introduced by Kenneth Craik (1943/1967) in his influential book, *The nature of explanation.* Craik proposed that the brain “imitates” a physical process by creating an “internal model of reality” with a similar “relation-structure,” thereby enabling prediction of external events in the physical world (p. 50-53, 81-82). In engineering, internal model control was developed to compensate for the time delays inherent in feedback control by incorporating an internal model of the controlled system (Conant & Ashby, 1970; Garcia & Morari, 1982). Similarly, internal models of the musculoskeletal system have been promoted in computational motor control (Kawato, 1999; Wolpert & Ghahramani, 2000), while world models have been incorporated into control architectures for mobile robots (Moravec, 1982; Thrun, 1997). Echoing Craik, Wolpert describes internal models as “putative neural systems that mimic physical systems outside the brain,” whose “primary role is to predict the behavior of the body and the world” (Davidson & Wolpert, 2005, p. S313; Wolpert & Ghahramani, 2000, p. 1212). The standard concept of an internal model thus satisfies Clark and Grush’s (1999) description of a “full-blooded” representation: an inner surrogate for an extra-neural state of affairs that can be decoupled (at least temporarily) from ongoing environmental input. Wolpert and Ghahramani (2000) offer the analogy of a flying ball, whose future path can be predicted by a model that includes the equations of projectile motion (Newton’s laws), the fixed parameters of the system (gravitational constant, air resistance, ball diameter), and takes information about the ball’s initial state (position, velocity, spin) as input.

Whereas the on-line approach emphasizes the perceiver’s coupling to the environment by means of optical information, the model-based approach emphasizes the role of an internal model of the actor-environment system. Successful action thus typically depends on a close correspondence between the physical world and its internal model. As an action unfolds, the state of the actor is continuously monitored, based on sensory information and/or motor efference, and is used to update the actor’s state with respect to the world model. The primary role in controlling action – whether or not visual information is concurrently available – is thus played by an internal representation of the world and the actor’s state. There is evidence that action can be guided without concurrent visual information in some circumstances, which I will refer to as off-line control. For example, in the blind walking task, blindfolded participants are able to walk successfully to a target they have previously viewed. Loomis and Beall (1998, 2004) proposed that visual and other sensory input is processed to construct an internal 3D model of the environment, which they called “perceptual space.” Based on this world model, they argued, locomotor behavior is planned and executed and the actor’s state is updated. Results from the blind walking paradigm imply that locomotion can be guided by some form of spatial memory.

One problem I face in trying to evaluate the two approaches is that the properties of internal world models invoked in the literature are seldom clearly specified. Some internal models appear to have a wide scope, such as the laws of projectile motion or a 3D spatial model of the environment. Others are said to represent specific situations with narrow scope, such as the extrapolated trajectory of a given object or the spatial location of a particular target. In addition, knowledge of fixed parameters, such as Earth's gravitational acceleration or a ball's diameter or elasticity, is sometimes referred to as an internal model. I will reserve the term for the standard notion of an internal surrogate that mimics an external physical process; fixed parameters do not meet this standard and will be treated as constants or calibrations. Further, the fidelity of an internal model, as well as its temporal duration, are rarely specified. This makes the expected accuracy, precision, and time course of model-based action difficult to operationalize. The concept is thus rather unconstrained and its predictions quite malleable, to the point where it may not be possible to test (Chemero, 2009; Haselager, de Groot, & van Rappard, 2003).

Both the on-line and model-based approaches have something to contribute to our understanding of the control of action. The on-line approach contributes by identifying specific information in natural environments and characterizing control laws that map the information into movement control variables. Its advantage lies in its parsimony, in reducing the computational burden of constructing and simulating a high-fidelity world model to guide every movement. The proper domain of the on-line approach is, by definition, action that is controlled by current visual information; it does not purport to apply to off-line situations in which environmental information is unavailable, such as blind walking. Conversely, the natural domain of the model-based approach is action that is performed off-line without concurrent visual information, like blind walking. The primary question at issue is whether the model-based approach normally applies to both domains, even in the presence of visual information that could be used to guide action on-line. A secondary question is whether a full-blooded internal model is necessary to account for off-line control, or whether weaker strategies are sufficient. The advantage of a strong model-based view is that it provides a common account of visual-motor control under both conditions.

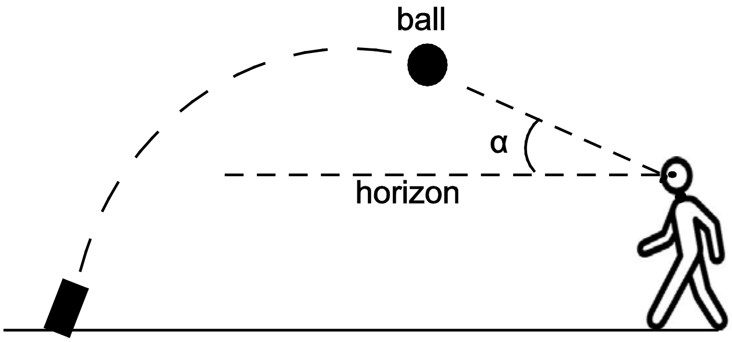

Figure 1. An outfielder catching a fly ball.

In this chapter, I evaluate two hypotheses regarding the control of action under both normal vision and visual occlusion conditions. To introduce the hypotheses, consider the classic outfielder problem, in which a baseball player runs to catch a fly ball (Figure 1). The ball is launched at a given distance and flies in the general direction of the fielder. First, according to the *strong on-line control* hypothesis (Figure 2a), action is normally controlled exclusively on the basis of current visual information, without the involvement of an internal model (e.g. Chapman, 1968; McBeath, Shaffer, & Kaiser, 1995). This hypothesis implies that performance would deteriorate if vision was withdrawn, depending on the spatio-temporal demands of the task, but it does not aim to account for action control in the absence of visual information. One way to test this hypothesis is to eliminate the current information by visually occluding the ball, and to measure the fielder's subsequent behavior. If performance is significantly impaired under such conditions, it would suggest that the fielder ordinarily uses current visual information to control catching.

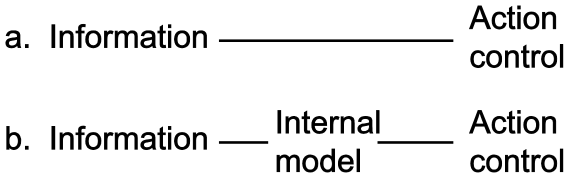

Figure 2. The two hypotheses of action control. a: Action is controlled by current information. b: Action is controlled by an internal model.

Another test is to manipulate the visual information about the ball's flight and determine the control law that guides the fielder's behavior in real time. For example, the Optical Acceleration Cancellation (OAC) theory proposes that the fielder moves forward or backward so as to null the vertical acceleration of the ball's optical projection, and left or right to keep the ball in a constant bearing (CB) direction (Chapman, 1968; McLeod, Reed, & Dienes, 2006, Michaels & Oudejans, 1992). If the ball's current vertical optical velocity ($d\tan a/d\mathrm{t}$ in Figure 1) is increasing, the fielder should speed up in the backward direction, whereas if $d\tan a/d\mathrm{t}$ is decreasing, the fielder should speed up in the forward direction. By keeping the upward optical velocity approximately constant, the fielder will arrive at the right place at the right time to catch the ball. Indeed, experimental manipulation of the ball's trajectory produces adjustments by the fielder that are consistent with this on-line control strategy (Fink, Foo, & Warren, 2009; McLeod, Reed, Gilson & Glennerster, 2008). This theory offers an illustrative example of anticipatory behavior arising from a specific coupling between actor and environment due to lawful regularities that govern the coupled system.

However, neither of these tests can rule out the possibility that current information is used to update an internal world model, which is in turn used to control action. On this hypothesis, information does not control action directly – only indirectly, via its effects on an internal model. Specifically, according to the *strong model-based control* hypothesis (Figure 2b), action is controlled exclusively by an internal world model. The world model is constructed using information about the physical environment and the actor's state, and is used to control action even when visual information is available. Under conditions of visual occlusion, the world model persists and continues to guide action. In the outfielder example (Figure 1), the fielder visually perceives the ball's initial distance and velocity, computes the ball's trajectory based on an internal model of the laws of projectile motion and knowledge of fixed parameters, and predicts its landing place and time (Saxberg, 1987). Consequently, the fielder should be able to catch the ball even when it is visually occluded shortly after launch. (I note that evidence for this particular theory is lacking: at outfield distances of 30 m, absolute distance and velocity are not accurately perceived, and even skilled baseball players cannot identify correct trajectories or predict landing points (Schaffer and McBeath, 2005)).

A critical issue is how long an internal model can be expected to persist and how accurately it can control behavior after decoupling from environmental information. If an internal model is assumed to decay rapidly, successful action would require continuous updating by current information. Withdrawal of that information would thus lead to increasing model error, resulting in impaired performance – depending, of course, on the spatio-temporal demands of the task. Positing a short-lived world model thus renders strong model-based control indistinguishable from strong on-line control, because both require continuous visual input and predict degraded performance under visual occlusion. Hence, a rapidly-decaying internal model is not an empirically testable hypothesis. It is also a more complex one, for it is not clear what a continuously-coupled internal model would add to the explanatory account if behavior can be controlled by environmental information itself. Finally, a rapidly-decaying internal model seems to undermine the raison d'etre of such an internal representation: to predict the state of the world when decoupled from environmental information. This proposal thus has obvious logical weaknesses, so I will assume that a world model persists long enough and is accurate enough to be empirically measurable.

In the remainder of this chapter, I proceed by reviewing relevant experimental studies on the visual control of locomotor and manual actions. The first section focuses on model-based control. My purpose here is to determine whether a hypothesized internal world model is sufficient for accurate and precise control of action, or whether current visual information is necessary. These studies typically manipulate the availability of information and analyze performance under different visual conditions. In the second section, I review the on-line control literature, with the aim of determining whether current information is sufficient for accurate and precise action control, and whether action is normally guided on-line. In the third section, I consider the literature on anticipatory control in interception tasks. Finally, I preview three experiments in which I investigate whether on-line or model-based control is used in a moving-target interception task.

1.1. Model-based control: Is an internal model sufficient?

According to the model-based approach, action is normally controlled on the basis of a 3D world model and/or action plan. This view implies that such an internal representation alone should be sufficient to control action in the absence of visual information, at a comparable level of performance, for some period of time. Numerous studies address this question by manipulating the availability of visual information. If visual input is withdrawn and task performance remains accurate and precise, this would imply that such an internal representation is sufficient to control action. But it would not imply that action is normally model-based when visual information is available. Conversely, if performance deteriorates, this would imply that concurrent visual information is necessary for normal levels of performance. But it would be agnostic as to whether the information is used to guide action directly or to update a short-lived internal model. Studies manipulating the duration of visual occlusion might shed some light on this question.

1.1.1. Visual occlusion leads to degraded performance

Research on *visually directed action* is often regarded as evidence for model-based control in human locomotion (Loomis & Beall, 2004; Loomis & Philbeck, 2008). For example, in the typical blind walking task, human participants briefly view a target on the ground at a distance, close their eyes, and walk without vision to the remembered target location. This task has been extensively investigated over the last three decades. It is usually reported that human actors are able to perform blind walking successfully with target distances up to 30 m (Loomis, DaSilva, Fujita, & Fukusima, 1992; Rieser, Ashmead, Talor, & Youngquist, 1990; Thomson, 1983). Participants are able to walk to the target location after viewing it for only 150 ms, and even without directly fixating the target (Philbeck, 2000). Successful performance is also observed in other directed walking tasks (Loomis et al., 1992; Philbeck, Loomis, & Beall, 1997). For example, in "triangulation by walking", participants view a target at a distance and then walk blindfolded along an oblique path until instructed to turn and walk to the remembered target location – which they can do with reasonable accuracy (Philbeck et al., 1992). This result suggests that blind walking is based on a spatial memory of the target location in the environment and updating of the actor's position, not simply a perceived egocentric distance, a pre-planned action, or a visual-motor mapping.

Studies of visually directed walking thus indicate that humans are able to perform certain actions without guidance by concurrent visual information. However, they do not imply that action is normally model-based when such information is available. This question hinges on a comparison of blind walking performance with that of sighted walking. Moreover, null results must be interpreted cautiously, for the degree of error is likely to depend on the spatial demands of the task. Very few studies have directly compared walking in visual and nonvisual conditions. Thomson (1983) originally asked participants to walk to a previewed target with or without vision. Participants walked with similar accuracy and precision in both conditions for target distances of 9 m or less, but variability in walked distance increased dramatically in the occlusion condition for targets at 12 m or more. In Farrell and Thomson (1999), participants walked to a target line and placed the toe of a specified foot against the line. Variability in final toe position was significantly greater in the occlusion condition than that in the normal vision condition. One might expect larger differences for tasks that place greater demands on spatial memory. These studies indicate that visual occlusion leads to degraded performance compared with normal vision, with greater variability implying spatial uncertainty. Therefore, spatial memory alone cannot guide locomotion with the same precision, demonstrating an ongoing role for current visual information.

Driving a car is an everyday activity with greater spatio-temporal demands than locomotion on foot because of higher speed and more complex maneuvers. Initial reports indicated comparable driving performance under full vision and visual occlusion conditions when participants changed lanes on a straight road or negotiated a curve (Godthelp, 1985, 1986). For example, Godthelp (1985) investigated whether drivers can change lanes without continuous visual information. Measures of steering-wheel activity and the car’s spatial path with full vision were compared with visual occlusion at start of the lane change. The occlusion duration lasted 1 s in a driving simulator and 3 s in a real car. In both cases, participants successfully performed lane changes under both the full vision and visual occlusion conditions.

With longer occlusion durations, however, greater performance degradation was subsequently observed (Cloete & Wallis, 2009; Wallis, Chatziastros, & Bulthoff, 2002; Wallis, Chatziastros, Tresilian, & Tomasevic, 2007). Wallis, et al. (2002) asked participants to perform a lane change on a straight road in a driving simulator, under normal light or dark-tunnel conditions. In the tunnel, all visual information was removed and participants did not receive visual feedback about their performance. Participants were able to change lanes very well in normal light, but they could not successfully perform the task in the dark-tunnel condition, and usually failed to adjust their driving direction in the new lane. This failure persisted even when visual feedback was provided at the end of each trial.

One possible reason for the severe performance degradation in Wallis, et al. (2002) is the extended visual occlusion, which lasted the whole course of lane change. Even with occlusion of 3 s, Godthelp's (1985) participants were usually in the midst of the lane change when visual information became available again, so they could make final corrections to their maneuvers in the new lane. However, in Wallis, et al. (2002), visual information was removed during the entire lane change, so participants could not make visual corrections and were completely dependent on spatial memory.

To analyze the influence of visual occlusion duration on driving performance, Hildreth, Beusmans, Boer, and Royden (2000) tested a lane correction task in a driving simulator, in which the car's position was perturbed and the screen went blank, and the driver tried to steer back to the center of the lane. Errors began to accrue in the second phase of correction with visual occlusion of only 1.5 s, and variability in steering angle and lateral position in the first phase increased significantly at 4 s. The results indicate that even short occlusion durations yield a decline in performance, consistent with on-line control.

I recently investigated the effect of occlusion in a more demanding locomotor task, walking a slalom course of five targets (Zhao and Warren, 2013). Participants walked in a virtual environment while the visibility of the upcoming targets was manipulated and the walking trajectory was recorded. An analysis of the passing distance for each target revealed that increasing the number of visible upcoming targets from 1 to 5 did not improve steering accuracy or precision, indicating no advantage of a longer preview. In contrast, when the next upcoming target was visually occluded, performance significantly deteriorated, and greater errors were observed with occlusion of the upcoming two targets. The same pattern of results was observed by Duchon and Warren (1997) when participants steered a slalom course with a joystick. These results imply that steering is normally guided to the next target in an on-line manner, one target at a time.

So far, the findings for walking and driving appear to be consistent. Withdrawal of visual information generally leads to a decline in performance, although the effect of occlusion duration depends on the spatio-temporal demands of the task. This emphasizes the importance of current visual information for accurate and precise performance, consistent with on-line control. It also provides evidence of off-line control strategies that can be used in the absence of current information, based on spatial memory that decays rapidly over a few seconds. The outstanding question is the role of this current information: whether it normally controls action on-line, or is used to update an internal model that continually controls action.

The research on manual actions such as reaching or catching is consistent with the findings for locomotion. Manual actions differ from locomotor actions with respect to both effectors and spatial-temporal scale, and often demand higher accuracy and/or precision for successful performance. In early studies on catching, Whiting and colleagues (Sharp & Whiting, 1974; Whiting & Sharp, 1974) found that participants were able to perform a one-handed catching task successfully when the ball was visually occluded for a short duration (less than 280 ms) before interception. But longer occlusion durations led to significantly degraded performance.

Westwood, Heath, and Roy (2001) asked participants to reach to a target in the midsagittal plane. The target was either fully visible, or was occluded 0 to 2 s before the reaching signal and remained occluded during the reach. Visual occlusion during the reach resulted in greater endpoint errors, with longer occlusion times producing even greater errors. Similar effects of occlusion duration have been reported in other studies of manual reaching (Elliott & Calvert, 1990; Heath, Westwood, & Binsted, 2004).

Binsted, Rolheiser, and Chua (2006) examined the time course of the decay of the remembered location of a target. Participants were asked to repeatedly tap between two targets presented in the transverse plane. Both targets were illuminated for the first 5 s, and then disappeared for the remaining 6 s of a trial. Tapping was highly accurate when the targets were visible, but endpoint variability significantly increased immediately after they disappeared, and continued to increase through the occlusion period. This result is consistent with on-line control when visual information is available, and off-line control that decays rapidly after information is withdrawn.

Related studies have investigated the effect of intermittent vision on catching and reaching. In general, performance degrades significantly when the gap between visual samples is more than 80 ms (Bennett, Elliott, Weeks, & Keil, 2003; Bennett, Ashford, & Elliott, 2003; Elliott, Chua, & Pollock, 1994; Elliott, Pollock, Lyons, & Chua, 1995; Lyons, Fontaine, & Elliott, 1997). For example, Bennett, et al. (2003) asked participants to catch an approaching tennis ball with visual samples of 20 ms separated by visual occlusion intervals of 0, 20, 40 or 80 ms. Catching performance with simultaneous binocular samples was unaffected by occlusion intervals of 0 to 40 ms, but performance deteriorated significantly with gaps of 80 ms, with both greater position error and a higher rate of failure. Thus, while continuous visual information may not be necessary for successful action, relatively short occlusion intervals significantly impair performance. This is quite consistent with on-line control, but indicates that any internal model of the ball’s trajectory is extremely short-lived, raising doubts about strong model-based control.

In sum, walking, driving, catching, and reaching tasks are generally impaired under visual occlusion conditions. Although some tasks can be performed successfully with short occlusion durations, it is consistently observed that longer occlusion leads to a larger decline in accuracy and/or precision. The magnitude of error obviously depends on the spatio-temporal demands of the task, and the literature demonstrates that more demanding tasks can produce significant errors with very short occlusion periods. This pattern of findings is consistent with strong on-line control, the claim that action is normally controlled by current visual information. They also cast doubt on strong model-based control, for the evidence indicates that any such representation decays extremely rapidly upon withdrawal of visual information. At a minimum, such an internal model would have to be continuously updated, and thus model-based control also critically depends on current visual information. Taken together, the occlusion paradigm indicates that an internal world model is by itself insufficient to account for the accuracy and precision of normal action; this level of performance appears to require concurrent visual information.

1.1.2. Visual occlusion leads to a different movement pattern

In the previous section, I reviewed literature on task performance under visual occlusion conditions, leading to the conclusion that a world model alone is not sufficient to account for ordinary levels of performance. In this section, I consider research showing that the pattern of movement changes under visual occlusion.

A number of studies have reported that visual occlusion can influence the movement pattern in manual catching (Dessing, Wijdenes, Peper, & Beek, 2009; Mazyn, Savelsbergh, Montagne, & Lenoir, 2007; Tijtgat, Bennett, Savelsbergh, Clercq, & Lenoir, 2011). Mazyn et al. (2007) asked participants to catch an approaching ball with full vision and in a visual occlusion condition in which the ball was occluded at the onset of catching hand-movement. First, participants performed a block of 10 trials of visually-guided catching. Then, they were trained in the occlusion condition on blocks of 10 trials until they reached a criterion (catching 7 out of 10 balls), followed by another block of occluded trials. Number of successful catches significantly dropped in the first occlusion block compared to the full vision block, then improved in the last occlusion block, but remained worse than with full vision. Of greater interest is an observed change in the spatial and temporal characteristics of the catching movement. Compared to the full vision block, the movement was initiated significantly later in the first visual occlusion block, and even later in the last occlusion block. Similarly, the movement time significantly decreased and the peak wrist velocity increased in the first occlusion block, and even more so in the last occlusion block. The peak hand aperture also increased and participants caught the ball closer to their bodies in the visual occlusion condition, compared to the full vision condition. Thus it appears that participants postponed their response to keep the ball visible for a longer time, and the movement kinematics compensated for the late initiation. The peak hand aperture also increased to facilitate successful catching in the occlusion condition.

Delaying movement initiation in the occlusion condition thus served to maintain the visibility of the flying target, enabling participants to detect more information about its motion before it disappeared. The shorter movement time also produced a shorter occlusion time before the catch, reducing uncertainty about the target's trajectory. Increasing the hand aperture helped to compensate for remaining uncertainty about the ball's trajectory. These coordinated changes in the movement pattern suggest that the visual-motor system adapts to reduced information by seeking to maximize the period of on-line control, minimize the period of off-line control, and compensate for uncertainty about the target's motion. This pattern of results is consistent with the hypothesis that on-line control is the preferred mode of action guidance.

The studies I reviewed in this section manipulated availability of visual information in action tasks, that is, visual information is either available or totally eliminated. The results indicate that visual occlusion usually leads to degraded action performance and/or different movement pattern, consistent with on-line control. However, there are very few studies testing the effect of degraded visual information on action tasks. This is an interesting test about action control. In some natural circumstances, visual information may be degraded such as walking in fog. Moreover, testing action task with degraded visual information may shed light on mechanisms underlying action control which might complement the findings reviewed in this section. Therefore, in my dissertation, I will investigate on-line or model-based control by manipulating quality of visual information in action tasks. Specifically, in Experiment 2, I will degrade the visual information to different levels about a moving target to test its effect on a locomotor interception task.

1.2. On-line control: Is current information sufficient?

Whereas model-based control emphasizes the role of an internal representation in guiding action, on-line control emphasizes the role of current visual information. The approach seeks to identify both the information that is used and the control laws that map that information into the control variables for action (Warren, 2006).

