Intercepting a moving target: On-line or model-based control?

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When walking to intercept a moving target, people take an interception path that appears to anticipate the target's trajectory. According to the constant bearing strategy, the observer holds the bearing direction of the target constant based on current visual information, consistent with on-line control. Alternatively, the interception path might be based on an internal model of the target's motion, known as model-based control. To investigate these two accounts, participants walked to intercept a moving target in a virtual environment. We degraded the target's visibility by blurring the target to varying degrees in the midst of a trial, in order to influence its perceived speed and position. Reduced levels of visibility progressively impaired interception accuracy and precision; total occlusion impaired performance most and yielded nonadaptive heading adjustments. Thus, performance strongly depended on current visual information and deteriorated qualitatively when it was withdrawn. The results imply that locomotor interception is normally guided by current information rather than an internal model of target motion, consistent with on-line control.

Introduction

In daily life, people are faced with the challenge of interacting with a complex, dynamic environment. How such behavior is controlled remains an open question, and contrasting approaches lead to a different understanding of the underlying mechanisms. Two general approaches to the control of action have been developed in the past few decades, often referred to as on-line control and model-based control (Davidson & Wolpert, 2005; Oostwoud, Gomi, & Brenner, 2015; Zhao & Warren, 2015). In this article, we investigate these approaches by examining the specific case of locomotor interception.

In *on-line control,* action is guided by current visual information during the ongoing movement. On this view, action is normally coupled to the environment by means of visual information, and the movement trajectory and even anticipatory behavior emerges from the dynamics of the coupled system (Stepp & Turvey, 2010; Warren, 2006). For visually guided locomotion, a number of optical variables are available that might be used to control steering, obstacle avoidance, following, and interception under normal conditions (Gibson, 1958, 1979; Warren, 1998). For instance, it has been shown that walking direction (heading) and walking speed are controlled by using optic flow, the bearing direction of the target, and the local optical expansion of the target (Bastin, Jacobs, Morice, Craig, & Montagne, 2008; Fajen & Warren, 2004; Lenoir, Musch, Thiery, & Savelsbergh, 2002; Rio, Rhea, & Warren, 2014; Warren, Kay, Zosh, Duchon, & Sahuc, 2001). This view implies that if visual information were withdrawn, performance would rapidly deteriorate, depending on the spatiotemporal demands of the task.

In *model-based control,* on the other hand, action is guided on the basis of an internal representation of the external world and the actor. Consistent with Craik's (1943/1967) original conception, Wolpert defines 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). Successful action depends on a close correspondence between the physical system and its internal model. As an action unfolds, the actor's state is continuously monitored and the internal model is updated accordingly. An essential property of an internal model is that it can serve to guide behavior when decoupled (at least temporarily) from concurrent environmental input (Clark & Grush, 1999). The primary role in controlling action—whether

or not visual information is currently available—is thus played by an internal representation of the external world.

In the context of locomotion, Loomis and colleagues (Loomis & Beall, 2004; Loomis & Philbeck, 2008) have proposed that the perceiver creates an internal representation of three-dimensional space, on the basis of which the locomotor path is planned and guided. Findings on *visually directed action* are often regarded as evidence for such an internal world model. For example, it has been shown that human participants are able to perform a blind walking task in which they view a target at a distance on the ground, and then walk without vision to the remembered target location (Loomis, DaSilva, Fujita, & Fukusima, 1992; Philbeck, 2000; Philbeck, Loomis, & Beall, 1997; Rieser, Ashmead, Talor, & Youngquist, 1990). We refer to the guidance of behavior in the absence of visual information as *off-line control*. However, off-line control could be based on heuristic strategies when needed, such as a spatial memory of the target's location. At issue is the existence of an internal world model that normally guides behavior whether or not visual information is concurrently available.