1.2.1. On-line control of locomotor behavior

According to the on-line approach, locomotion is normally controlled on the basis of current visual information, without relying on an internal representation such as a world model or a pre-planned path. Under normal circumstances, humans control their actions by detecting current information and coupling it to movement control variables in real time (with a visual-motor delay), avoiding the computational demands of maintaining an internal model and a path plan in a complex environment that is continuously changing.

Much evidence has shown that multisensory information is used to perceive one's current direction of travel (heading) and control steering, including optic flow (Bruggeman, et al., 2007; M.G. Harris & Carre, 2001; Li & Cheng, 2013; Turano, et al., 2005; Warren, et al., 2001), proprioception (J.M. Harris & Bonas, 2002; Rushton, et al., 1998; Wilkie & Wann, 2002), and vestibular information (Butler, et al., 2010). The steering dynamics model developed by Warren and his colleagues (see Warren & Fajen, 2008) offers an existence proof that on-line control based on such information is sufficient to account for basic locomotor behavior, including steering to stationary and moving targets, and avoiding stationary and moving obstacles (see also Wilkie & Wann, 2003, 2005). The model is a nonlinear dynamical system that takes information about the current heading and the directions and distances of objects as input, and generates a new heading direction as output, without an internal representation of the environment or the future path.

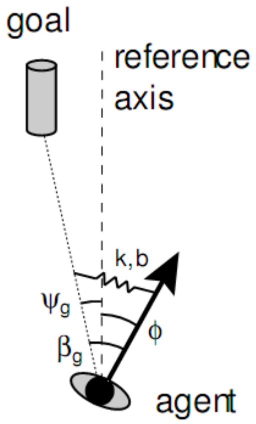

Figure 3. Definition of variables as an agent walk to a stationary goal: heading direction(Φ), goal direction( ), target-heading angle( ), metaphorical spring stiffness (*k*) and damping coefficient(*b*). Adapted from Warren (2006).

Consider the example of steering to a stationary goal. Fajen and Warren (2003) modeled steering with a second-order differential equation in which the angular acceleration of turning is a function of the current difference between the heading direction and the goal direction ( ) and the distance of the goal (d_g):

(1)

This model can be thought of as an angular mass-spring system (Figure 3). The model effectively nulls the target-heading angle by creating an attractor of heading in the goal direction. The damping term reflects a frictional force that is proportional to the turning rate, preventing oscillations about the goal. The stiffness term reflects the observation that the strength of the attractor linearly increases with the target-heading angle. The stiffness is modulated by goal distance , reflecting the observation that the attractor strength decays exponentially with distance.

Fajen, and Warren (2003) found that this model closely reproduces walking trajectories as goal distance and target-heading angle are varied. Participants turned onto a straight path to the goal in the early part of a trajectory, and they did so earlier when the goal was closer and when the target-heading angle was greater. The model generalizes to new conditions with fixed parameter values (b, k, c_1, c_2). Moreover, similar components for other elementary behaviors have been developed, which can be linearly combined to account for more complex behavior (Warren & Fajen, 2008).

Taken together, the steering dynamics model demonstrates that on-line control is sufficient to explain basic human locomotor behavior, when concurrent information is available. Of course, it is also possible to create conditions that invoke off-line control, by removing information (e.g. blind walking), imposing task demands that render the available information inadequate, or introducing a strategic element (e.g. team sports). But it does not follow that model-based strategies are normally used to guide locomotion when on-line control is sufficient.

1.2.2. On-line control of manual actions

It is widely observed that manual action is adjusted based on incoming visual information even after movement onset (Brenner & Smeets, 1997; Brenner, Smeets, & de Lussanet, 1998; Caljouw, van der Kamp, & Savelsbergh, 2006; Diedrichsen, Nambisan, Kennerley, & Ivry, 2004; Gosselin-Kessiby, Messier, & Kalaska, 2008; Sarlegna, Blouin, Bresciani, Bourdin, Vercher, & Gauthier, 2003; Saunders & Knill, 2003, 2004). Brenner and Smeets (1997) found that participants rapidly adjust their hand movement to the target's perturbed position in a manual hitting task. Participants were asked to hit a stationary disk with a rod as soon as the disk appeared on a screen. In some trials, the disk was suddenly displaced to the left or right as participants initiated their hand movement. Hand trajectories indicated that participants shifted their hand movement toward the disk's new position about 110 ms after its displacement. In another study (Brenner et al., 1998), participants hit a moving target with a rod; on some trials, the target velocity suddenly increased or decreased after movement initiation. The results indicated that participants adjusted their hand movement on-line with a visual-motor delay about 200 ms, responding to the perturbation on the target's velocity.

Gosselin-Kessiby et al. (2008) required participants to first align their hand with the orientation of a target then reach to the target. Participants were explicitly instructed not to change their hand orientation during reaching, yet the initial alignment error was reduced during the reach. This result suggests that on-line adjustment of hand movements may be carried out involuntarily based on the available information.

In the previous section, I found that when manual tasks are performed under visual occlusion, performance typically deteriorates and movement patterns change to compensate for the loss of visual information (e.g. Mazyn et al. 2007). The results imply that an internal representation is by itself insufficient to account for normal levels of performance, inconsistent with model-based control. Conversely, the present studies indicate that manual actions are continuously guided by the available information and are rapidly adjusted in response to new information. The evidence thus demonstrates that current information is sufficient to account for the guidance of locomotor and manual actions, consistent with on-line control.

In contrast with the findings that manual actions are rapidly adjusted in response to new information, there are very few studies testing whether humans could rapidly adjust their locomotor interceptions according to new information about a moving target. Moreover, it is an interesting question whether the steering dynamics model (see Warren & Fajen, 2008) is able to account for humans' locomotor interception of a target that changes its movement. I will test this in two experiments. Specifically, in Experiment 1, I will vary target speed to test participants' interception behavior. By simulating interception paths, I will test whether the steering dynamics model could sufficiently account for interception behavior or an internal model of target movement estimated over a temporal window could improve simulation performance. Then in Experiment 3, I will test whether participants could learn the movement of a speed-varying target through a block of trials and, if they did, whether a learned internal model of target movement could guide interception of an occluded target.

1.3. Anticipatory control of interceptive actions: Is an internal model necessary?

To interact successfully and efficiently with a dynamic environment, action is often anticipatory. In this section, I will examine whether anticipatory control of interceptive action is based on current information, or whether some form of prediction based on an internal world model is necessary. Two anticipatory control strategies have been proposed for interceptive action: predictive control, which is model-based, and on-line control, which is information-based in a continuous or prospective manner (Lee & Young, 1985; Warren, 2006; Zago, McIntyre, Senot, & Lacquaniti, 2009)[1]. I note that these terms are used inconsistently in the literature, so I will define our usage here.

According to *predictive control,* an internal world model is used to predict the future state of the environment, the prediction is used to plan an action, which is then executed. For instance, in the outfielder problem, the initial velocity of the ball and a model of projectile motion would be used to predict its landing point and plan a running trajectory. Predictive control is thus a form of model-based control. In contrast, anticipatory action could be based on current information,in two ways. In *continuous control,* movement is governed by information that continuously leads the actor to the right place at the right time, according to a control law such as the OAC and CB strategies. *Prospective control* is based on current information that specifies the future state of the actor-environment system, and guides the actor to that endpoint according to a control law. For example, the relative rate of optical expansion (*tau*) of an object approaching at a constant velocity specifies its time-to-contact (TTC) with the actor – the time that remains before a future collision (Lee, 1976; Hecht & Savelsbergh, 2004). Instead of a future state being predicted by a world model, the future state is specified by current information, which is used in a control law. Both continuous and prospective control are thus forms of on-line control.

1.3.1. Locomotor interception

In locomotor interception, the actor travels to intercept a moving target, which is typically moving in the horizontal plane. In initial studies, participants travelled on a linear path (e.g. a track or a treadmill) and only controlled their speed. The results were consistent with the constant bearing strategy, in which speed was varied to keep the target in a constant direction, leading to successful interception (Bastin, Craig, & Montagne, 2006; Bastin, Jacobs, Morice, Craig, & Montagne, 2008; Chardenon, Montagne, Laurent, & Bootsma, 2005; Lenoir, Musch, Janssens, Thiery, & Uyttenhove, 1999; Lenoir, Musch, Thiery, & Savelsbergh, 2002). Fajen and Warren (2004) asked participants to intercept a moving target by walking in a virtual environment, allowing them to control both heading and speed. Instead of heading toward the target’s current position, participants led the target, maintaining it in a constant bearing direction in space. When tested against other possible control strategies, the constant bearing strategy best explained the data, indicating that it is sufficient to account for locomotor interception (Fajen & Warren, 2007).

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[1] A third strategy of *strong anticipation* has been developed for temporally coupled movements (Stepp & Turvey, 2010; Stephen, Stepp, Dixon, & Turvey, 2008), but I do

Subsequently, Diaz, Philips, and Fajen (2009) suggested that prediction might play a role in guidance of interception. In a virtual environment projected on a large screen, participants used a foot pedal to control their simulated speed on a straight path, in order to intercept a moving target. In the first experiment, the target moved at 3 initial speeds, then after 2.5 to 3.25s it changed speed. The new speed was sampled from a normal distribution with a mean greater than the initial speed, so the target usually accelerated. Contrary to the constant bearing strategy, the bearing direction of the target increased prior to the speed change – that is, participants typically accelerated more than required by the CB strategy. The authors suggested that participants learned from previous trials that the target usually increased its speed, and thus the accelerated prior to the target.

In their second experiment (Diaz et al., 2009), participants intercepted a target that moved on linear, concave, or convex curvilinear paths. On the concave trials, participants accelerated early then decelerated later in a trial, consistent with the constant bearing strategy. On the convex trials, participants mostly accelerated early in a trial as the target approached, thereby avoiding the target getting away when it turned perpendicular to their path, inconsistent with the constant bearing strategy. The authors fit this data with a model combining the constant bearing strategy with a short-term prediction of the target's motion during a future time interval (Δt = 0.5-3.5s), based on a learned internal model of the target's trajectory. Travel speed is then adjusted to null change in the bearing angle at that future time ($t+\Delta t$). Diaz, et al. (2009) thus suggested

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not have space to consider it here.

that an internal model of the target's trajectory plays a part in guiding interception, together with the CB strategy.

However, the spatio-temporal demands in Diaz, et al. (2009) were such that on-line control was often inadequate for successful interception. Target trajectories were explicitly designed so that the CB strategy would often fail, and indeed participants missed the target in nearly half the trials, even after practice (~ 45% in the last block of both experiments). These are precisely the conditions that invoke off-line control strategies. In Experiment 2, the authors note that performance was best on linear and concave trials, when the speed profile was consistent with the CB strategy, and worst on convex trials, when it was not. That is, participants appeared to use the CB strategy in conditions when it was likely to succeed (linear and concave paths), and added a predictive component in the condition when it was insufficient (convex path). I note that, contrary to other studies, initial walking speed in Diaz, et al. (2009) was 0 m/s at the onset of target motion, with an interception time of 5 s or less. This required acceleration early in the trial, consistent with the observed early-acceleration strategy.

Morice, Francois, Jacobs, and Montagne (2010) performed a similar experiment, in which participants walked on a treadmill in a virtual environment to intercept a target that moved on rectilinear, concave or convex paths. In this case, however, it was possible to intercept the target (about 90% success) and participants adopted a moderate walking speed before the target appeared. With the concave target path, participants usually accelerated and decelerated, whereas with the convex path they decelerated from the initial speed and then accelerated, consistent with the CB strategy. This result suggests that participants prefer an on-line control strategy when it is sufficient to perform the task.

Morice, et al.’s (2010) second experiment was similar, except that the target’s path was marked on the ground with a colored stripe on half the trials. The participants’ speed profiles were less consistent with the constant bearing strategy when the stripe was visible, and more consistent with a required velocity model. That strategy is based on the ratio of the actor’s distance from the interception point and target’s TTC with the interception point. Marking the target’s path specifies the interception point during straight walking and thus makes these variables visually available, providing prospective information for on-line control. Under these conditions, prediction based on an internal model is not necessary to explain the experimental results.

The work of Diaz et al. (2009) and Morice et al. (2010) suggests that the CB strategy is not the only solution for locomotor interception: human actors are able to adopt different strategies under different conditions, demonstrating a certain flexibility in visual-motor control. Recall, however, that participants could only control their speed in these studies, whereas in normal locomotion both speed and heading must be controlled. Research by Owens and Warren (described in Warren & Fajen, 2008) asked participants to intercept a target that moved on a circular path while walking in a virtual environment on the ground plane. The results indicated that participants usually walked a smoothly curved trajectory at a preferred speed to intercept the target, consistent with the CB strategy (Owen & Warren, 2004). When the target traveled repeatedly on the same circular path, some participants learned a heuristic after 6 to 10 trials: they took a short-cut across the circle and picked up the target on at the far side using the CB strategy (Owen & Warren, 2005). But when the target could move on two different circular paths, this heuristic was abandoned and participants reverted to the CB strategy for the entire interception path (Owen & Warren, 2006).

These results indicate that the constant bearing strategy is a basic and robust strategy for locomotor interception. Although heuristics can be learned under certain conditions, they are approximate, specific to those conditions, and unstable. In this case, with a repeated target path, a heuristic was adopted for the early stage of interception when precise control was not essential, but the CB strategy was phased in during the late stage, when the spatio-temporal demands of the task were high. Such a heuristic-then-online strategy is another manifestation of the flexibility in human visual-motor control, yet it did not generalize to highly similar situation with only two possible targets. Even when an off-line strategy is adopted, it appears to be a rough heuristic that applies under narrow conditions, rather than an accurate, generalizable world model.

1.3.2. Manual interception

Anticipatory manual interception might also be based on current visual information or an internal world model. Whereas locomotor interception takes place over many seconds and tolerates relatively large errors, manual interception often occurs within a second and demands a great degree of accuracy. These spatio-temporal demands imply even greater difficulty in the face of a visuomotor delay of about 200ms, widely recognized as the duration for visual information processing and action initiation (Nijhawan, 2008).

Numerous studies indicate that online control is sufficient to account for manual interception of an approaching ball (Bootsma, Fayt, Zaal, Laurent, 1997; Dessing, Bullock, Peper, & Beek, 2002; Dessing, Peper, Bullock, & Beek, 2005; Montagne, Laurent, Durry, & Bootsma,1999; Peper, Bootsma, Mestre, & Bakker, 1994). For example, Peper, et al. (1994; Bootsma, et al. 1997) originally proposed the required velocity model to account for ball catching behavior. According to this model, the lateral hand velocity is continuously controlled by information about the current lateral distance between hand and ball, divided by the ball's current TTC. However, recent evidence favors a prospective control strategy (Peper, et al, 1994), in which the interception point of the approaching ball is specified by the ratio between its lateral optical velocity and its TTC, which is used to control hand position on-line (Arzamarski, Harrison, Hajnal, & Michaels, 2007; Craig, Goulon, Berton, Rao, Fernandez, & Bootsma, 2009; Jacobs & Michaels, 2006; Michaels & Jacobs, 2006). There is no indication that an internal model of the ball's trajectory must be introduced to account for these interception data.

The need for an internal model has been more pointedly raised for the case of catching a free-falling object, where gravitational acceleration significantly influences the timing of interception. Although the *tau* variable was originally proposed to specify TTC with an object moving at a constant velocity, Lee, Young, Reddish, Lough, and Clayton (1983) argued that it could also be used to time hitting an accelerating object. A ball was dropped from different heights, which accelerated under gravity. Participants stood beneath the ball, crouched and leapt to punch it straight back up. The results indicated that they geared the timing of their leg and arm movements to the first-order estimate of TTC given by *tau*. This suggested that prospective information is used to control interception on-line, even with accelerating objects.

In contrast, Lacquaniti and his colleagues argued that interception of a free falling object is predictively controlled based on an internal model of earth's gravity (Lacquaniti & Maioli, 1989a , 1989b; Mcintyre, Zago, Berthoz, & Lacquaniti, 2001; Senot, Zago, Lacquaniti, & McIntyre, 2005; Zago, Bosco, Maffei, Iosa, Ivanenko, & Lacquaniti, 2004). For example, Mcintyre, et al. (2001) asked participants to catch a ball that was projected downward with three initial velocities (0.7, 1.7 and 2.7 m) from a height 1.6m above their hand. On Earth, catching responses were closely synchronized with the arrival of the ball regardless of its initial velocity. Participants rotated their forearm upward about 200 ms before contact and the peak bicep EMG occurred about 40 ms before contact. However, when the task was performed in microgravity (about 0 g) on board the space shuttle, the anticipatory peak bicep EMG occurred earlier before contact; the shifts were inconsistent with using first-order TTC or the ball's actual motion, and implied that participants were still correcting for Earth's gravitational acceleration despite being in microgravity. Considering that object acceleration is poorly perceived (Brouwer, Brenner, & Smeets, 2002, Werkhoven, Snippe, & Toet, 1992), the authors proposed that a "second-order internal model of gravity" is used to predict the object's movement during catching.

Baures, Benguigui, Amorim, and Siegler (2007) raised some methodological concerns about these studies. Moreover, the results are actually consistent with an approximate heuristic strategy and do not require an internal model of gravitational motion. Indeed, the authors (Zago, et al., 2008) subsequently backed away from their initial interpretation concluding that their findings were "indicative of a rather unsophisticated model of effects of gravity," and stressing "the notion of implicit, approximate, probabilistic knowledge of the effects of gravity on object motion, as opposed to the notion of explicit, precise, analytic knowledge of Newtonian mechanics."

Other studies have shown that visual information is not necessary for participants to intercept an object in free fall (Katsumata & Russell, 2012; Lacquaniti & Maioli 1989b). Lacquaniti and Maioli (1989b) reported that participants were able to catch a ball that was dropped from different heights and was occluded after its release. However, they did not produce consistent anticipatory EMG activity in the occlusion condition compared with the visual condition. Moreover, successful catches in occlusion condition could be attributed to an off-line mapping strategy based on time retention (Baures, et al., 2007). Lacquaniti and Maioli (1989b) only tested three drop heights (0.4, 0.8 and 1.2 m). Thus, participants could have learned a simple mapping from the ball's height to the temporal interval between release and interception in early trials, and used the mapping to guide interception in the occlusion condition. Indeed, in a study of rhythmic ball bouncing, Siegler, Bardy, and Warren (2010) found that participants use the temporal interval of the ball's ascent to control the timing of racket motion. Specifically, participants adapted immediately to a change in the gravitational constant when bouncing a virtual ball, demonstrating that racket motion was not controlled based on an internal model of Earth's gravity.

Such a temporal mapping strategy could also be used to intercept fast-moving objects when there is insufficient time to detect information about the trajectory. In major league baseball, for example, a fastball takes about 410 ms from release to arrive at the plate, and passes the batter at speeds approaching 100 mph (44.7 m/s), an angular velocity greater than 500 deg/s. The batter's pre-swing usually begins about 200 ms before bat-ball contact. Thus, the batter must rely on brief visual information early in the ball’s flight, sometimes prior to release, to control hitting.

Gray (2002) asked experienced baseball players to use a bat to hit a simulated approaching baseball displayed on a computer monitor. The ball was launched horizontally from a simulated distance of 18.5 m, and was only affected by the force of gravity. In the first experiment, pitch speed varied randomly within a large range (28.2-35.8 m/s). The temporal accuracy of hitting was significantly better than the spatial accuracy. In the second experiment, only slow (about 31.3 m/s) and fast (about 38.0 m/s) pitch speed were randomly presented, and performance greatly improved. Batters hit significantly more balls and spatial accuracy was significantly higher. If batting were based on an internal model of each trajectory, there is no reason to expect such an improvement. A possible explanation is that the small set of initial conditions in the second experiment facilitated the development of a mapping strategy, in which the ball’s optical motion in the early part of its trajectory was mapped into the spatial parameters of the swing. By contrast, the variation in initial conditions in the first experiment was presumably too great to acquire a simple mapping.

In addition, a pitch sequence effect was observed in the second experiment. For example, performance on a fast pitch was better when it followed several fast pitches than when it followed several slow pitches. The authors explained this as an expectancy effect, such that after several fast pitches players came to expect the next one to be fast again. But a mapping strategy could provide a mechanism for this effect of “expectancy” on performance. Specifically, a fast-pitch mapping may be activated and tuned by a sequence of fast pitches, resulting in better performance on the next fast pitch. Switching to a slow-pitch mapping would have to be based on the first couple hundred milliseconds of the next pitch, incurring a cost in performance.

Recently, Hayhoe and her colleagues (Diaz, Cooper, Rothkopf, & Hayhoe, 2013; Hayhoe, McKinney, Chajka, & Pelz, 2012; Hayhoe, Mennie, Sullivan, & Gorgos, 2005; also Land & McLeod, 2000) have reported anticipatory eye movements in ball interception tasks. They proposed that an internal model of the world's dynamics is constructed and used to predict upcoming events and plan movements. Diaz, et al. (2013) asked participants to hit a ball with a racquet in a virtual environment, after it bounced once on the ground. The ball was projected toward them from a distance of 9 m on three sets of parabolic paths, which simulated natural trajectories under gravity. The ball then bounced near a fixed location (about 3.25 m away), with two possible values of elasticity (0.58 and 0.73), which determined the ratio of prebounce to postbounce vertical velocity. Eye movement records indicated that participants usually tracked the ball after it was released and then made a saccade about 150-200 ms before the bounce. They maintained that gaze direction until the ball bounced up near the line of sight, after which they tracked the ball again before hitting it.

Based on an analysis of the visual angle between the fixed gaze direction and the ball direction at the time of the bounce, Diaz, et al. (2013) concluded that participants made accurate predictive saccades. Specifically, the line of fixation was close the ball's post-bounce trajectory, given its pre-bounce velocity and elasticity, consistent with a prediction based on an internal model of the ball's dynamics. Unfortunately, the within-participant variability of this angle was not reported, which bears on the required precision of any internal model.

To assess the accuracy of the predictive saccade, Diaz, et al. (2013) analyzed the minimum visual angle between the gaze direction and ball direction after the bounce, and reported that it was quite small, with low within-participant variability. I note, however, that the ball's post-bounce trajectory spans a rather large visual angle, and thus a saccade does not need to be very accurate or precise to land near this trajectory. Specifically, as long as the saccade is not too small, the gaze direction will be low enough for the ball to pass near the line of fixation, so the eye can then track the ball. This suggests that a simple not-too-small-saccade heuristic may be enough to fixate near the post-bounce trajectory, with a simple mapping from the three initial trajectories to a saccade target for both ball elasticities. Such an off-line strategy may be able to account for anticipatory saccades more parsimoniously than assuming a generative dynamic world model. Potential tests of this claim include analyzing the accuracy and precision actually required for successful and unsuccessful saccades in this task, and studying whether experience with a small set of ball trajectories and elasticities generalizes to new conditions or requires learning a new mapping.

Overall, here is little evidence suggesting that an internal model of gravity or elasticity is necessary to explain control of manual interception. In general, interception appears to be controlled on-line by visual information when it is available. In certain circumstances, when information is unavailable (e.g., visual occlusion), near threshold (e.g. baseball batting), or object trajectories are stereotyped, simple heuristic or mapping strategies appear be used. The advantage of these simple task-specific strategies over an accurate internal model is their parsimony in explaining interception behavior. However, it is a challenge to empirically distinguish on-line control and simple off-line strategies from a predictive internal model that is continually updated by current information.

1.4. The current studies

In this chapter, I reviewed studies indicating that visual occlusion usually leads to degraded performance and/or different movement pattern. This implies that an internal model is not sufficient to guide action. In those studies, visual information was either available or totally eliminated. In my dissertation, I will probe intermediate levels of information availability by degrading the visibility of a moving target to different levels in a locomotor interception task. If interception is controlled on-line by current visual information, increasingly degraded visibility should lead to progressively impaired performance. Total occlusion of the target should lead to worst performance for there is no information about target motion at all. If interception is controlled by an internal model of target motion, interception performance should depend on the fidelity of the internal model. If a high-fidelity internal model is created before target visibility degradation and persists, it should be able to guide interception accurately and precisely. If a medium- or low-fidelity internal model is created before target visibility degradation and persists, interception performance should progressively decline as target visibility is degraded, until it plateaus at some level: the plateau provides an estimate of the model’s fidelity. If an internal model is created and continuously updated by incoming visual information, interception performance should progressively decline as target visibility is degraded. Total occlusion of the target should result in intermediate level of performance that provides estimate of the internal model without updating by the degraded target information.

I also reviewed studies indicating that current information is sufficient to guide actions. The steering dynamics model (see Warren & Fajen, 2008) offers an existence proof that on-line control based on such information is sufficient to account for basic locomotor behavior. In addition, studies concerning manual actions indicated that hand movement is adjusted based on incoming visual information even after movement onset (e.g. Brenner & Smeets, 1997). In my dissertation, I will test whether locomotor interception can be adjusted in response to new information about target movement. In Experiment 1, I will vary target speed in the midst of a trial, that is, the target will randomly speed up or slow down. If locomotor interception is controlled on-line based on current information, interception should be rapidly adjusted in response to new target speed. Moreover, the steering dynamics model should be able to account for interception of the speed-varying target. I will also test whether an internal model of target movement estimated over a temporal window contributes to account for interception behavior. If the internal model does make contribution, involvement of the internal model as input to the steering dynamics model should improve simulation of interception paths. Otherwise, it implies that the internal model is not necessary to account for interception behavior.

In the last section of this chapter, I reviewed studies indicating that locomotor and manual interception are guided based on anticipatory control. Generally speaking, interceptive actions can be accounted for by either on-line control based on current information, or by some off-line strategies such as heuristics and mapping strategy. However, some studies suggested that a learned internal model of target movement could be used to guide interception. Such internal models could be learned from everyday life, e.g. an internal model of earth’s gravity (see McIntyre, et al., 2001), or from repeated practice, e.g. a fixed target trajectory (see Diaz, et al., 2009). In my dissertation, I will test whether an internal model of target behavior could be learned and subsequently used to control interception. If so, the internal model should be available to guide interception of the same target even when the latter is visually occluded.

Chapter 2. Experiment 1: Intercepting a speed-varying target

2.1. Introduction

As described above, humans walk to intercept a moving target by nulling change in the current direction of the target, consistent with the constant bearing strategy (Bastin, Craig, & Montagne, 2006; Bastin, Jacobs, Morice, Craig, & Montagne, 2008; Chardenon, Montagne, Laurent, & Bootsma, 2005; Lenoir, Musch, Janssens, Thiery, & Uyttenhove, 1999; Lenoir, Musch, Thiery, & Savelsbergh, 2002). For example, in Fajen and Warren (2004), participants intercepted a moving target by walking in a virtual environment. It was found that, instead of heading toward the target's current position, participants led the target, maintaining it in a constant bearing direction in space (Figure 4).

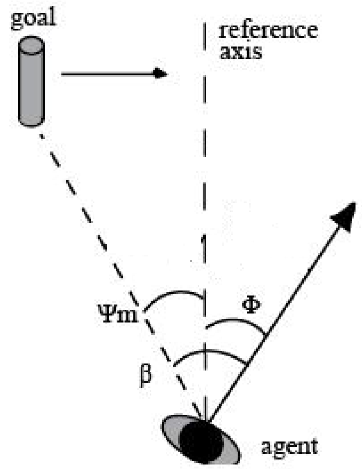

Figure 4. Definition of variables as an agent is intercepting a moving goal: heading Direction (Φ), goal direction ( ), target-heading angle ( ).

Fajen & Warren (2007) reported that the constant bearing strategy best explained participants' interception behavior over other possible control strategies. A steering dynamics model based on the constant bearing strategy accurately reproduced participants' interception path in different conditions (See Equation 2).

(2)

This theoretical model effectively nulls change in the target's bearing direction (, establishing an attractor in the direction of the interception path. The damping term represents a frictional force that is proportional to agent's turning rate, reducing oscillations. The stiffness term reflects the observation that the strength of the attractor linearly increases with the rate of change in the target's bearing. The stiffness term is modulated by target distance , reflecting the observation that the attractor strength decreases with target distance.

Besides the constant bearing model, Fajen & Warren (2007) also tested other possible theoretical models. These included a model that nulls the target-heading angle, a model that computes a required interception angle and a model that nulls change in the target-heading angle. Simulation performance indicated that the constant bearing model best explained participants' interception behavior.

In contrast to an on-line interception strategy, a model-based strategy could create an internal model by extrapolating the target's previous motion to estimate its future trajectory. For example, Saunders and Knill (2003, 2004) proposed an auto-regressive linear model for a manual reaching task. According to this model, finger position is estimated by computing the weighted sum of the finger's previous positions over a temporal window. In effect, the model predicts the next finger position by integrating over its previous positions. I evaluated this class of internal models for extrapolating target motion. In this case, interception behavior is guided by an estimate of the target's future speed that is based on integrating its previous speed over some temporal window.

In Experiment 1, I tested whether this kind of internal extrapolation model makes a contribution to locomotor interception, or whether current visual information is sufficient to explain interception behavior. Participants walked to intercept a moving target that randomly increased or decreased its speed in the midst of a trial. These interception trajectories were simulated using the constant bearing strategy (with a fixed visual-motor delay), but different kinds of input about target motion were compared. Specifically, I either input information for the target's current speed, or an estimate of the target's speed based on integration over a previous temporal window. The size of the temporal window was varied to identify the optimal integration interval. If such an internal model of target motion contributes to interception behavior, it would improve simulation performance. In contrast, if current visual information is sufficient to explain behavior, no improvement would be observed.

2.2. Method

2.2.1. Participants

10 graduate and undergraduate students (six females, 4 males) participated in this experiment. Their ages ranged from 19 to 30, and all had normal or corrected-to-normal vision. Participants read and signed the informed consent prior to the experiment, and were paid for their participation. Brown’s Institutional Review Board approved the research protocol.

2.2.2. Apparatus

The experiment was carried out in the Virtual Environment Navigation Lab (VENLab) at Brown University. Participants walked freely in a 12 m × 12 m tracking area while viewing a virtual environment in a head-mounted display (HMD; Proview SR80-A, Rockwell Collins, Carlsbad, CA). The HMD provided stereoscopic viewing with a 53° (vertical) × 63° (horizontal) field of view, at a resolution of 1024 × 1280 pixels in each eye. The virtual environment was generated using Vizard software (WorldViz, Santa Barbara, CA) on a Dell XPS 730 workstation, and the images were presented at frame rate of 60 Hz. Head position and orientation were measured using a hybrid ultrasonic-inertial system (Intersense IS-900, Billerica, MA) with 6 degrees of freedom, at a sampling rate of 60 Hz. Head coordinates from the tracker were used to update the display with a latency of approximately 50 ms.

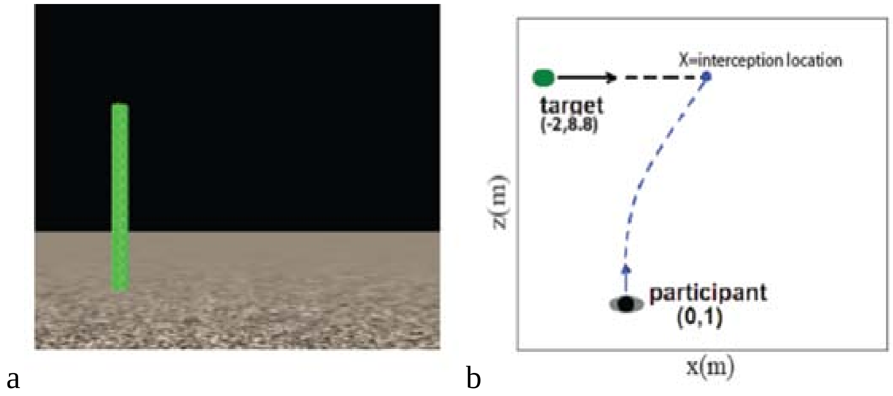

Figure 5. Display of the experimental environment. a: A target pole appears on the participant’s left and moves rightward. b: A top-down view at the moment the target appears.

2.2.3. Displays

The virtual environment consisted of a ground plane (50 m^2) mapped with a random noise texture of black and white squares, a black sky, a home pole, an orientation pole, and a target pole (See Figure 5). The home pole was a blue granite-textured cylinder, 3.0 m tall with a radius of 0.2 m; the orientation pole was a red granite-textured cylinder, 1.8 m tall with radius of 0.2 m; the target pole was a green granite-textured cylinder, 2.0 m tall with a radius of 0.1 m. When participants stood at the home pole and faced the orientation pole (5 m away), the target pole appeared 8.8 m ahead and 2.0 m to the left or right of the participant and immediately began moving. If the target appeared on the left, it would move rightward (and vice versa) on a path perpendicular to the line between the home and orientation poles.

2.2.4. Design and procedure

The target pole initially moved at one of the two speeds, 0.6 or 0.8 m/s. Three seconds later, it changed its speed by -0.3, -0.2, 0, +0.2 or +0.3 m/s. This yielded a 2 (initial speed) x 5 (speed change) factorial design, with a total of ten target conditions.

At the beginning of an experimental session, the HMD was set up and calibrated for the participant according to the procedure described in Fajen and Warren (2003). This was followed by 8 practice trials in which the target's initial speed was 0.7 m/s, different from test trials. The target speed increased by 0.2 m/s in 2 practice trials, decreased by 0.2 m/s in 2 trials, and remained constant in the remaining 4 trials, which were presented in a random order. The participant then completed 8 test trials in each target condition (initial speed x speed change), for a total of 80 test trials. The order of test trials was also randomized.

At the beginning of each trial, the home pole and orientation pole appeared. The participant was instructed to walk to and stand at the home pole, facing the orientation pole. After 1.5 s, the orientation pole turned yellow and the participant was instructed to walk straight toward the orientation pole. After the participant walked 0.5 m, the home and orientation poles disappeared; after another 0.5 m, the target pole appeared and started moving. The participant was instructed to walk to intercept the target without running. When the participant arrived within 0.4 m of the center of the target pole, the trial ended and next trial began, with the home and orientation poles appearing at new locations. All instructions were pre-recorded and delivered over headphones. An experimental session lasted about 50 min.

2.3. Results

2.3.1. Interception locations

I first examined the influence of the different target conditions on interception location. Figure 6 illustrates the interception location in the different speed change conditions for Participant 10 (note that the z-axis is exaggerated relative to the x-axis). When the target speed increased, it traveled farther in the lateral direction (x-axis) before interception, with a progressively greater effect for larger increases; if the target speed decreased, it traveled a disproportionately shorter distance before interception.

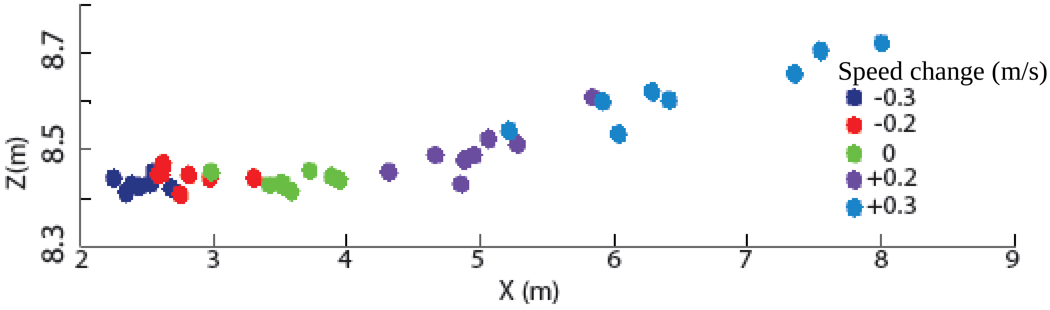

Figure 6. Example interception locations from Participant 10 with target initial speed 0.8 m/s.

Because the target moved in the x direction with a constant z position, I analyzed only the x interception location (the variation in z, only about 0.3 m, was due to the angle of approach to the target pole). The mean x interception location in each target condition appears in Figure 7. A 2-way repeated-measures ANOVA revealed significant main effects of initial speed, F (1,9) = 582.59, $p < 0.01$,$\eta_p^2 = 0.99$, speed change F (4,36) = 257.93, $p < 0.01$, $\eta_p^2 = 0.96$, and an interaction, F (4,36) = 24.65, $p < 0.01$, $\eta_p^2 = 0.73$.

The results indicate that the speed manipulation was sufficient to affect the participants' interception behavior.

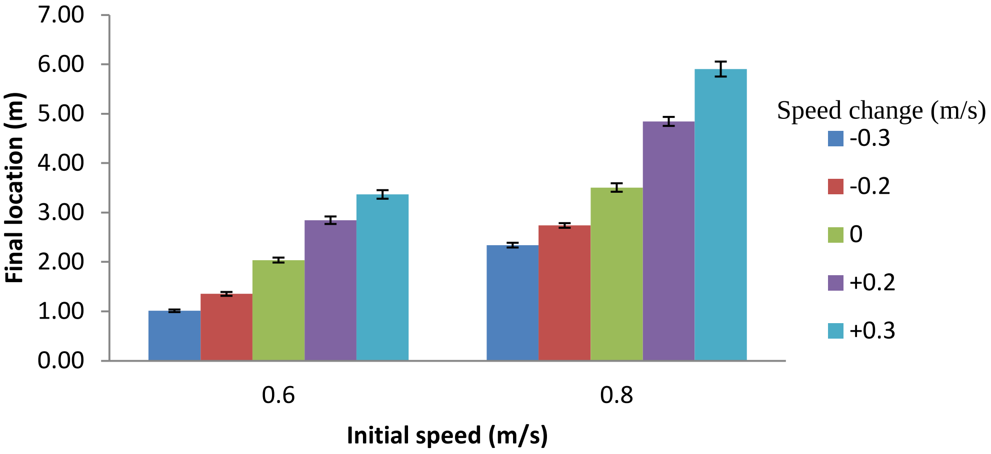

Figure 7. Mean final locations in each target condition in Experiment 1.

2.3.2. Simulation of interception path

I simulated interception paths using the constant bearing model (Equation 2), according to which participants intercept the target by nulling change in the target's bearing direction. I used the parameter values from Fajen and Warren (2007), that is, b =7.75 s^{-1}, k_m=6.00 $m^{-1}s^{-1}$, and c_1=1.00 m, fixed across all conditions. I input the target's current speed to the model, with a fixed visuo-motor delay of 400 ms from Cinelli and Warren (2012), reflecting the interval between a target speed change and observable adjustments in a walking participant's trajectory.

To examine whether an internal model of target motion contributes to locomotor interception, I also ran simulations of the constant bearing model using the extrapolated target speed as input. Specifically, the distal target speed was estimated by computing its mean prior speed over a temporal window (See Equation 3), and treating the size of window as a free parameter (Figure 8a).

(3)

The integration interval influences the estimate of target speed, such that a larger window results in a longer delay before the current target speed is accurately estimated following a speed change (Figure 8b). I varied the temporal window from 50 to 1000 ms in increments of 50 ms. The resulting estimate of the target's proximal angular velocity and distance were fed into the simulation of the constant bearing model.

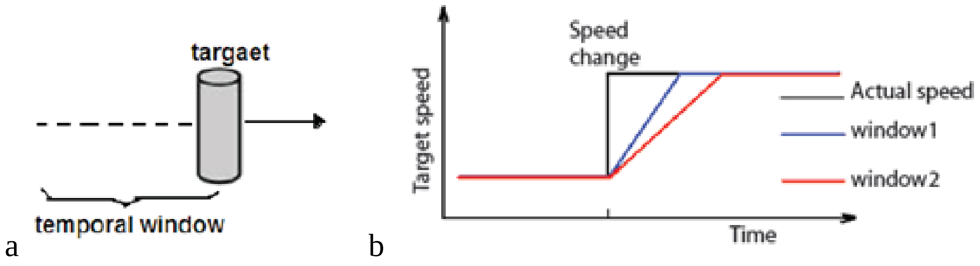

Figure 8. a: As a target is moving right, its movement is estimated within a temporal window. b: Example target speed profile and its estimations within different temporal windows with window2 longer than window1.

To simulate each trial, the model was initialized with the participant's initial position and initial heading, and the time series of actual walking speed was input into the model along with the target speed and distance. The model was integrated in Matlab using the Runge-Kutta method to generate a time series of the actor's position and heading direction. Sample paths from participant N and simulated paths from both models appear in Figure 9. The on-line constant bearing model (red) appears to match the participant’s actual path (blue) quite closely. When the extrapolated estimate of target speed with a temporal window of 800 ms is used as input in the simulation, the simulated paths (green) are no closer and appear to deviate more from the participant paths in some conditions (Figure 9b).

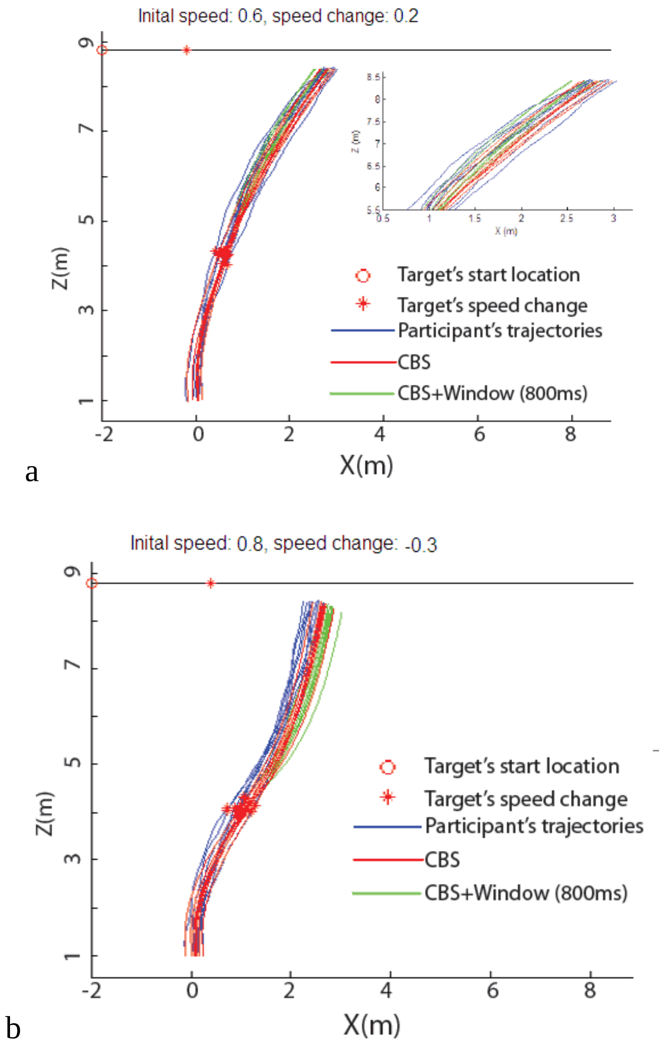

Figure 9. Example trajectories. CBS: simulated trajectories based on constant bearing model (red trajectories). CBS+window (800ms): simulated trajectories based on constant bearing model with estimate of target speed over 800 ms (green trajectories). a: Initial target speed 0.6 m/s with speed change +0.2 m/s. b: Initial target speed is 0.8 m/s with speed change -0.3 m/s.

To measure simulation performance, I computed the distance between the participant's actual trajectory and the corresponding simulated trajectory at every time step. Then I computed the mean distance of that trajectory across all time steps. Figure 10 presents the mean distance as a function of window size for all target conditions, where a temporal window of 0 ms is equivalent to on-line control; the shorter the mean distance, the better is the simulation performance. With a slow initial speed of 0.6 m/s (Figure 10a), mean distance increased with window size when the target sped up (speed change +0.2 and +0.3 m/s). One-way repeated-measures ANOVAs for each speed change condition indicated a significant main effect of window size in the +0.2 m/s condition, F (20,180) = 16.90, $p < 0.01$, and in the +0.3 m/s condition, F (20,180) = 32.66, $p < 0.01$, indicating that performance declined with temporal integration. The size of window did not significantly affect simulation performance in the other three speed change conditions for this initial speed, indicating no improvement with temporal integration of target motion.

With a fast initial target speed of 0.8 m/s (Figure 10b), the mean distance increased significantly with window size when the target slowed down (speed change of -0.3 m/s), F (20,180) = 8.82, $p < 0.01$. However, when the target sped up by +0.3 m/s, mean distance significantly decreased with a longer window, F (20,180) = 2.11, $p < 0.01$. The size of temporal window did not significantly affect simulation performance in the other three speed change conditions. In sum, an internal extrapolation model increased simulation accuracy in only one of ten conditions, actually reduced simulation accuracy in three conditions, and did not contribute to performance in the remaining six conditions.