In a recent review of the literature (Zhao & Warren, 2015), we found that when visual information is removed, performance deteriorates significantly and rapidly for a variety of actions, including catching, reaching, driving, and walking. Studies directly comparing sighted and blind walking, for example, indicate that visual occlusion leads to degraded performance. Thomson (1983) asked participants to walk to a previewed target with or without vision. The accuracy and precision of walked distance were comparable for targets at 9 m or less, but precision dropped dramatically for blind walking with targets at 12 m or more. When task demands were increased by asking participants to align the toe of a specified foot with a target line at 8–12 m, Farrell and Thomson (1999) found that variability in final toe position was significantly higher in blind than sighted walking.

Similar declines in performance with the removal of visual information have been reported in driving tasks (Cloete & Wallis, 2009; Hildreth, Beusmans, Boer, & Royden, 2000; Wallis, Chatziastros, & Bülthoff, 2002; Wallis, Chatziastros, Tresilian, & Tomasevic, 2007). For example, Wallis et al. (2002) found that participants changed lanes very well in normal light, but they failed to adjust their driving direction in the new lane after visual information was withdrawn. This failure persisted even when visual feedback was provided at the end of each trial. These experiments tested locomotion in a static environment, implying that a spatial memory of the layout is not sufficient to guide locomotion at normal levels of performance.

In a dynamic environment, locomotion must be controlled with respect to moving objects, such as walking to intercept a moving target. A variety of species have been observed to intercept moving targets in accordance with the *constant bearing strategy* (CBS). In this strategy, the actor approaches the target while holding the target's bearing direction constant (i.e., its direction with respect to an exocentric reference axis). The CBS has been observed in dragonflies (Olberg, Worthington, & Venator, 2000), fish (Lanchester & Mark, 1975), bats (Ghose, Horiuchi, Krishnaprasad, & Moss, 2006) and humans, for both heading control in the two-dimensional horizontal plane (Fajen & Warren, 2004, 2007) and speed control on a one-dimensional track (Bastin, Craig, & Montagne, 2006; Bastin et al., 2008; Chardenon, Montagne, Buekers, & Laurent, 2002; Chardenon, Montagne, Laurent, & Bootsma, 2004, 2005; Lenoir, Musch, Janssens, Thiery, & Uyttenhove, 1999; Lenoir et al., 2002; see Bastin, Fajen, & Montagne, 2010, on limitations of CBS).

According to CBS, interception is guided on the basis of current information about the bearing direction of the target, without relying on an internal model of target motion. Fajen and Warren (2007) showed that on-line control based on CBS is sufficient to account for human data on walking to intercept a moving target. They modeled interception as a second-order differential equation that controls steering to null change in the bearing direction of the target. Specifically, angular acceleration in the agent's heading direction ($\ddot{\phi}$) is a function of the current change in the target's bearing direction ($\dot{\psi}_m$) and the distance to the target (d_m; see Figure 1):

$$\ddot{\phi} = -b\dot{\phi} - k\dot{\psi}_m(d_m + c). \quad (1)$$

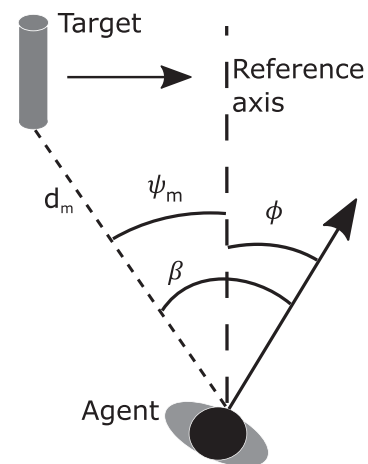This theoretical model includes a stiffness term $k\dot{\psi}_m$

Figure 1. Definition of variables for interception of a moving target: heading direction (ϕ), bearing direction of the moving target (ψ_m), distance of the moving target (d_m), and target-heading angle ($\beta = \phi - \psi_m$).

Figure 2. The target visibility conditions, as viewed from a distance of 3 m.

that acts to null change in the target's bearing direction, a damping term $b\dot{\phi}$ that prevents oscillation in the heading direction, and a distance term ($d_m + c$, where $c = 1$) that compensates for the decrease in the angular speed of a moving target with distance.