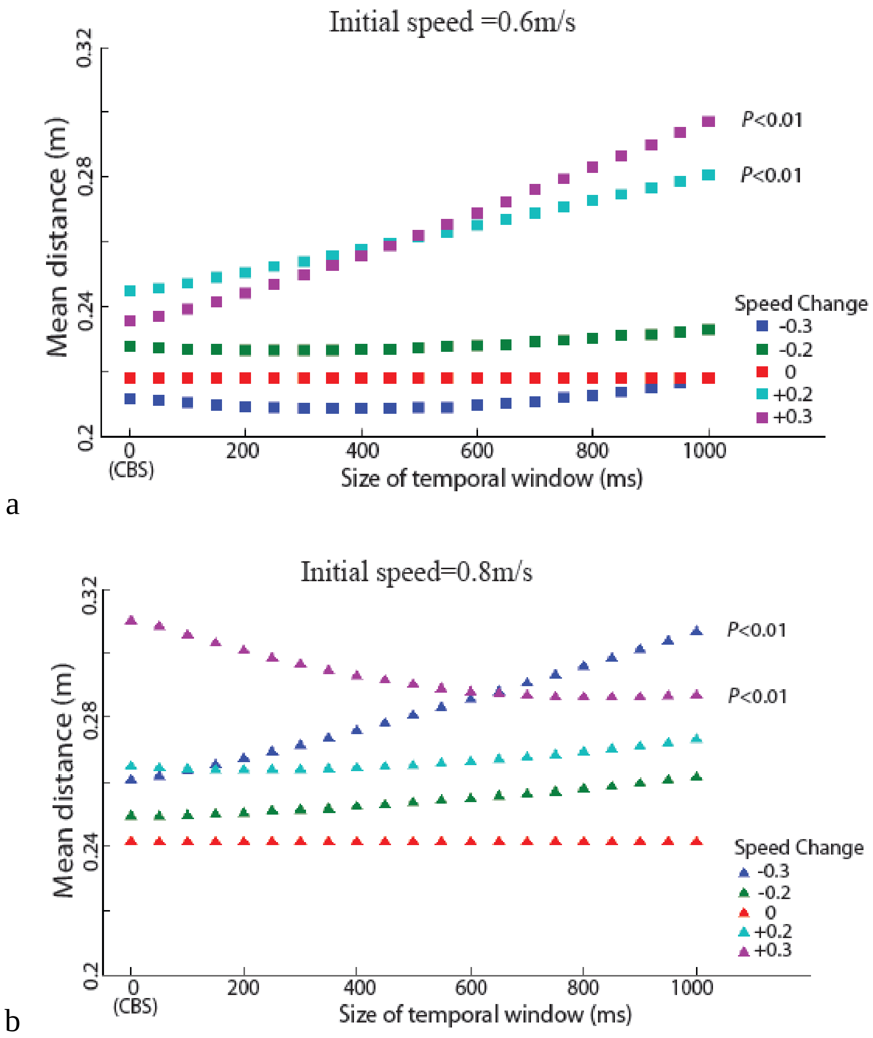

Figure 10. Mean distance between participants' and simulated Trajectories in Experiment 1. a: Initial target speed is 0.6 m/s. b: Initial target speed is 0.8 m/s

2.4. Discussion

In Experiment 1, I manipulated the initial speed of the target and the direction and magnitude of a speed change during interception. Analysis of the interception location indicated that the higher the initial speed, the farther was the interception location in the lateral (x) direction, and that a greater speed increase led to a farther interception location while a greater decrease led to a closer interception location. The results indicated that the speed manipulation was sufficient to measurably affect participants' interception trajectories.

Simulations of these interception trajectories using the constant bearing model with different temporal integration windows were used to compare on-line control based on current visual information (0 ms window) with an internal model that extrapolated the target's motion based on its preceding speed (up to a 1000 ms window). The simulation results indicated that adding an internal model of target motion failed to improve simulation performance in nine out of ten conditions. On the contrary, temporal integration actually impaired performance in three speed-up conditions, inconsistent with model-based control. The one condition in which a longer integration window improved performance occurred when a fast initial speed (0.8 m/s) increased by +0.3 m/s.

In conclusion, in the vast majority of trials, a constant bearing strategy based on current visual information is sufficient to account for target interception without an internal model of target motion. Indeed, the introduction of a temporal integration estimate of target speed impairs performance more often than it improves performance. The pattern of results thus rules out this class of extrapolation models in locomotor interception. The findings of Experiment 1 are thus consistent with on-line control.

Chapter 3. Experiment 2: Intercepting a blurred target

3.1. Introduction

In Chapter 1, I reviewed studies indicating that visual occlusion usually leads to degraded performance across different action tasks, including manual, locomotion and driving tasks. This implies that an internal model is not sufficient to guide action at the same level of performance as current visual information, consistent with on-line control. In those studies, there were usually two visual conditions: visual information was either totally available or totally removed. In this experiment, I probed intermediate levels of information availability by degrading the visibility of a moving target during locomotor interception. This allowed me to make some qualitative predictions.

There is evidence that reducing a target’s contrast results in decreasing perceived target speed (Brooks, 2001; Thompson, 1982), and so does reducing a target’s spatial frequency (Diener, Wist, Diehgans, & Brandt, 1976). In this experiment, target visibility was thus degraded by horizontally “blurring” a vertical bar, yielding a target with a Gaussian luminance profile that varied in width and in contrast, with six visibility conditions. Each trial began with a fully-visible moving target, which then appeared to move behind a translucent occluder, and continued at the same speed. The participant’s task was again to walk to intercept the moving target.

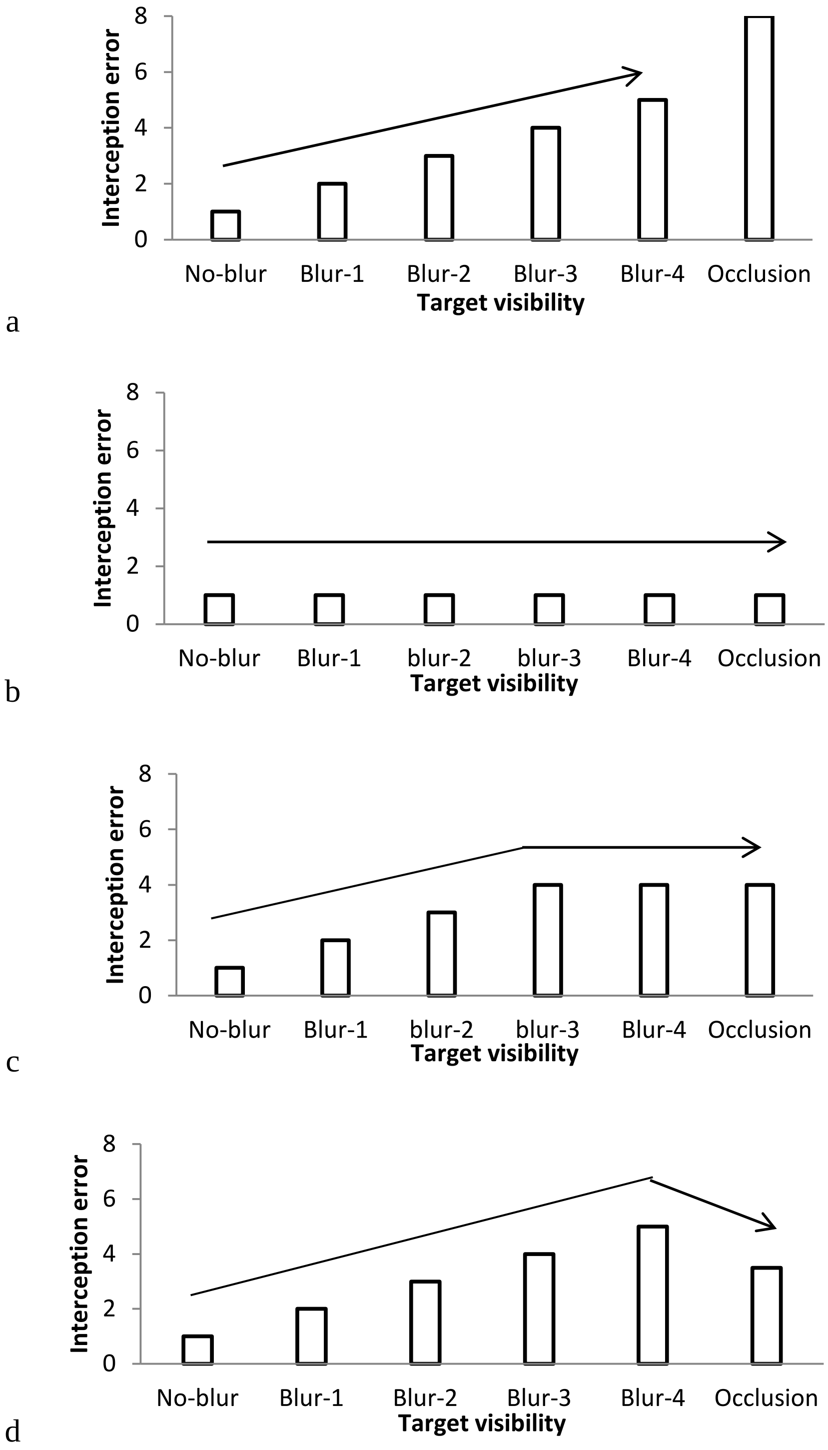

Figure 11. Three predictions about interception error due to increasingly degraded visibility a: Prediction based on on-line control hypothesis. b: Prediction based on a high-fidelity internal model. c: Prediction based on a medium- or low-fidelity internal model without updating after target occlusion. d: Prediction based on a medium- or low-fidelity internal model with updating after target occlusion.

According to the on-line control hypothesis, performance is dependent on current visual information. Thus, this hypothesis predicts that as visual information for the target's bearing direction and angular velocity is degraded, interception error should begin to increase (The Blur conditions in Figure 11a). Since there is no visual information available in the Occlusion condition, performance in this condition should be worst (The Occlusion condition in Figure 11a).

According to the model-based control hypothesis, an internal model of target motion should be created early in a trial when the target is clearly visible, and it should persist and guide interception with some degree of accuracy after removal of visual information. Degrading target visibility to different levels may thus allow us to estimate the fidelity of such an internal model. For example, a high-fidelity internal model would result in accurate and precise interception across all levels of visibility (Figure 11b), whereas a medium- or low-fidelity model would yield an increase in error as visibility is reduced, until it plateaus at some level (Figure 11c); the plateau provides an estimate of the model's fidelity.

It is also possible that an internal model of target motion is continuously updated based on incoming visual information, regardless of information quality. Therefore, in the Blur conditions, even though an accurate internal model might be created when the target is clearly visible, after the target is blurred it would be updated based on the degraded visual information, which leads to increasing decay of the internal model and thus increasing interception error (Blur conditions in Figure 11d). In the Occlusion condition, the internal model created early in a trial with clear target should persist, for there is no updating information, and it should more accurate than the degraded Blur conditions. The interception accuracy in the Occlusion condition provides an estimate of the persisting fidelity of the internal model later in the trial (the Occlusion condition in Figure 11d).

3.2. Method

3.2.1. Participants

10 graduate and undergraduate students (5 females, 5 males) participated in this experiment. Their ages ranged from 20 to 29, and all had normal or corrected-to-normal vision. All participants read and signed the informed consent prior to the experiment, and were paid for their participation. Brown's Institutional Review Board approved the research protocol.

3.2.2. Apparatus and displays.

The apparatus and displays were the same as in Experiment 1, with one exception. Instead of a 3D pole, the target was a green 2D bar (0.2m wide x 2.0 m tall), which appeared to move in front of a virtual wall. The wall was a translucent gray patch (400 m wide x 200 m tall), which was visible throughout a trial and was actually located 2 cm behind the target's path. 2.5 s after the target appeared, it arrived at a virtual occluder and then moved behind it (Figure 12). The occluder was invisible through a trial. The bar was progressively blurred as it passed the edge of the occluder, so it appeared to move behind a translucent occluder of varying opacity.

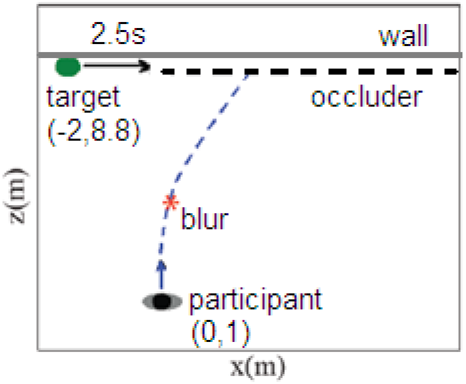

Figure 12. A top-down view at the moment the target appeared. The red asterisk on participant path indicated the moment the target was occluded by the occluder.

There were six different levels of target visibility. In the No-blur condition, the rectangular bar (0.2 m wide) was fully visible. In the Blur-1 to Blur-4 conditions, the bar was blurred in the x direction and its contrast was reduced (0.4, 0.6, 0.8, 1.0 m wide, respectively). In the Occlusion condition, the bar was totally occluded as it passed the virtual occluder. To create these different levels of blur, the alpha value of the target was determined as a Gaussian function centered on target:

$$a(x) = g\ (\ x\text{-}c,\ w/6\ ) \qquad (3)$$

where x refers horizontal coordination within a target, *c* refers coordination of target center, and *w* refers target width. Figure 13 showed the targets in different Blur conditions viewed straight ahead from a distance of 3 m.

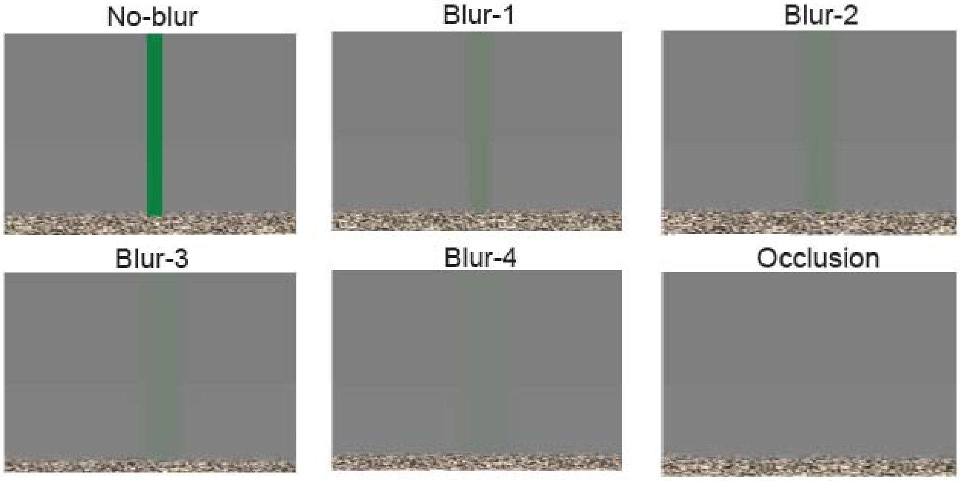

Figure 13. The targets of different blur levels viewed 3 m straight ahead.

3.2.3. Design and procedure.

In this experiment, three target speeds (0.6, 0.8 or 1.0 m/s) were crossed with six levels of visibility (No-blur, Blur-1 to Blur-4, and Occlusion), yielding a 3 (speed) x 6 (blur) factorial design with a total of 18 target conditions.

The task and procedure were similar to those in Experiment 1. On each trial, the target appeared 8.8 m ahead and 2 m to the left or right, and began to move (Figure 12). After 2.5 s, the target appeared to move behind the occluder and the participant continued to intercept it. The trial ended when participant came within 0.4 m of the occluder. Participants were told that the target would be blurred or totally occluded in some trials, and in that case they were to intercept the target as if it was fully visible.

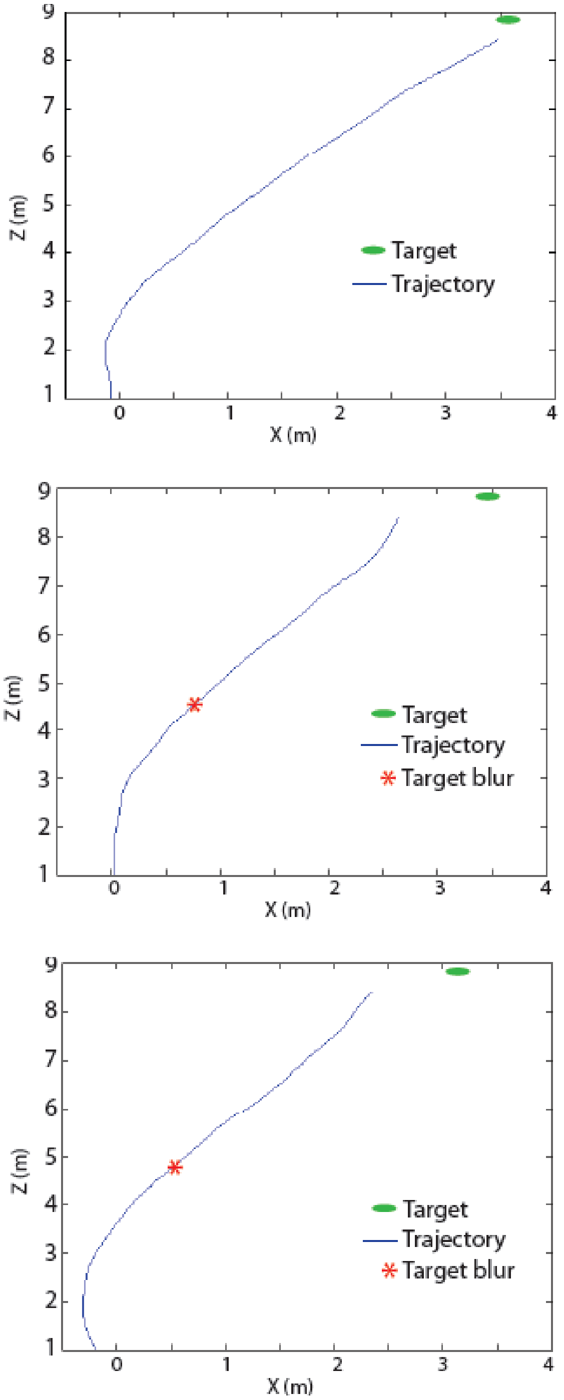

Figure 14. Example trajectories in No-blur, Blur4 and Occlusion conditions. The asterisks represent the blur points where the targets went behind an occluder. The targets were clearly visible before the blur points and then be occluded after the blur points. Heading adjustment before the blur points is the mean angle participants turned before blur point; heading adjustment after blur point is the mean angle participants turned after blur point.

Participants performed 12 practice trials, 2 in each target blur condition. The three target speeds were randomly assigned to the practice trials. Then they performed 144 test trials, with 8 repetitions in each of the 18 target conditions. The order of the trials was randomized for each participant. An experimental session lasted about an hour.

3.3. Results

3.3.1. Interception performance

I first examined the effect of target blur on interception performance. Three sample interception trajectories from the No-blur, Blur-4 and Occlusion conditions, with a target speed of 1.0 m/s, appears in Figure 14. Note the increasing deviation from a straight path and undershooting of the target. As before, I analyzed the x position at interception. The constant error was computed as the distance between the participant's x position and the target's x position at the end of the trial; positive values indicate overshooting and negative values undershooting. The variable error is the within-subject standard deviation of constant errors in each condition.

The mean constant error in each condition appears in Figure 15. When the target moved slowly (0.6 m/s), the constant errors were close to zero across different levels of target blur, indicating quite accurate interception. This could be because participants completed the initial turn onto a straight path before the target reached the occluder. When the target moved at 0.8 or 1.0 m/s, constant errors were increasingly negative with greater target blur, indicating more undershooting with more blur. A 2-way repeated-measures ANOVA indicated significant main effects of target speed, $F(2,18) = 68.82$, $p <$

0.01, $\eta_p^2 = 0.88$, and target blur, $F(5,45) = 9.70$, $p < 0.01$, $\eta_p^2 = 0.52$, and a significant interaction, $F(10,90) = 28.14$, $p < 0.01$, $\eta_p^2 = 0.76$. Simple main effect test found a significant main effect of target blur in both the 0.8 m/s condition, $F(5,45) = 6.97$, $p < 0.05$, and the 1.0 m/s condition, $F(5,45) = 6.73$, $p < 0.05$, but not in 0.6 m/s, $F(5,45) = 1.72$, $p = 0.28$. Thus, undershooting increased monotonically as target visibility was degraded.

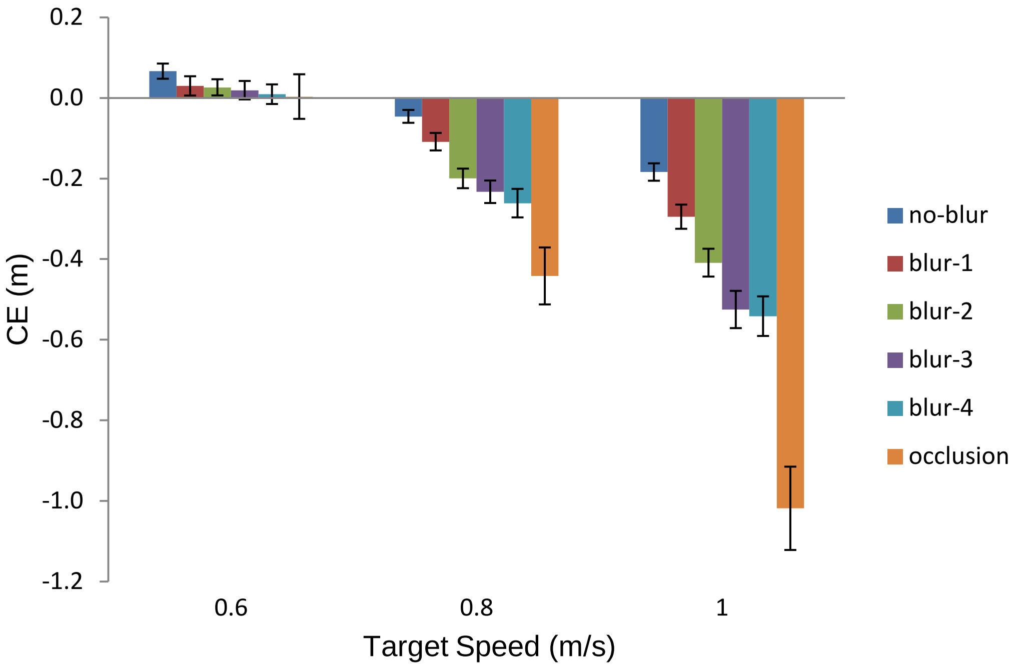

Figure 15. Constant errors in each target condition in Experiment 2.

The mean variable error in each condition is presented in Figure 16. It appears that variable errors increased with target blur for all target speeds, indicating greater variability in interception behavior as target visibility was degraded. A 2-way repeated-measures ANOVA indicated significant main effects of target speed, $F(2,18) = 3.69$, $p < 0.05$, $\eta_p^2 = 0.29$, and target blur, $F(5,45) = 40.36$, $p < 0.01$, $\eta_p^2 = 0.82$, but no interaction, $F(10,90) = 1.39$, $p = 0.19$, $\eta_p^2 = 0.13$. Simple main effect test found a significant main effect of target blur in the 0.6 m/s condition, $F(5,45) = 18.06$, $p < 0.01$, and 1.0 m/s condition, $F(5,45) = 6.25$, $p < 0.05$, but not in 0.8 m/s, $F(5,45) = 3.59$, $p = 0.09$.

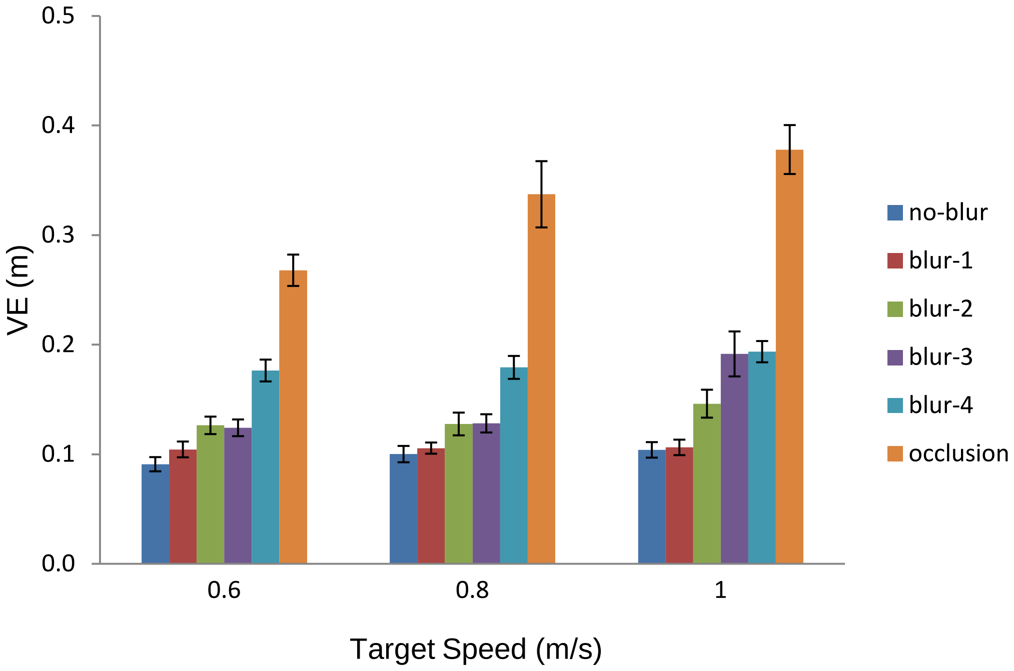

Figure 16. Variable errors in each target condition in Experiment 2.

The results so far indicate that participants generally undershot the target when it moved at speeds of 0.8 or 1.0 m/s. To investigate the reason for the undershooting, I analyzed the participant’s walking speed and final location. The mean final location in each condition appears in Figure 17. A 2-way repeated-measures ANOVA found significant main effects of target speed, $F(2,18) = 237.37$, $p < 0.01$, $\eta_p^2 = 0.96$, and target blur, $F(5,45) = 5.57$, $p < 0.01$, $\eta_p^2 = 0.38$, and a significant interaction, $F(10,90) = 7.08$, $p < 0.01$, $\eta_p^2 = 0.44$. One-way ANOVAs for each target speed confirmed a significant main effect of target blur in the 0.8 m/s condition, $F(5,45) = 3.34$, $p < 0.05$, and the 1.0 m/s condition, $F(5,45) = 7.64$, $p < 0.01$. These results indicate that participants undershot the target by walking a shorter distance in the x direction as target blur increased, at higher target speeds. This effect is most obvious in the total Occlusion condition with a target speed of 1.0 m/s. The results indicated that degrading target visibility results in different interception paths, which lead to undershooting.

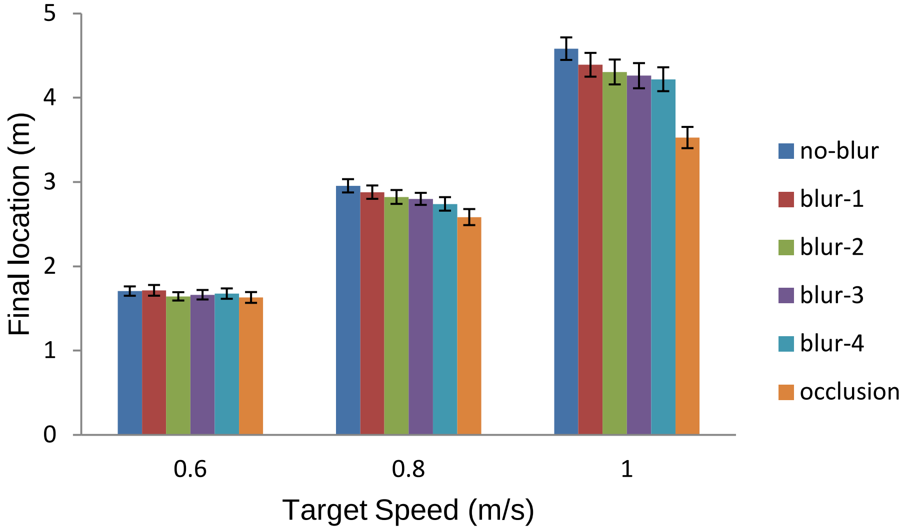

Figure 17. Mean final locations in each target condition in Experiment 2.

The mean walking speed in each condition is presented in Figure 18. Although walking speeds are fairly stable across conditions, a 2-way repeated-measure ANOVA revealed significant main effects of target speed, $F(2, 18) = 81.39$, $p < 0.01$, $\eta_p^2 = 0.90$, and target blur, $F(5,45) = 11.33$, $p < 0.01$, $\eta_p^2 = 0.38$, as well as a significant interaction, $F(10,90) = 4.81$, $p < 0.01$, $\eta_p^2 = 0.21$. One-way repeated-measures ANOVAs for each target speed demonstrated a significant main effect of blur in both the 0.8 m/s condition, $F(5,45) = 6.01$, $p < 0.01$ and the 1.0 m/s condition, $F(5,45) = 20.08$, $p < 0.01$. These results indicate that participants walked more slowly as target visibility was degraded in the faster speed conditions. One possible explanation is that degrading target's visibility results in decreasing perceived target speed. This would contribute to target undershooting.

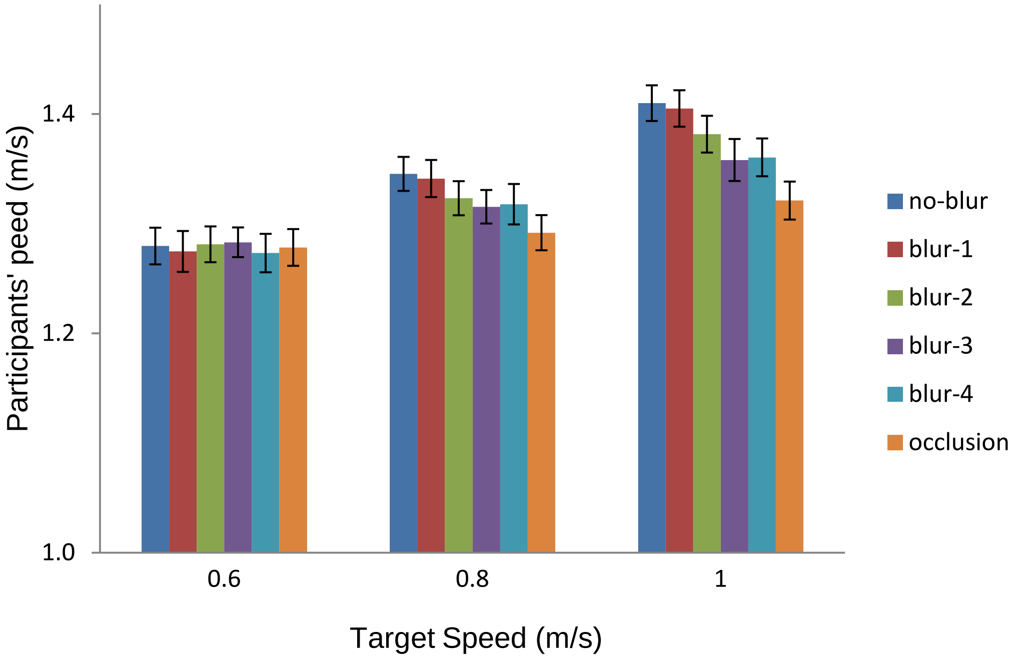

Figure 18. Mean walking speed in each target condition in Experiment 2.

To examine whether participants adjusted their heading in response to the target's motion, I measured the angle they turned within a trial. First, to determine whether viewing the target for 2.5 s is enough for participants to differentially respond to target speed, I measured the total angle through which they turned in the first part of the trial, before the target was blurred (red asterisk in Figure 14). Participants turned more with faster targets in all conditions (Figure 19). A 2-way repeated-measure ANOVA found a significant main effect of target speed, $F(2, 18) = 221.28$, $p < 0.01$, $\eta_p^2 = 0.96$, but no main effect of blur level, $F(5, 45) = 0.42$, $p = 0.84$, $\eta_p^2 = 0.04$, nor any interaction, $F(10, 90) = 1.21$, $p = 0.29$, $\eta_p^2 = 0.12$. The results indicate that viewing the target for 2.5 s is enough for participants to distinguish target speeds and adjust their heading adaptively.

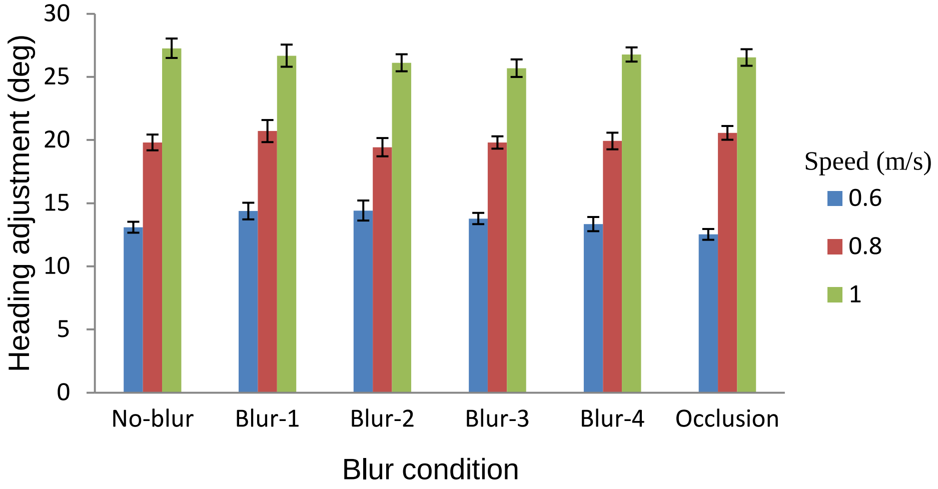

Figure 19. Heading adjustment before blur point in Experiment 2.

Second, to determine whether participants also adaptively adjusted their heading during blur or occlusion, I measured the angle they turned after the blur point (red asterisk in Figure 14). Participants adjusted for target speed in the Blur conditions, but not in the Occlusion condition (Figure 20). A 2-way repeated-measures ANOVA found significant main effects of target speed, $F(2,18) = 85.48$, $p < 0.01$, $\eta_p^2 = 0.91$, target blur, $F(5,45) = 4.81$, $p < 0.01$, $\eta_p^2 = 0.35$, and a significant interaction, $F(10,90) = 8.82$, $p < 0.01$, $\eta_p^2 = 0.49$. Simple effect tests found a significant effect of target speed in each of the five Blur conditions ($p < 0.01$ for all blur conditions), but not in the Occlusion condition ($p = 0.24$). The results indicate that participants adjusted their heading adaptively during target blur; however, they just turned constant angle when the target was totally occluded.

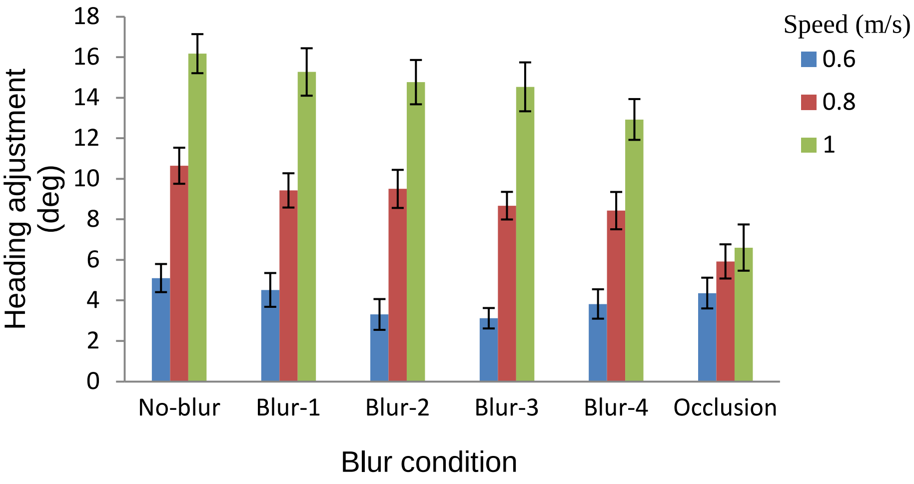

Figure 20. Heading adjustment after blur point in Experiment 2.

3.3.2. Recurrence quantification analysis (RQA)

Variable error is a measure of the total amount of variability in interception performance across trials. Other measures can be used to quantify the temporal structure of variability within single trials. Specifically, Recurrence Quantification Analysis (RQA) is a technique that measures repeating patterns at multiple time scales that may present in what appears to be random variability. RQA was developed in early 1990's (Zbilut & Webber, 1992; Webber & Zbilut, 1994) and it has been used to analyze variability in psychophysical and behavioral tasks (Zbilut, Thomasson, & Webber, 2002; Riley, Balasubramaniam, & Turvey, 1999).

To measure the nested structure of variability within a trial, I performed RQA on the locomotor trajectory from each test trial. For each trial, I first filtered the time series of x and z position using a forward and backward 4th-order low-pass Butterworth filter with a cutoff frequency of 5 Hz. Then I computed the time series of heading direction from the spatial displacement at each time step. Finally, I ran RQA on the heading time series with the following parameters: delay = 20, embedding dimension = 5, radius = 25 and Linemin = 2. Specifically, for each heading time series, I created four delayed time series, each with increasing delay of 20 data samples, which derived five time series in total. With each heading time series representing a dimension, the heading values of the five time series formed a trajectory in a 5-dimension space. Then for each point along the trajectory, I searched all other points that fall within a radius of 25. Thus the point numbers of any pair of points falling within the radius (25) formed a 2D coordinate. For example, if the first point falls within 25 from the 40th point, this pair gives rise to a coordinate of (1, 40). Then the coordinates was represented by a black dot in a 2D recurrence plot, with each dimension representing the point number. Thus, the black area in a recurrence plot represents the amount of recurrent points. See Charles & Webber (2005) for detailed procedure of RQA.

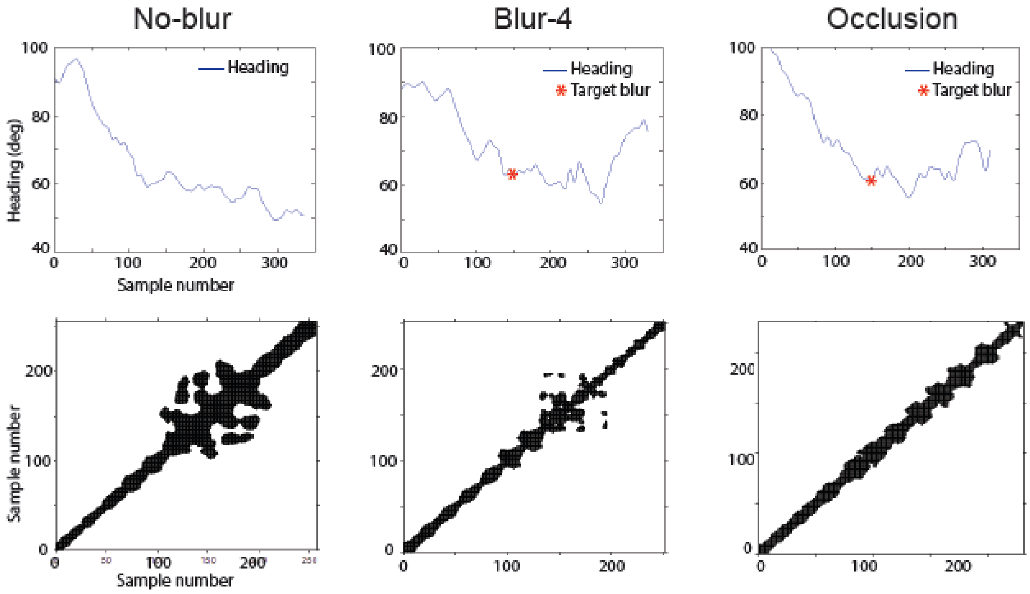

Figure 21. Example heading time series and recurrence plot.

The heading time series and the RQA recurrence plot for three sample trials appear in Figure 21. As the target was increasingly blurred, black area appears to decrease, indicating that greater target blur results in less recurrence points. Several measures of nested temporal structure can be derived from the recurrence plot, such as percent recurrence, which quantifies the degree of pattern repetition across different time scales. Specifically, it is the percentage of recurrence points over all possible points, represented by ratio of black area within a recurrence plot. Regarding the current study, low percent recurrence may characterize more variable interception behavior.

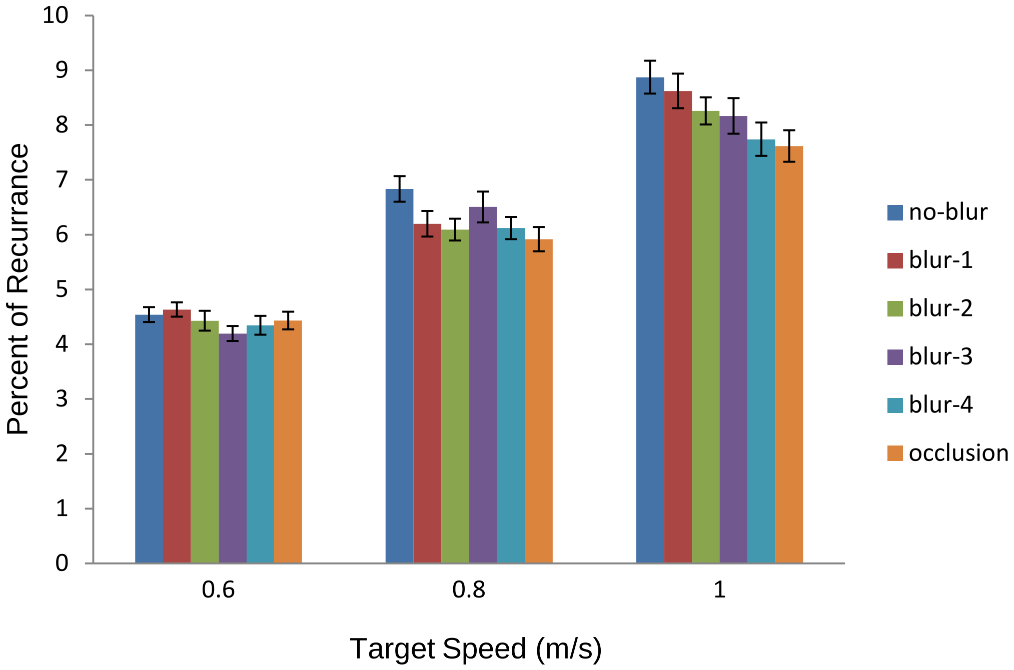

Figure 22. Mean percent recurrence in each target condition in Experiment 2.

The mean percent recurrence in each condition appears in Figure 22. The pattern of results suggests that temporal structure within a trial decreased as target blur increased, and also at lower target speeds. A 2-way repeated-measures ANOVA found significant main effects of target speed, $F(2, 18) = 84.73$, $p < 0.01$, $\eta_p^2 = 0.90$, and target blur,

$F(5,45) = 4.50$, $p < 0.01$, $\eta_p^2 = 0.33$, but no interaction, $F(10, 90) = 1.58$, $p = 0.125$, $\eta_p^2 = 0.15$. A one-way repeated-measures ANOVA for each target speed obtained significant main effect of blur in both the 0.8 m/s condition, $F(5,45) = 3.67$, $p < 0.01$ and the 1.0 m/s condition, $F(5,45) = 2.98$, $p < 0.05$. Thus, consistent with the preceding analyses, degrading target visibility resulted in more variable interception trajectories, having less temporal structure, at higher target speeds.

3.4. Discussion

In the current study, I manipulated target visibility using different levels of blur, ranging from full visibility to total occlusion, as the target moved behind a virtual occluder. The results indicated that degrading target visibility progressively impaired both the accuracy and precision of locomotor interception. That is, greater target blur led to more undershooting, higher variability in final position, and less temporal structure in interception trajectories. Total occlusion resulted in the most severely impaired performance. Moreover, participants did not adjust their heading adaptively if the target was totally occluded. Instead they just turned a constant angle regardless of different target speed.

Thus, interception performance strongly depended on current visual information. If interception were guided by an internal model of target motion that persists after information is degraded, interception error would either remain low (Figure 11b) or would plateau at a blur level that reflects the model’s fidelity (Figure 11c). On the contrary, I showed that interception error increased monotonically as information was degraded. This result suggests that interception of a blurred target is based either on current visual information (Figure 11a) or an internal model continuously updated by current visual information, even though it is degraded (Figure 11d). I showed that interception performance is worst in the Occlusion condition, which is consistent with the on-line control prediction (Figure 11a). Therefore, the results suggest that interception is controlled only based on current visual information, consistent with on-line control.

In Chapter 1, I reviewed numerous studies that manipulated the availability of current visual information in visual-motor tasks (for example, Wallis, et al., 2002). The findings of those studies show that removal of visual information usually leads to impaired performance. In Experiment 2, I created intermediate levels of target visibility and found that greater target blur led to progressively impaired performance. The current study thus goes beyond previous research and lends greater support to a strong dependence on current information, as expected by on-line control.

When the target moved at higher speeds (0.8 or 1.0 m/s), increased target blur resulted in greater undershooting. Analysis of participants' final x location and walking speed indicated that increasing target blur resulted in a slower walking speed and less distance traveled in the x direction. This may be due to that target speed was perceived lower when the target was increasingly blurred. Thus, target blur influenced both participants' walking speed and locomotor path, and both of these factors contributed to target undershooting.

On the other hand, the results indicate that higher target speeds effectively led to final positions that were farther along the x-axis. This holds true even in the total

Occlusion condition, when the target disappeared from view. This raises the question of how locomotor interception is controlled in off-line situations.

I found that participants adaptively adjusted their heading before the blur point according to different target speed. This also holds true in the Occlusion condition. Therefore heading adjustment before the blur point might be sufficient to account for participants' increased final x location with faster targets. After the blur point, participants continued to adaptively adjust their heading according to the target's speed if the target was visible or blurred. But if the target was totally occluded, they turned a constant angle regardless of target speed. Specifically, it appears that they did not turn more with faster targets. This stereotyped turn results in undershooting of the faster targets in the Occlusion condition. Moreover, it implies that there is no internal model simulation or prediction of the occluded target's motion.

The constant bearing model (Equation 2) may help understand participants' stereotyped heading adjustment after target occlusion. With the target totally occluded, the constant bearing model loses its stiffness term (   ), for there is no current information about bearing angle, however still maintaining the damping term (   ). If participants were still turning at the blur point, the damping term would allow participants to decrease their turning rate and then probably walk straight ahead at the end of a trial. To test this, I will analyze participants' heading time series to examine whether participants were still turning at blur point and then decreased their turning rate.

Participants accurately intercepted the target when the target moved at 0.6 m/s regardless of blur levels. This result indicates that participants did understand the task and walked to the center of the target even when the target is blurred. One possible reason of the accurate interception in this target condition is that slower target speed demands less adjustment in participant’s interception path or walking speed. With respect to walking speed, participants walked most slowly when target moved at 0.6 m/s, with mean speed of 1.28 m/s in both No-blur and Occlusion conditions. In contrast, when target moved at 0.8 m/s, participants’ mean speed is 1.35 m/s in No-blur condition and 1.28 m/s in Occlusion condition, and 1.41 and 1.32 m/s in these two conditions with target speed of 1.0 m/s. The decline in walking speed from No-blur to Occlusion condition may imply that lower walking speed might be the more comfortable one compared with higher speed. Thus when target moved at slower speed (0.6 m/s), it may demand little adjustment in participants walking speed (speeding up in this case) to accurately intercept the target. To further test this hypothesis, I plan to examine adjustment in interception path.

Target blur appears to have increased uncertainty about the target’s position and speed, resulting in progressively impaired performance. Nevertheless, performance in the Blur-1 to Blur-4 conditions was better than in the Occlusion condition. This implies that, although the target’s visibility was degraded, some visual information was still available to guide interception. For example, even with a greatly blurred target, participants might be able to estimate the center of the target and reduce its positional uncertainty. In stationary psychophysical tasks, human observers can be quite accurate in judging the center of a wide object (Cavezian, Valadao, Hurwitz, Saoud, & Danckert 2012; Elias, Robinson, & Saucier, 2005).

Whereas the amount of variability in performance across trails is expressed by the variable error, RQA characterized the structure of variability on an interception path within a single trial. The RQA found that mean percent recurrence (the degree of repeating pattern) decreased with greater target blur. This result suggests that degrading target visibility yields interception trajectories with less temporal structure and more random variability. The RQA results are quite consistent with the interception errors and support the primary role of current information in action control.

In sum, Experiments 1 and 2 offer no support for the model-based control hypothesis that interception is guided by a persisting internal model that extrapolates the trajectory of a moving target on individual trials. In contrast, the results thus far indicate a strong dependence on current visual information, consistent with the on-line control hypothesis. In Experiment 3, I turn to the possibility that an internal model of a target’s motion is learned over multiple trials and subsequently used to guide interception behavior.

Chapter 4. Experiment 3: Intercepting an occluded target after learning its movement

4.1. Introduction

The previous two experiments have found no evidence that an internal model of target motion is created on the basis of the target's initial trajectory and used to guide interception during an individual trial. However, it remains possible that an internal model of target behavior might be learned over multiple trials and subsequently used to guide interception on later occasions. Experiment 3 is designed to investigate this hypothesis.

Some studies have suggested that a learned internal model of target movement could be used to guide interception. For example, Lacquaniti and his colleagues argued that an internal second-order model of earth's gravity, including the law of motion, is used to control interception of a free falling object (e.g. McIntyre, et al., 2001). Gravity is ubiquitous on earth and humans experience it all the time. Such an internal model might thus be learned from everyday human experience with falling bodies.

In another study, Diaz, et al. (2009) suggested that prediction of a target's future motion could be used to intercept a velocity-varying target. The authors assumed both "perfect knowledge" of the target's future movement and that this knowledge could be used to compute the required velocity for interception. This knowledge might be acquired during repeated trials in which the target moved the same way.

These studies seem to suggest that an internal model of target behavior could be learned and subsequently used to control interception. If so, then according to model-based control, the internal model should be available to guide interception of the same target even when the latter is visually occluded. I tested this hypothesis in the present experiment.

First, during a block of learning trials, participants intercepted a visible moving target that always underwent the same speed change (increasing or decreasing its speed by 0.2 or 0.3 m/s). This was followed by a block of test trials, in which participants were told to intercept the same target, but it was visually occluded before the speed change. If a reasonably accurate internal model of target motion is learned and used to guide interception, this predicts that performance in test trials should not be greatly impaired by target occlusion. On the other hand, if action is not based on a learned internal model but model but depends on current information, this predicts that interception performance should deteriorate significantly in test trials.

4.2. Method

4.2.1. Participants

10 graduate and undergraduate students (6 females, 4 males) participated in this experiment. Their ages ranged from 19 to 27 years, and all had normal or corrected-to-normal vision. All participants read and signed the informed consent prior to the experiment, and were paid for their participation. Brown’s Institutional Review Board approved the research protocol.

4.2.2. Apparatus and displays

This apparatus was the same as in the previous experiments. The target bar (with no blur) and virtual occluder were taken from Experiment 2, and the target's motion was the same as in Experiment 1.

4.2.3. Design and procedure

As in Experiment 1, the initial target speed was 0.6 or 0.8 m/s, and three seconds later its speed changed by -0.3, -0.2, 0, +0.2 or +0.3 m/s. This again yielded a 2 (initial speed) x 5 (speed change) factorial design, with a total of ten target conditions.

However, in this experiment the five speed-change conditions were blocked and run in separate experimental sessions, with at least 24 hours between them. Each session consisted of a learning block followed by a test block. In the learning block, the target was visible throughout a trial and the speed-change was the same on every trial, although the target's initial speed varied in a random order. Participants performed 20 trials at each initial speed, yielding 40 trials in a learning block. In the test block, the target disappeared behind the virtual occluder 2.5 s after it appeared, so it was totally occluded before the speed change. Participants were told that the target would speed up or slow down the same way it had in the learning block, and they were instructed to intercept the target as if it were fully visible. There were 12 trials at each initial speed, presented in a random order, yielding 24 trials in a test block. A session lasted about 40 min, and the session order was counterbalanced across participants.

The procedure was the same as in Experiment 1, with the exception that practice trials were replaced by a virtual reality familiarization period at the beginning of the first session, in which participants walked to several stationary green poles. Thus, they only intercepted moving targets during learning trials. Participants were instructed to walk to intercept the target, but were not explicitly instructed to learn or remember the target motion.

4.3. Results

To examine participants' interception performance, I analyzed final constant errors in each target condition for learning and test blocks (Figure 23). Participants tended to overshoot the target when it initially moved at the low speed and then slowed down, and tended to undershoot the target when it initially moved at the high speed and then sped up; the converse conditions tended to be more accurate. This pattern is most obvious in the test block, where participants under- and overshot the target by as much as 80 cm. An omnibus 3-way repeated-measures ANOVA found significant main effects of initial target speed, $F(1,9) = 78.76$, $p < 0.01$, $\eta_p^2 = 0.89$, and speed change, $F(4,36) = 31.24$, $p < 0.01$, $\eta_p^2 = 0.78$, but not block type (learning or test), $F(1,9) = 0.04$, $p = 0.849$, $\eta_p^2 = 0.00$. However, all two-way interactions were significant, although the three-way interaction was not.

To examine these effects more closely, I performed a 2-way repeated-measures ANOVA (block type x speed change) for each initial target speed. With the slow initial speed of 0.6 m/s, there was a significant main effect of speed change, $F(4,36) = 20.68$, p

< 0.01, $\eta_p^2 = 0.69$, no main effect of block type, $F(1,9) = 4.35$, $p = 0.07$, $\eta_p^2 = 0.33$, but a significant interaction, $F(4,36) = 13.75$, $p < 0.01$, $\eta_p^2 = 0.60$,. This result confirms that participants overshot the target more in the test block than in the learning block when the target slowed down. Simple main effect test only found significant effect of speed change for test block, $F(4,36) = 10.79$, $p < 0.01$, but not for learning block, $F(4,36) = 3.13$, $p < 0.10$.

For the fast initial speed of 0.8 m/s, a 2-way repeated-measures ANOVA revealed a significant main effect of speed change, $F(4,36) = 37.25$, $p < 0.01$, $\eta_p^2 = 0.81$, no effect of block type, $F(1,9) = 2.92$, $p = 0.12$, $\eta_p^2 = 0.25$, but a significant interaction, $F(4,36) = 15.19$, $p < 0.01$, $\eta_p^2 = 0.63$. This result indicates that participants undershot the target more in the test block than in the learning block when the target speed was constant or increased. Simple main effect test found significant effect of speed change for both learning block, $F(4,36) = 9.00$, $p < 0.05$, and test block, $F(4,36) = 14.42$, $p < 0.01$.

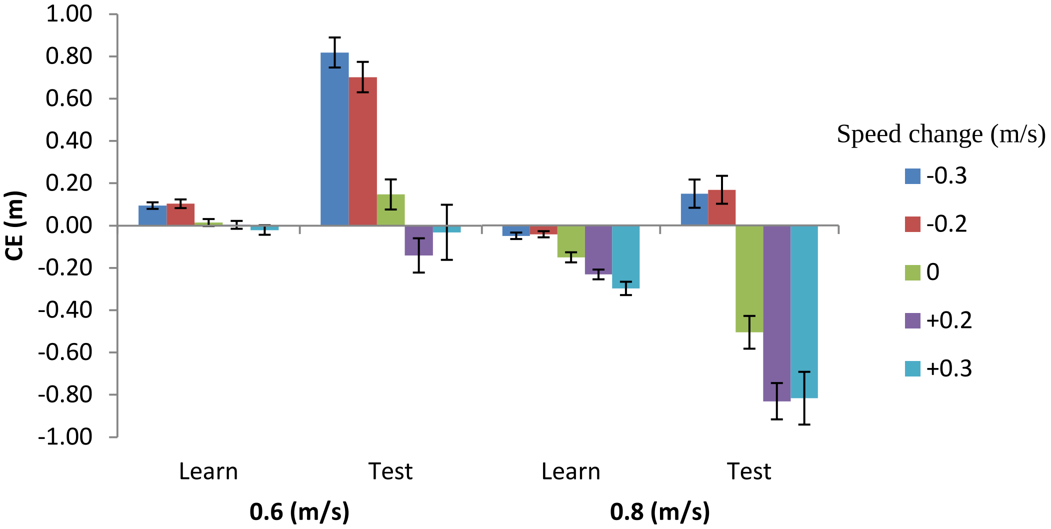

Figure 23. Constant errors in each target condition for learning and test blocks in Experiment 3.

The mean variable error in each condition is presented in Figure 24. It appears that variable errors increased in test block when the target was totally occluded compared with learning block where the target was visible. An omnibus 3-way repeated-measures ANOVA indicated only a main effect of block type, $F(1,9) = 116.05$, $p < 0.01$, $\eta_p^2 = 0.93$, but no effect of target initial speed, $F(1,9) = 1.42$, $p = 0.26$, $\eta_p^2 = 0.14$, or speed change, $F(4,36) = 1.61$, $p = 0.19$, $\eta_p^2 = 0.15$, nor any interaction. The results indicate that target occlusion resulted in higher interception variability.

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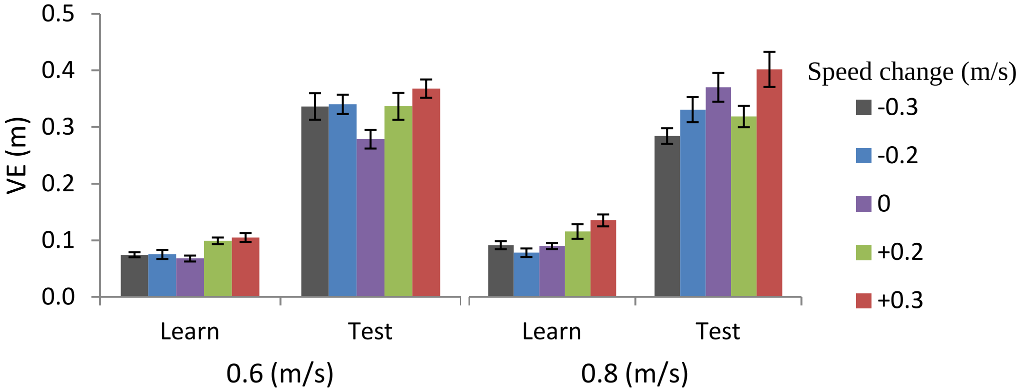

Figure 24. Variable errors in each target condition for learning and test blocks in Experiment 3.

Both constant and variable errors were computed with respect to target's final location. Thus neither of them can directly reveal how different target conditions influence interception paths. To better understand this, I examined participants' final x locations in each condition over time. Figure 25 presents the mean final location for sub-blocks of 5 trials during a session. The pattern of final locations suggests a regression toward the mean initial target speed of 0.7 m/s when the target was occluded in the test block. For the initial speed of 0.6 m/s, the solid curves appear to converge slightly upward on test trials, and for the initial speed of 0.8 m/s, the dashed curves appear to converge slightly downward. This observation implies that participants learned the mean initial speed of the target, not the specific speed change in a learning block. This would account for the pattern of over and under-shooting.

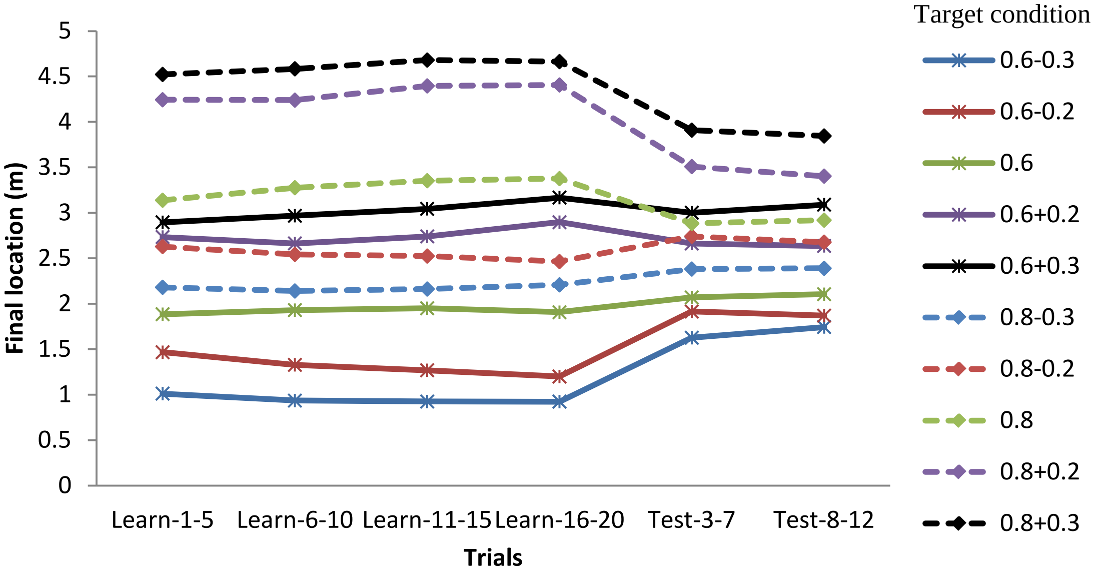

Figure 25. Final location averaged every 5 trials across participants in each target condition for learning and test blocks in Experiment 3.

The mean final x location in each condition appears in Figure 26. A 3-way repeated-measures ANOVA indicated significant main effects of initial target speed, $F(1,9) = 203.36$, $p < 0.01$, $\eta_p^2 = 0.96$, and speed change, $F(4,36) = 22.44$, $p < 0.01$, $\eta_p^2 = 0.71$, but no effect of block type, $F(1,9) = 0.02$, $p = 0.89$, $\eta_p^2 = 0.00$, although the three-way interaction was significant, $F(4,36) = 3.15$, $p < 0.05$, $\eta_p^2 = 0.26$. To examine this effect more closely, I performed a 2-way repeated-measures ANOVA for each initial target speed. With an initial speed of 0.6 m/s, there was significant main effect of speed change, $F(4,36) = 23.80$, $p < 0.01$, $\eta_p^2 = 0.73$, no effect of block type, $F(1,9) = 3.59$, $p = 0.09$, $\eta_p^2 = 0.29$, but a significant interaction, $F(4,36) = 7.30$, $p < 0.01$, $\eta_p^2 = 0.45$, consistent with a compression of the range of final locations in the test block. One-way repeated-measures ANOVAs for each block indicated a significant main effect of speed change in both the learning block, $F(4,36) = 36.59$, $p < 0.01$ and test block, $F(4,36) = 9.93$, $p < 0.01$.

For the initial speed of 0.8 m/s, a 2-way repeated-measures ANOVA similarly revealed a significant main effect of speed change, $F(4,36) = 20.82$, $p < 0.01$, $\eta_p^2 = 0.69$, no effect of block type, $F(1,9) = 3.11$, $p = 0.11$, $\eta_p^2 = 0.26$, but a significant interaction, $F(4,36) = 8.63$, $p < 0.01$, $\eta_p^2 = 0.49$, again confirming a compression of the response range in the test block. One-way repeated-measure ANOVAs for each block indicated significant main effect of speed change in both the learning block, $F(4,36) = 27.92$, $p < 0.01$, and the test block, $F(4,36) = 8.86$, $p < 0.01$. In sum, the results of final x location indicate that, although participants distinguished the initial speed and speed-change conditions, the adjustment of the interception path in the test block was significantly compressed compared to the learning block. This is consistent with the analysis of constant error and absolute error, which indicated greater errors in the test block.

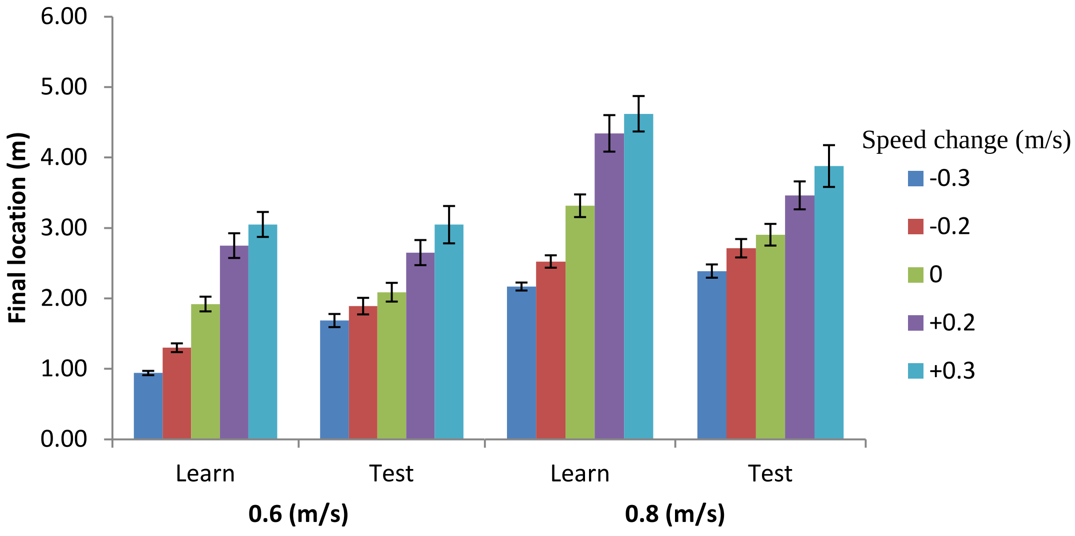

Figure 26. Mean final locations in each target condition for learning and test blocks in Experiment 3.

To examine whether participants adjusted their speed in different target conditions, I also examined participants' walking speed. The mean walking speed in sub-blocks of 5 trials during a session appears in Figure 27. The walking speeds also exhibit a regression toward the mean on test trials, when the target was occluded. That is, participants' walking speed increased from the learning block to test block when the target initially moved at lower speed and then slowed down. This result is consistent with the finding that participants overshot the target more in those conditions during test block. Moreover, participants' walking speed decreased from the learning block to test block when the target initially moved at higher speed and then sped up. This result is consistent with the finding that participants undershot the target more in those conditions during test block.

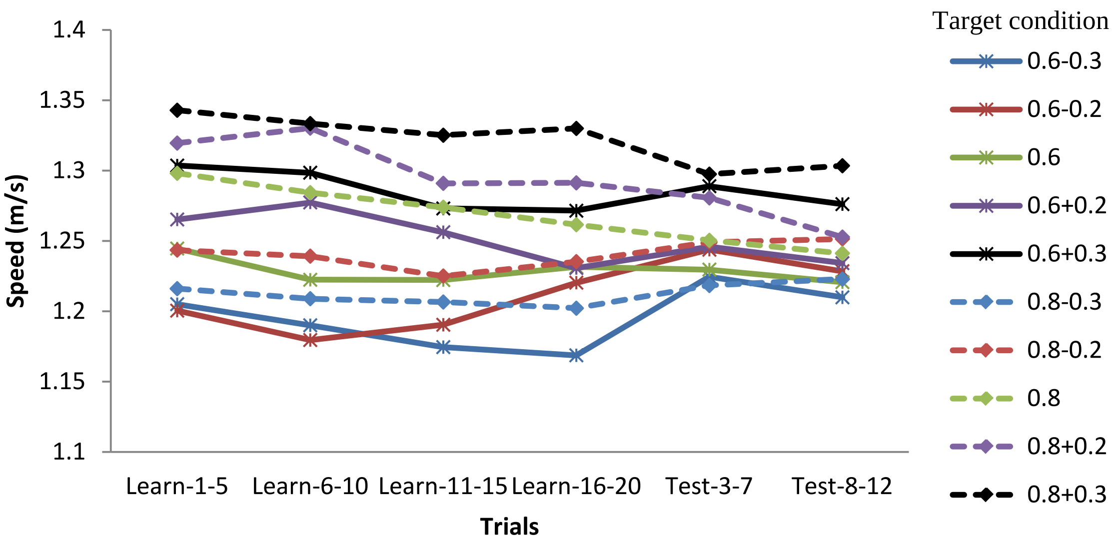

Figure 27. Walking speed averaged every 5 trials across participants in each target condition for learning and test blocks in Experiment 3.

The Mean walking speed in each target condition appears in Figure 28. A 3-way repeated-measure ANOVA indicated significant main effect of initial target speed, $F(1,9) = 67.86$, $p < 0.01$, $\eta_p^2 = 0.88$, and speed change, $F(4,36) = 3.56$, $p < 0.05$, $\eta_p^2 = 0.28$, but no effect of block type, $F(1,9) = 0.02$, $p = 0.89$, $\eta_p^2 = 0.00$, nor the three-way interaction, $F(4,36) = 0.13$, $p = 0.97$, $\eta_p^2 = 0.01$. To examine the walking speed more closely, I performed a 2-way repeated-measure ANOVA for each target initial speed. For the initial speed of 0.6 m/s, there was a revealed significant main effect of speed change, $F(4,36) = 2.84$, $p < 0.05$, $\eta_p^2 = 0.24$, and significant interaction between block type and speed change, $F(4,36) = 3.78$, $p < 0.05$, $\eta_p^2 = 0.29$, but no effect of block type, $F(1,9) = 1.01$, $p = 0.34$, $\eta_p^2 = 0.10$. One-way repeated-measure ANOVA within each block type indicated significant main effect of speed change only in the learning block, $F(4,36) = 4.57$, $p < 0.01$.

For initial speed of 0.8 m/s, there was a significant main effect of speed change, $F(4,36) = 4.24$, $p < 0.01$, $\eta_p^2 = 0.32$, and significant interaction between block type and speed change, $F(4,36) = 4.02$, $p < 0.01$, $\eta_p^2 = 0.31$, but no effect of block type, $F(1,9) = 1.13$, $p = 0.32$, $\eta_p^2 = 0.11$. One-way repeated-measure ANOVA within each block type indicated significant main effect of speed change only in the learning block, $F(4,36) = 6.78$, $p < 0.01$. In sum, the results of participants' walking speed indicated that participants did not adjust their walking speed effectively in different target conditions in the test block while they did so in the learning block. This is consistent with the analysis of constant error and absolute error which indicated higher errors were observed in the test block.

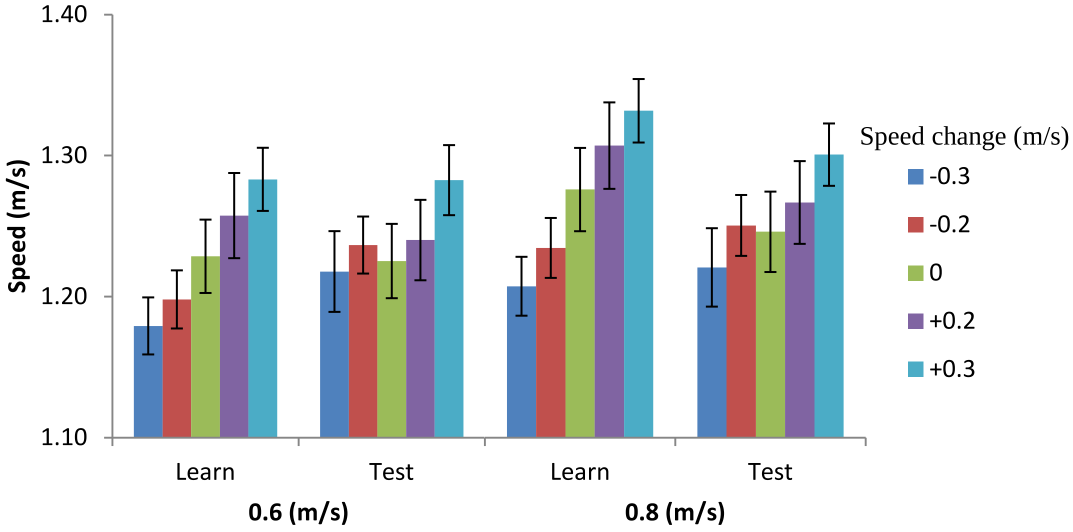

Figure 28. Mean walking speed in each target condition for learning and test blocks in Experiment 3.

To examine how participants adjusted their heading in different target conditions, I measured the angle they turned within a trial. First, to determine whether participants learned to anticipate the target speed change, I measured the total angle through which they turned before the occlusion point at 2.5 s (i.e. before the speed change). When the target initially moved at 0.6 m/s, participants turned more when the target speed would subsequently increase, and turned less when the target speed would decrease (Figure 29). This pattern of adjustment was observed in both learning and test blocks. A 2-way repeated-measure ANOVA indicated significant main effect of block type, $F(1,9) = 6.22$, $p < 0.05$, $\eta_p^2 = 0.41$, and speed change, $F(4,36) = 20.44$, $p < 0.01$, $\eta_p^2 = 0.69$, but no interaction, $F(4,36) = 2.25$, $p = 0.08$, $\eta_p^2 = 0.20$. A similar pattern of heading adjustment was observed with an initial target speed of 0.8 m/s. A 2-way repeated-measure ANOVA indicated only a significant main effect of speed change, $F(4,36) = 15.68$, $p < 0.01$, $\eta_p^2 = 0.64$. The results indicate that participants learned to anticipate the upcoming target speed change by adjusting their heading in advance.

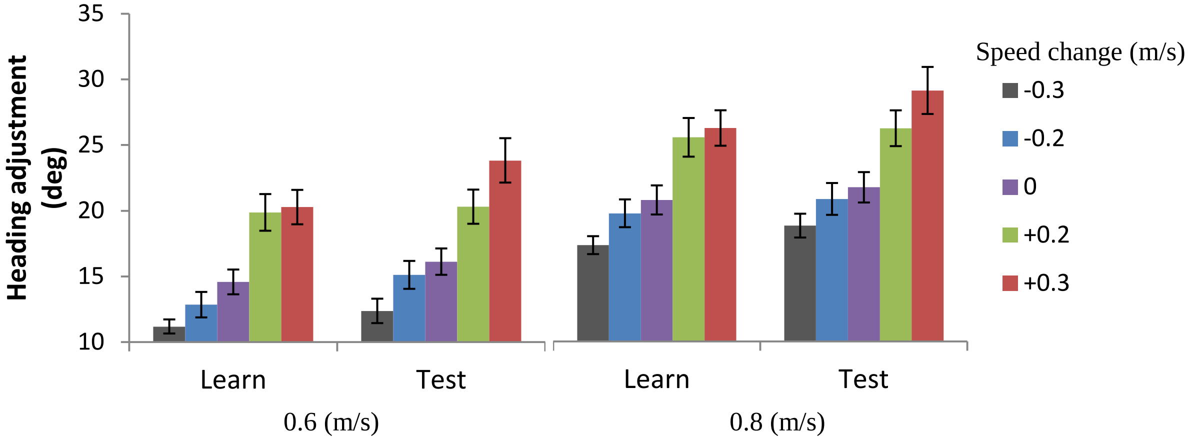

Figure 29. Heading adjustment before occlusion point in each target condition for learning and test blocks in Experiment 3.

Second, to determine whether participants learned to adjust for the speed change during occlusion, I measured the angle they turned after the occlusion point (Figure 30). In the learning block when the target was always visible, participants turned more when target speed increased and turn less when target speed decreased. However, in the test block when the target was occluded, participants appeared to turn a constant angle regardless of the target speed change. When target initially moved at 0.6 m/s, a 2-way repeated-measure ANOVA indicated significant main effect of speed change, $F(4,36) = 10.31$, $p < 0.01$, $\eta_p^2 = 0.53$, no effect of block type, $F(1,9) = 0.36$, $p = 0.56$, $\eta_p^2 = 0.04$, and significant interaction $F(4,36) = 20.04$, $p < 0.01$, $\eta_p^2 = 0.69$. Simple effect tests found a significant effect of target speed change in the learning block ($p < 0.01$), but not in the test block ($p = 0.89$). With an initial target speed of 0.8 m/s, a 2-way repeated-measure ANOVA indicated significant main effect of speed change, $F(4,36) = 11.99$, $p < 0.01$, $\eta_p^2 = 0.57$, block type, $F(1,9) = 6.73$, $p < 0.05$, $\eta_p^2 = 0.43$, and their interaction, $F(4,36) = 18.56$, $p < 0.01$, $\eta_p^2 = 0.67$. Simple effect tests found a significant effect of target speed change in the learning block ($p < 0.01$), but not in the test block ($p = 0.10$). The results indicate that participants adaptively adjusted their heading with a visible target in the learning block; in contrast, they turned a constant angle when the target was occluded in the test block. Thus, participants did not learn to adjust their heading to the target's speed change during occlusion.

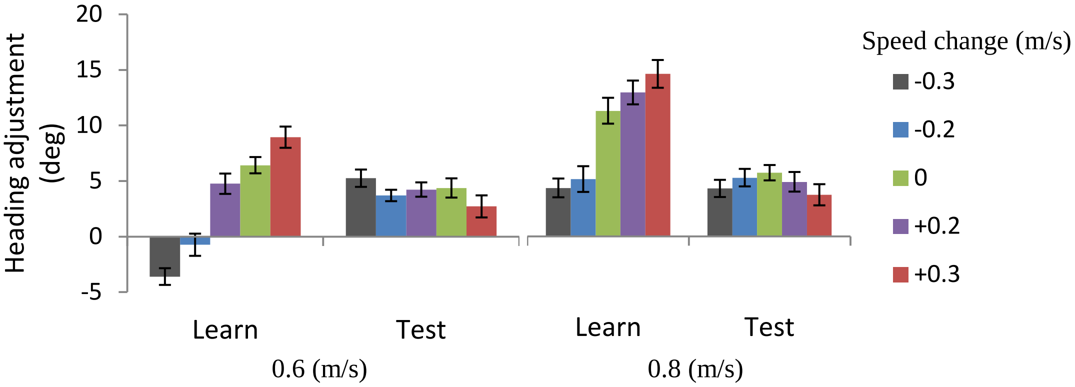

Figure 30. Heading adjustment after occlusion point in each target condition for learning and test blocks in Experiment 3.

4.4. Discussion

In the current study, participants first learned target movement in a learning block with the visible target, and then they were tested in a test block with the target visually occluded. The analysis of performance errors indicated that higher errors were observed in the test block than in the learning block. Moreover, participants tended to overshoot the target more in the test block than in the learning block when the target initially moved at slower speed and then slowed down; they tended to undershoot the target more in the test block than in the learning block when the target initially moved at higher speed and then sped up. The impaired performance in the test block with occluded target is consistent with the results of Experiment 2 in which degrading target visibility progressively impaired interception performance.

The results also revealed a pattern of regression to the mean in final location and walking speed when the target was occluded. That is, participants' final x position and walking speed increased from the learning block to test block when the target's initial speed was low and then slowed down; their final location and walking speed decreased from the learning block to test block when the target initially moved at higher speed and then sped up. This result indicated that participants did not adjust their interception path and walking speed in the test block as effectively as in the learning block. This may account for the increased interception error in the test block.

As in Experiment 2, participants' final location indicated that different target speed changes effectively resulted in different final locations, and hence different interception paths. That is, speeding-up led to greater final x locations, while slowing-down led to smaller final x locations. This holds true even in the test block, when the target was totally occluded. However, this does not necessarily imply that an accurate internal model of target motion was learned and used to guide interception. Indeed, interception performance in the test block was significantly impaired, as reflected by the constant and absolute errors, and the range of responses was significantly compressed. Moreover, participants made adaptive adjustments for the upcoming speed change before the target was occluded, which may be sufficient to account for their final x locations.

These adaptive adjustments prior to the occlusion point indicate that participants did learn to anticipate the upcoming target speed change. A possible heuristic might be called the “adaptive bearing strategy”. That is, in a block of trials in which the target speeds up, participants increase the bearing angle before the occlusion point; and in a block in which the target slows down, they decrease the bearing angle. This heuristic only applies before the occlusion point. In a learning block, when the target remains visible, the constant bearing strategy may fade in to control interception after the speed change. But in a test block, when the speed change is occluded, participants turn a constant angle after the occlusion point. This stereotyped adjustment was also observed in Experiment 2. There is thus no evidence of an adaptive or predictive adjustment once the target was occluded. The constant bearing model (Equation 2) with only a damping term might be able to account for the stereotyped heading adjustment. To examine participants' heading adjustment strategy in different conditions, I will examine their heading time series.

Lacquaniti and his colleagues argued that an internal model of earth's gravity could be used in interception of a free falling object (e.g. Mcintyre, et al., 2001). And Diza, et al. (2009) suggested prediction based on knowledge of a target's future movement could be used to intercept a velocity-varying target. In those studies, participants didn't purposely learn an internal model of target movement if there was one. In contrast, in the current study I had participants learned a target's movement in a block of trials in which the target underwent the same speed change. Moreover, in those studies, the target underwent more complicated velocity change, e.g. the free falling target continuously accelerated due to earth's gravity. In contrast, in the current study the target underwent less complicated speed change, that is, it only changed its speed once. Nevertheless, I found impaired interception performance and a stereotyped heading adjustment during occlusion. There is thus no evidence that an internal model of target motion was learned and used to guide interception.

Chapter 5. Discussion

5.1. The current experiments

In three experiments, I used a moving-target interception task to investigate whether locomotor interception is normally controlled on-line by current information or by an internal model. One of the reasons that I used this task is that locomotor interception is a fundamental daily activity. Another reason is that locomotor interception complements previous work with blind walking tasks. Research on blind walking is often regarded as evidence for model-based control in human locomotion (Loomis & Beall, 2004; Loomis & Philbeck, 2008). However, the spatio-temporal demands of blind walking are relatively low compared to those of blind interception. Specifically, the blind walking task only implicates an internal representation of the spatial position of a stationary object, which might be satisfied by spatial memory for the target's approximate location in a static environment. In contrast, the blind interception task implicates a dynamic internal model that mimics an object's motion through the environment and enables prediction of its trajectory. Moving-target interception thus places greater demands on the control of action and enables tests of a "full-blooded" internal model.

In Experiment 1, I tested whether an internal model of target position and speed, computed over a preceding temporal window (Saunders & Knill, 2003, 2004), would help explain human interception behavior. I found that using this internal model as input to the constant bearing strategy did not improve simulations of the human data, compared to using current information as input. Thus, target extrapolation models of this sort do not appear to contribute to human interception behavior. Although this is a likely candidate, of course, there are other possible types of internal models of target motion, such as Kalman filter models, that I plan to test against the current data.

In Experiment 2 and 3, to test on-line or model-based control, I manipulated availability or quality of current visual information to test on-line or model-based control. The results of Experiment 2 indicate that degrading target visibility progressively impaired both the accuracy and precision of locomotor interception. In Experiment 3, even when participants experienced the same target speed-change for a block of 40 trials, visual occlusion again resulted in impaired interception performance. These results clearly demonstrate the primary role of current information in locomotor interception. On the other hand, participants did learn to anticipate upcoming target speed change in Experiment 3. An adaptive bearing strategy might be able to account for participants' adaptive heading adjustment before occlusion point. According to this strategy, participants increase the bearing angle before occlusion point if they anticipate the target speeding up; they decrease the bearing angle if they anticipate the target slowing down.

In Experiment 2 and 3, participants turned a constant angle after the target was totally occluded in contrast with the adaptive heading adjustment when target was visible. This result indicates no evidence for an internal model that predicts the target's motion during occlusion. This finding also suggests that different control strategies may be used in visual and occlusion conditions. This stereotyped heading adjustment might be able to be accounted for by the constant bearing model (Equation 2) with only the damping term.

To closely examine how participants adjust their heading, I will analyze their heading time series.

5.2. The three hypotheses

5.2.1. Strong model-based control

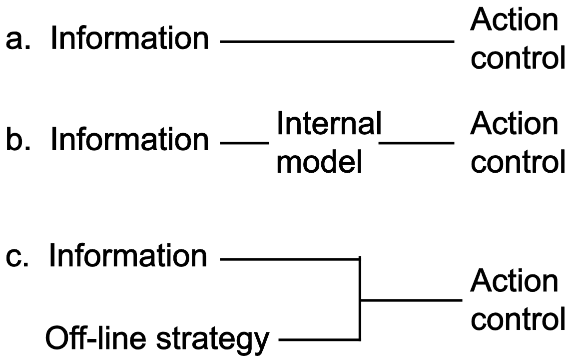

Figure 31. The three hypotheses of action control.

The model-based approach seeks to account for the control of action based on an internal representation such as a world model and/or an action plan. In particular, the strong model-based hypothesis states that vision is used to construct an internal model of the environment, and action is controlled exclusively based on this world model, whether or not visual information is concurrently available. However, the properties of an internal world model are seldom clearly specified, making the hypothesis difficult to test.

Successful performance in visually directed action such as blind walking is regarded as an existence proof of an internal world model. However, it does not follow that such a world model guides walking when the eyes are open. Indeed, the literature shows that performance with vision is significantly more precise than performance without vision, increasingly so as the spatio-temporal demands of the task increase. Moreover, it is widely reported that longer occlusion times lead to progressively impaired performance. All these findings suggest that an internal model by itself is not sufficient to guide action, contrary to the strong model-based control hypothesis. The difficulty is that the temporal persistence of a world model is unspecified, and thus degraded performance under occlusion, no matter how rapid, can be attributed to the decay of an internal model.

A world model is often posited to account for anticipatory actions as well, for example in locomotor or manual interception of a moving target. On this view, interceptive actions are predicatively controlled, where the prediction is based on an internal model of the target's motion. A few studies have claimed that participants learn a predictive model of target motion, but I contend that the results may be explained by simpler heuristic or visual-motor mapping strategies. Generally speaking, the existing data are insufficient to justify the strong model-based control hypothesis in the face of more parsimonious explanations.

In sum, without clear specification, the existence and role of an internal world model are difficult to test empirically. First, an internal model cannot be directly manipulated to test its influence on action control. In contrast, the available visual information can be manipulated or withdrawn and the corresponding on-line control laws can be identified and tested empirically.

Second, the expected time course of an internal model upon removal of visual information is unspecified. Although humans can perform certain tasks under visual occlusion, longer occlusion usually leads to progressive deterioration in performance.

There is no agreement on the level of performance predicted by a world model, its expected rate of decay, or the frequency of visual updating required to maintain performance. If decay is rapid and updating frequent, at some point the model-based hypothesis collapses into the on-line control hypothesis, for action is continuously dependent upon current information. Given that both approaches thus recognize the crucial role of current information, I conclude that on-line control is more parsimonious than model-based control.

Third, the content and scope of an internal world model remain ill-specified. In the literature I reviewed, a world model could be a spatial memory (e.g., Loomis & Beall, 2004), a model of Earth’s gravitational acceleration (e.g., McIntyre, et al., 2001), knowledge of an object’s dynamic properties (e.g. ball elasticity in Diaz, et al., 2013), or a spatiotemporal model of a specific trajectory (e.g. a convex path in Diaz, et al., 2009). The concept of a world model appears to be too unconstrained to serve as a useful scientific construct, subject to operationalization and empirical test (Haselager, et al., 2004). In contrast, visual information and on-line control laws can be operationalized and tested experimentally. Nevertheless, I believe that common usage of the term “internal model” entails a representation of intervening states of the actor-environment system, and a generative capacity to extend to new situations within the model’s domain. Such properties may be empirically evaluated, but testable predictions depend on specifying the content and scope of the model.

In sum, there is little evidence to support the use of model-based control when visual information is concurrently available. When visual information is removed, task performance deteriorates rapidly, implying that an internal world model alone is not sufficient to guide action. The evidence thus demonstrates that current information is necessary for normal levels of performance, given the spatio-temporal demands of the task, consistent with on-line control. Under these circumstances, positing an internal world model is gratuitous. Even proponents of the concept (Zago et al., 2008) have conceded the lack of support for “precise, analytic knowledge” and accepted “unsophisticated, approximate knowledge” that I would term heuristic. I conclude that the facts militate against the strong model-based hypothesis.

5.2.2. Strong on-line control

The strong on-line control hypothesis states that action is controlled on the basis of current visual information, when such information is available. The literature review indicates that visual information is sufficient for on-line control of a variety of locomotor and manual tasks. A growing number of studies have identified the specific informational variables and control laws used to guide a wide range of human actions. In addition, as summarized in the previous section, performance is generally impaired by visual occlusion, leading to the conclusion that current information is necessary for normal levels of performance. Taken together, these findings indicate that action is normally controlled by current information, consistent with the strong on-line control hypothesis.

However, strong on-line control is not a comprehensive account of the control of action, for does not attempt to explain behavior under conditions when visual information is unavailable. For a complete theory, an account of off-line control is also needed.

5.2.3. The hybrid hypothesis

I propose a hybrid hypothesis of action control (Figure 27). The hybrid hypothesis aims to be a comprehensive account of the control of action by combining strong on-line control with complementary off-line control strategies. This hypothesis accepts that action is normally controlled online by current information. But under exceptional conditions, such as visual occlusion, near visual threshold, or with highly regular object motion, action may be controlled by simple off-line strategies such as heuristics, mappings, or spatial memory. For example, in visually directed locomotion, an approximate spatial memory of target location appears to guide blind walking after vision is removed.

These off-line strategies do not guarantee successful or general control of action. Spatial memory is approximate, capacity-limited, and subject to interference and decay over time. A heuristic is a qualitative rule without much predictive accuracy, but gets the actor into the ball-park for the task. A mapping strategy is a learned relationship between initial information variables and action control variables or end-states. For example, a simple mapping from three drop heights to interception times may be learned during normal catching, and then used when the target is occluded (Lacquaniti and Maioli, 1989b).

Alternatively, consider the possibility that off-line control is based on a full internal world model rather than heuristics and mappings. Despite the vagueness of the concept, I believe that an internal model can be distinguished from these weaker strategies. As used in the literature, the term entails computing or simulating intervening states of the actor-environment system with some degree of accuracy. It also implies that the model is generative, such that model-based control should generalize to new conditions within the model’s domain. For instance, an internal model of projectile motion would represent intervening states of a ball’s trajectory, and may be expected to generalize to new initial velocities, wind conditions, and ball elasticities, depending on its scope.

I find that the existing evidence does not call for an accurate world model, and can often be explained by a simple heuristic or mapping. For example, participants walking to intercept a target that moved on a fixed circular path learned a short-cut strategy (Owen & Warren, 2005), but it did not enable successful interception; rather, on-line control phased in on the far side of the circle. Moreover, the strategy was context-specific and did not generalize to multiple target paths with different radii and directions. This has the hallmarks of a heuristic. Or consider a baseball batter operating near the limits of visual performance (Gray, 2002). Batters appeared to learn a mapping from the ball’s initial optical motion to its arrival location at the plate. Moreover, different mappings appear to be learned for fast pitches and slow pitches, potentially explaining the pitch sequence effect. Such results are more consistent with context-specific mappings than a general internal model of the projectile motion. However, experiments on off-line control are still needed, which are explicitly designed to disentangle the predictions of an internal model from situation-specific heuristics and mappings.

In Experiment 2 and 3, stereotyped heading adjustment was observed and interception performance was impaired when the target was occluded. This indicates no evidence for an internal model that predicts or simulates target’s motion. A simple heuristic might rather be used. Specifically, participants may just maintain approximately the same walking direction after target occlusion. The constant angle they turned after target occlusion may be due to inertia, which may be accounted for by the constant bearing model (Equation 2) with only the damping term.

5.3. Conclusion

In conclusion, I performed three experiments to test whether locomotor interception of a moving target is controlled on-line by current visual information or by an internal model. I used different ways to test this question, including comparing simulation performance of different control models and comparing interception performance in different visual conditions. Generally speaking, the results of the experiments suggest the primary role of current visual information in control of locomotion interception. Based on the current results and by reviewing literature in this area, I conclude that a hybrid hypothesis, which combines one-line control and off-line heuristics, provides a comprehensive and coherent account of visually controlled action.

References

Arzamarski, R., Harrison, S.J., Hajnal, A., & Michaels, C.F. (2007) Lateral ball interception: hand movements during linear ball trajectories. *Experimental Brain Research, 177,* 312-323.

Bastin, J., Jacobs, D. M., Morice, A. H. P., Craig, C., & Montagne, G. (2008). Testing the role of expansion in the prospective control of locomotion. *Experimental Brain Research, 191*, 301-312.

Bastin, J., Craig, C., & Montagne, G. (2006). Prospective strategies underline the control of interceptive actions. *Human Movement Sciences, 25,* 718-732.

Baures, R., Benguigui, N., Amorim, M-A., & Siegler, I. A. (2007). Intercepting free falling objects: Better use occam's razor than internalize Newton's law. *Vision Research, 47,* 2982-2991.

Bennett, S. J., Ashford, D., & Elliott, D. (2003). Intermittent vision and one-handed catching: The temporal limits of binocular and monocular integration, *Motor Control, 7,* 378-387

Bennett, S. J., Elliott, D., Weeks, D. J., & Keil, D. (2003). The effects of intermittent vision on prehension under binocular and monocular viewing. *Motor Control, 7,* 46-56.

Binsted, G., Rolheiser, T. M., & Chua, R. (2006). Decay in visuomotor representations during manual aiming. *Journal of Motor Behavior, 38,* 82-87.

Bootsma, R. J., Fayt, V., Zaal, F. T. J. M., & Laurent, M. (1997). On the information-based regulation of movement: Things Wann(1996) may want to consider, *Journal of Experimental Psychology: Human perception and performance*, *23,* 1282-1289.

Brenner, E., & Smeets, J. B. J. (1997). Fast responses of the human hand to changes in target position. *Journal of Motor Behavior*, *29,* 297-310.

Brenner, E., Smeets, J. B. J., & de Lussanet, M. H. E. (1998). Hitting moving targets, continuous control of the acceleration of the hand on the basis of the target's velocity. *Experimental Brain Research, 122*, 467-474.

Books, K. (2001). Stereomotion speed perception is contrast dependent. *Perception, 30*, 725-731.

Brouwer, A., Brenner, E., & Smeets, J. B. J. (2002). Perception of acceleration with short presentation times: Can acceleration be used in interception? *Perception & Psychophysics, 64*, 1160-1168.

Bruggeman, H., Zosh, W., & Warren, W. H. (2007). Optic flow drives human visuo-locomotor adaptation. *Current Biology, 17,* 2035-2040.

Caljouw, S. R., van der Kamp, J., & Savelsbergh, G. J. P. (2006). The impact of task-constraints on the planning and control of interceptive hitting movements. *Neuroscience Letters, 392*, 84–89.

Cavezian, C., Valadao, D., Hurwitz, M., Saoud, M., & Danckert, J. (2012). Finding centre: Ocular and fmri investigations of bisection and landmark task performance. *Brain Research, 1437,* 89–103.

Chapman, S. (1968). Catching a baseball. *American Journal of Physics, 36,* 868-870.

Chardenon, A., Montagne, G., Laurent, M., & Bootsma, R. J. (2005). A robust solution for dealing with environmental changes in intercepting moving balls. *Journal of Motor Behavior, 37*, 52-64.

Charles, L., & Webber, Jr. (2005). Recurrence quantification analysis of nonlinear dynamical systems. In M. A. Riley, & G. C. Van Orden (Eds.), *Tutorials in Contemporary nonlinear methods for the behavioral sciences*. Retrieved from http://www.nsf.gov/sbe/bcs/pac/nmbs/nmbs.jsp

Chemero, A. (2009) *Radical embodied cognitive science*. Cambridge: MIT Press.

Cinelli, M., & Warren, W. H. (2012). Do walkers follow their heads: Investigating the role of head rotation in locomotion control. *Experimental Brain Research, 219,* 175–190

Cloete, S., & Wallis, G. (2009). Limitations of feedforward control in multiple-phase steering movements. *Experimental Brain Research*, *195*, 481-487.

Conant, R.C., & Ashby, W.R. (1970). Every good regulator of a system must be a model of that system. *International Journal of Systems Science, 1*, 89-97.

Craig, C.M., Goulon, C., Berton, E., Rao, G., Fernandez, L., & Bootsma, R. (2009) Optic variables used to judge future ball arrival position in expert and novice soccer players. *Attention, Perception & Psychophysics, 71,* 515-522.

Craik, K.J.W. (1943/1967). *The nature of explanation*: Cambridge University Press.

Davidson, P.R., & Wolpert, D.M. (2005). Widespread access to predictive models in the motor system: a short review. *Journal of Neural Engineering, 2*, S313-S319.

Dessing, J. C., Bullock, D., Peper, C. L., & Beek, P. J. (2002). Prospective control of manual interceptive actions: Comparative simulations of extant and new model constructs. *Neural Network*, *15*, 163-179.

Dessing, J. C., Peper, D. L., Bullock, D., & Beek, P. J. (2005). How position, velocity and temporal information combine in the prospective control of catching: data and model. *Journal of Cognitive Neurosciences*, *17*, 668-686.

Dessing, J. D., Wijdenes, L. O., Peper, C. E., & Beek, P. J. (2009). Adaptations of lateral hand movements to early and late visual occlusion in catching. *Experimental Brain Research*, *192*, 669-682.

Diaz, G., Cooper, J., Rothkopf, C., & Hayhoe, M. (2013). Saccades to future ball location reveal memory-based prediction in a virtual-reality interception task. *Journal of Vision*, *13*, 1-14.

Diaz, G. J., Phillips, F., & Fajen, B. R. (2009). Intercepting moving targets: A little foresight helps a lot. *Experimental Brain Research, 195,* 345-360.

Diedrichsen, J., Nambisan, R., Kennerley, S. W., & Ivry, R. B. (2004). Independent on-line control of the two hands during bimanual reaching. *European Journal of Neuroscience, 19*, 1643-1652.

Diener, H. C., Wist, E. R., Diehgans, J., & Brandt T. (1976). The spatial frequency effect on perceived velocity. *Vision Research, 16*, 169-176.

Duchon, A. P., & Warren, W. H. (1997). Path planning vs. on-line control in visually guided locomotion. *Investigative Ophthalmology and Visual Science, 38*, S79.

Elias, L. J., Robinson, B., & Saucier, D. M. (2005). Rightward biases in free-viewing visual bisection tasks: Implications for leftward responses biases on similar tasks. *Brain and Cognition, 59,* 296–298.

Elliott, D., & Calvert, R. (1990). The influence of uncertainty and premovement visual information on manual aiming. *Canadian Journal of Psychology, 44*, 501-511.

Elliortt, D., Chua, R., & Pollock, B. J. (1994). The influence of intermittent vision on manual aiming. *Acta Psychologica, 85,* 1-13.

Elliott, D., Pollock, B.J., Lyons, J., & Chua, R. (1995). Intermittent vision and discrete manual aiming. *Perceptual and Motor Skills*, *80*, 1203-1213.

Fajen, B. R., & Warren, W. H. (2003) Behavioral dynamics of steering, obstacle avoidance, and route selection. *Journal of Experimental Psychology: Human Perception and Performance*, *29*, 343-363.

Fajen, B. R., & Warren, W. H. (2004). Visual guidance of intercepting a moving target on foot. *Perception, 33,* 689-715.

Fajen, B. R., & Warren, W. H. (2007). Behavioral dynamics of intercepting a moving target. *Experimental Brain Research, 180*, 303-319.

Farrell, M. J., & Thomson, J. A. (1999). On-line updating of spatial information during locomotion without vision. *Journal of Motor Behavior, 31*, 39-53.

Fink, P. W., Foo, P. S., & Warren, W. H. (2009). Catching fly balls in virtual reality: A critical test of the outfielder problem. *Journal of Vision*, *9,* 1-8.

Garcia, C.E., & Morari, M. (1982). Internal model control. A unifying review and some new results. *Industrial and Engineering Chemistry Process Design and Development, 21*, 308-323.

Gibson, J. J. (1958). Visually controlled locomotion and visual orientation in animals. *British Journal of Psychology, 49*, 182-194.

Gibson, J. J. (1979). *The Ecological Approach To Visual Perception*. Boston, MA: Houghton Mifflin Company.

Godthelp, J. (1985). Precognitive control: Open- and closed-loop steering in a lane-change maneuver. *Ergonomics, 28,* 1419-1438.

Godthelp, H. (1986). Vehicle control during curve driving. *Human Factors, 28,* 211-221.

Gosselin-Kessiby, N., Messier, J., & Kalaska, J. F. (2008). Evidence for automatic on-line adjustments of hand orientation during natural reaching movements to stationary targets. *Journal of Neurophysiology, 99*, 1653-1671.

Gray, R. (2002). Behavior of college baseball players in a virtual batting task. *Journal of Experimental Psychology: Human Perception and Performance*, *28*, 1131-1148.

Haselager, P., de Groot, A., & van Rappard, H. (2003). Representationalism vs. anti-representationalism: A debate for the sake of appearance. *Philosophical Psychology, 16*, 5–24.

Hayhoe, M., McKinney, T., Chajka, K., & Pelz, J. B. (2012). Predictive eye movements in natural vision. *Experimental Brain Research*, *217*, 125-136.

Hayhoe, M., Mennie, N., Sullivan, B., & Gorgos, K. (2005). The role of internal models and prediction in catching balls. *Proceedings of AAAI*, Fall 2005.

Heath, M., Westwood, D. A., & Binsted, G. (2004). The control of memory-guided reaching movements in peripersonal space. *Motor Control, 8*, 76-106.

Hecht, H., & Savelsbergh, G.J.P. (Eds.). (2004). *Theories of time to contact*. North-Holland: Elsevier.

Hildreth, E. C., Beusmans, J. M. H., Boer, E. R., & Royden, C. S. (2000). From vision to action: Experiments and models of steering control during driving. *Journal of Experimental Psychology: Human Perception and Performance*, *26*, 1106–1132.

Jacobs, D. M., & Michaels, C., F. (2006). Lateral interception I: Operative optical variables, attunement, and calibration. *Journal of Experimental Psychology: Human Perception and Performance, 32*, 443-458.

Katsumata, H., & Russell, D. M. (2012). Prospective versus predictive control in timing of hitting a falling ball. *Experimental Brain Research,216*, 499-514.

Kawato, M. (1999). Internal models for motor control and trajectory planning. *Current Opinion in Neurobiology, 9*, 718-727.

Lacquaniti, F., & Maioli, C. (1989a). The role of preparation in tuning anticipatory and reflex responses during catching. *Journal of neuroscience*, *9*, 134-148.

Lacquaniti, F., & Maioli, C. (1989b). Adaptation to suppression of visual information during catching. *Journal of Neuroscience, 9*, 149-159.

Land, M.F., & McLeod, P. (2000). From eye movements to actions: How the batsmen hit the ball. *Nature Neuroscience, 3*, 1340-1345.

Lee, D. N. (1976). A theory of visual control of braking based on information about time-to-collision. *Perception*, *5*, 437-459.

Lee, D. N., & Young, D. S. (1985). Visual timing of interceptive action. In D. J. Ingle, & M. Jeannerod (Eds.), *Brain mechanisms and spatial vision*. Dordrecht, The Netherlands: Nartinus Nijhoff.

Lee, D. N., Yound, D., S., Reddish, P., E., Lough, S., & Clayton, T., M., H. (1983). Visual timing in hitting an accelerating ball. *Quarterly Journal of Experimental Psychology*, *35A*, 333-346.

Lenoir, M., Musch, E., Janssens, M., Thiery, E., & Uyttenhove, J. (1999). Intercepting moving objects during self-motion. *Journal of Motor Behavior*, *31*, 55-67.

Lenoir, M., Musch, E., Thiery, E., & Savelsbergh, G. J. (2002). Rate of change of angular bearing as the relevant property in a horizontal interception task during locomotion. *Journal of Motor Behavior*, *34*, 385-404.

Li, L. & Cheng, J.C.K. (2013). Visual strategies for the control of steering toward a goal. *Displays, 34,* 97–104.

Loomis, J.M., & Beall, A.C. (1998). Visually controlled locomotion: Its dependence on optic flow, 3-D space perception, and cognition. *Ecological Psychology, 10*, 271-285.

Loomis, J. M., & Beall, A. C. (2004). Model-based control of perception/action. In L. M. Vaina, S. A. Beardsley, & S. K. Rushton (Eds.), *Optic flow and beyond* (pp. 421-441). Dordrecht: Kluwer.

Loomis, J. M., DaSilva, J., Fujita, N., & Fukusima, S. (1992). Visual space perception and visually directed action. *Journal of Experimental Psychology: Human Perception and Performance*, *18*, 906-921.

Loomis, J. M., & Philbeck, J. W. (2008). Measuring spatial perception with spatial updating and action. In Klatzky, R. L., MacWhinney, B., & Behrmann, M. (Eds). *Embodiment, Egospace, and Action.* New York: Taylor & Francis.

Lyons, J., Fontaine, R., & Elliott, D. (1997). I lost it in the lights: The effects of predictable and variable intermittent vision on unimanual catching. *Journal of Motor Behavior*, *29*, 113-118.

Mazyn, L. I. N., Savelsbergh, G. J. P., Montagne, G., & Lenoir, M. (2007). Planning and on-line control of catching as a function of perceptual-motor constrains. *Acta Psychologica*, *126*, 59-78.

McBeath, M.K., Shaffer, D.M., & Kaiser, M.K. (1995). How baseball outfielders determine where to run to catch fly balls. *Science*, *268*, 569-573.

McIntyre, J., Zago, M., Berthoz, A., & Lacquaniti, F. (2001). Does the brain model Newton’s laws? *Nature Neuroscience, 4,* 693–694.

McLeod, P., Reed, N., & Dienes, Z. (2006). The generalized optic acceleration cancellation theory of catching. *Journal of Experimental Psychology: Human Perception and Performance, 32,* 139–148.

McLeod, P., Reed, N., Gilson, S., & Glennerster, A. (2008). How soccer players head the ball: A test of optic acceleration cancellation theory with virtual reality. *Vision Research, 48,* 1479–1487.

Michaels, C.F., & Oudejans, R.D. (1992). The optics and actions of catching fly balls: Zeroing out optic acceleration. *Ecological Psychology, 4,* 199-222.

Michaels, C. F., Jacobs, D., M., & Bongers, R., M. (2006). Lateral interception II: Predicting hand movements. *Journal of Experimental Psychology: Human Perception and Performance*, *32*, 459-472.

Montagne, G., Laurent, M., Durry, A., & Bootsma, R. (1999). Movement reversals in ball catching. *Experimental Brain Research*, *129,* 87-92.

Moravec, H. (1982). The Stanford cart and the CMU rover. *Proceedings of the IEEE, 71*, 872-884.

Morice, A. H. P., Francois, M., Jacobs, D. M., & Montagne, G. (2010). Environmental constraints modify the way an interceptive action is controlled. *Experimental Brain Research, 202*, 397-411.

Nijhawan, R. (2008). Visual prediction: Psychophysics and neurophysiology of compensation for time delays. *Behavioral and brain sciences, 31*, 179-239.

Peper, L., Bootsma, R. J., Mestre, D. R., & Bakker, F. C. (1994). Catching balls: How to get the hand to the right place at the right time. *Journal of Experimental Psychology: Human Perception and Performance, 20*, 591-612.

Philbeck, J. W. (2000). Visually directed walking to briefly glimpsed targets is not biased toward fixation location. *Perception*, *29*, 259-272.

Philbeck, J. W., Loomis, J. M., & Beall, A. C. (1997). Visually perceived location is an invariant in the control of action. *Perception & Psychophysics, 59*, 601-612.

Rieser, J. J., Ashmead, D, Talor, C., & Youngquist, G. (1990). Visual perception and the guidance of locomotion without vision to previously seen targets. *Perception, 19*: 675-689.

Riley, M. A., Balasubramaniam, R., & Turvey, M. T. (1999). Recurrence quantification analysis of postural fluctuations. *Gait and Posture, 9*, 65–78.

Sarlegna, F., Blouin, J., Bresciani, J-P., Bourdin, C., Vercher, J-L., & Gauthier, G. M. (2003). Target and hand position information in the online control of goal-directed arm movements. *Experimental Brain Research*, *151*, 524-535.

Saunders, J. A., & Knill, D. C. (2003). Human use continuous visual feedback from the hand to control fast reaching movements. *Experimental Brain Research, 152,* 341–352.

Saunders, J. A., & Knill, D. C. (2004). Visual feedback control of hand movements. *The Journal of Neuroscience, 24,* 3223–3234.

Saxberg, B. V. (1987). Projected free-fall trajectories. 1. Theory and simulation. *Biological Cybernetics, 56,* 159–175.

Shaffer, D. M., & McBeath, M. K. (2005). Naïve beliefs in baseball: Systematic distortions in perceived time of apex for fly balls. *Journal of Experimental Psychology: Learning, Memory & Cognition*, *31*, 1492–1501.

Senot, P., Zago, M., Lacquaniti, F., & McIntyre, J. (2005). Anticipating the effects of gravity when intercepting moving objects: Differentiating up and down with non-visual cues. *Journal of neurophysiology*, *94*, 4471-4480.

Sharp, R. H., & Whiting, H. T. A. (1974). Exposure and occluded duration effects in a ball-catching skill. *Journal of Motor Behavior*, *6*, 139–147.

Siegler, I. A., Bardy, B. G., & Warren, W. H. (2010). Passive vs. active control of rhythmic ball bouncing: The role of visual information. *Journal of Experimental Psychology: Human Perception and Performance, 36*, 729-750.

Stephen, D.G., Stepp, N., Dixon, J.A., & Turvey, M.T. (2008). Strong anticipation: Sensitivity to long-range correlation in synchronization behavior. *Physica A, 387,* 5271-5278.

Stepp, N., & Turvey, M.T. (2010). On strong anticipation. *Cognitive Systems Research, 11*, 148-164.

Thompson, P. (1982). Perceived rate of movement depends on contrast. *Vision Research, 22*, 377-380

Thomson, J. A. (1983). Is continuous visual monitoring necessary in visually guided locomotion? *Journal of Experimental Psychology: Human Perception and Perception, 9*, 427-443.

Thrun, S. (1997). To know or not to know: On the utility of models in mobile robotics. *AI Magazine, 18*, 47-54.

Tijtgat, P., Bennett, S. J., Savelsbergh, G. J., Clercq, D. D., & Lenoir, M. (2011). To know or not to know: Influence of explicit advance knowledge of occlusion on interceptive actions. *Experimental Brain Research*, *214*, 483-490.

Wallis, G. M., Chatziastros, A., Tresilian, J., & Tomasevic, N. (2007). The role of visual and non-visual feedback in a vehicle steering task. *Journal of Experimental Psychology: Human Perception and Performance*, *33*, 1127–1144.

Wallis, G. M., Chatziastros, A., & Bulthoff, H. H. (2002). An unexpected role for visual feedback in vehicle steering control. *Current Biology*, *12*, 295–299.

Warren, W. H. (1998).Visually controlled locomotion: 40 years later. *Ecological Psychology*, *10*, 177–219.

Warren, W.H. (2009) How do animals get about by vision? Visually controlled locomotion and orientation after 50 years. *British Journal of Psychology, 100,* 277-281.

Warren, W. H. (2006). The dynamics of perception and action. *Psychological Review, 113*, 358-389.

Warren, W. H., & Fajen, B. R. (2008). Behavioral dynamics of visually-guided locomotion. In A. Fuchs, & V. Jirsa (Eds.), *Coordination: Neural, behavioral, and social dynamics*. Heidelberg: Springer.

Warren, W. H., Kay, B. A., Zosh, W. D., Duchon, A. P., & Sahuc, S. (2001). Optic flow is used to control human walking. *Nature Neuroscience, 4,* 213–216.

Webber, C. L., & Zbilut, J. P. (1994). Dynamical assessment of physiological systems and states using recurrence plot strategies. *Journal of Applied Physiology, 76,* 965–973.

Werkhoven, P., Snippe, H. P., & Toet, A. (1992). Visual processing of optic acceleration. *Vision Research*, *32*, 2313-2329.

Westwood, D. A., Heath, M., & Roy, E. A. (2001). The accuracy of reaching movements in brief delay conditions. *Canadian Journal of Experimental Psychology, 55,* 304–310.

Whiting, H. T. A., & Sharp, R. H. (1974). Visual occlusion factors in a discrete ball-catching task. *Journal of Motor Behavior, 6*, 11–16.

Wilkie, R.M., & Wann, J.P. (2003). Controlling steering and judging heading: Retinal flow, visual direction, and extra-retinal information. *Journal of Experimental Psychology: Human Perception and Performance, 29*, 363-378.

Wilkie, R.M., & Wann, J.P. (2005). The role of visual and nonvisual information in the control of locomotion. *Journal of Experimental Psychology: Human Perception and Performance, 31*, 901-911.

William, T. S., & Underwood, J. (1982). *The science of hitting.* New York: Simon and Schuster.

Wolpert, D.M., & Ghahramani, Z. (2000). Computational principles of movement neuroscience. *Nature Neuroscience, 3*, 1212-1217.

Yilmaz, E. H., & Warren, W. H. (1995). Visual control of Braking: A test of the tau-dot hypothesis. *Journal of Experimental Psychology: Human Perception and Performance*, *21,* 996-1014.

Zago, M., Bosco, G., Maffei, V., Iosa, M., Ivanenko, Y. P., & Lacquaniti, F. (2004) Internal models of target motion: Expected dynamics overrides measured kinematics in timing manual interceptions. *Journal of Neurophysiology*, *91*, 1620–1634.

Zago, M., Bosco, G., Maffei, V., Iosa, M., Ivanenko, Y. P., & Lacquaniti, F. (2005). Fast adaptation of the internal model of gravity for manual interceptions: Evidence for event-dependent learning. *Journal of Neurophysiology*, *93*, 1055-1068.

Zago, M., & Lacquaniti, F. (2005). Internal model of gravity for hand interception: Parametric adaptation to zero-gravity visual targets on Earth. *Journal of Neurophysiology*, *94*, 1346–1357.

Zago, M., McIntyre, J., Senot, P., & Lacquaniti, F. (2008). Internal models and prediction of visual gravitational motion. *Vision Research*, *48*, 1532-1538.

Zago, M., McIntyre, J., Senot, P., & Lacquaniti, F. (2009). Visuo-motor coordination and internal models for object interception. *Experimental Brain Research*, *192*, 571-604.

Zbilut, J. P., Thomasson, N., & Webber, C. L. (2002). Recurrence quantification analysis as a tool for nonlinear exploration of nonstationary cardiac signals. *Medical Engineering & Physics, 24*, 53–60.

Zbilut, J. P., & Webber, C. L. (1992). Embeddings and delays as derived from quantification of recurrence plots. *Physics letters A*, *171*, 199–203.

Zhao, H., & Warren, W.H. (2013). On-line and off-line control of locomotion: Steering a slalom course. Unpublished manuscript.