In contrast, it has been proposed that both manual and locomotor interception are controlled by internal world models. For example, Lacquaniti and colleagues argued that an internal model of Earth's gravity is used to guide manual interception of falling bodies (Lacquaniti & Maioli, 1989; Mcintyre, Zago, Berthoz, & Lacquaniti, 2001), while Hayhoe and colleagues proposed that an internal model of an object's dynamic properties (e.g., a ball's elasticity) guides predictive eye movements in manual interception (Diaz, Cooper, & Hayhoe, 2013; Diaz, Cooper, Rothkopf, & Hayhoe, 2013; Hayhoe, McKinney, Chajka, & Pelz, 2012; Hayhoe, Mennie, Sullivan, & Gorgos, 2005).

In the case of locomotion, Diaz, Phillips, and Fajen (2009) suggested that a model of an object's speed profile and path can guide interception. They asked participants to intercept a moving ball displayed on a large screen, using a foot pedal to control their simulated speed on a straight path. When the target moved on a linear path and usually accelerated in the midst of a trial, participants learned to accelerate before the target actually changed its speed, contrary to CBS. When the target moved on a concave path, participants accelerated early and then decelerated later in a trial, consistent with CBS. But they also accelerated early for targets on convex path, contrary to CBS. To fit this data, Diaz et al. (2009) suggested a control model that combines CBS with a short-term prediction of the target's future position and speed. Specifically, by assuming "perfect knowledge of both the controller dynamics and the target's behavior from t to $t + \Delta t$," (p. 354), the model predicts the target's motion at time Δt in the future, and nulls change in the target's bearing direction at that point. By varying Δt

to fit the data, they found the best value of Δt was 0.5–1.0 s. This implies that an accurate internal model of the target's motion could play a role in locomotor interception, in combination with CBS. However, the participants missed the target on nearly half the trials, casting doubt on a perfect internal model. The authors concluded that participants may have learned a mapping from a desired future constant bearing state at time $t + \Delta t$ to the required velocity adjustment at time t, closer to what we could call a heuristic strategy (Zhao & Warren, 2015).

In the present study, we examine locomotor interception in an open environment, where participants primarily control their heading direction while walking at a preferred speed. We tested the role of current information in interception by degrading the visibility of the target. By manipulating the level of target blur, we sought to influence the perceived speed and position of the target. This allowed us to test qualitative predictions of on-line and model-based control strategies in interception performance, and to probe a range of hypothetical internal models.

There is evidence that reducing a target's spatial frequency yields a decrease in perceived speed (Brooks, Morris, & Thompson, 2011; Diener, Wist, Diehgans, & Brandt, 1976; Smith & Edgar, 1990). Similarly, it has been reported that reducing the chromatic contrast of the target in a near-equiluminant display also reduces perceived target speed (Cavanagh, Tyler, & Favreau, 1984; Lu, Lemes, & Sperling, 1999). We thus manipulated target visibility by progressively blurring a green bar on a gray background as it passed behind a virtual gray occluder, using a function that simultaneously reduced its spatial frequency and its chromatic contrast, while leaving its luminance contrast close to zero. This operation yielded a target with a Gaussian saturation profile at six levels of visibility (see Figure 2). As the degree of blur increased, we thus expected that the perceived speed of the target behind the occluder
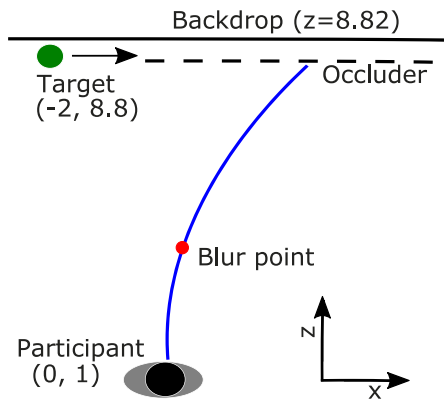
Figure 3. A top-down view of the experimental scenario. The green target appears, moves at a constant speed in front of a gray backdrop, and passes behind a virtual occluder (dashed line). The participant's path is indicated by the blue curve, and the red dot indicates their position when the target moves behind the occluder and is blurred; note that steering adjustments continue after the blur point.
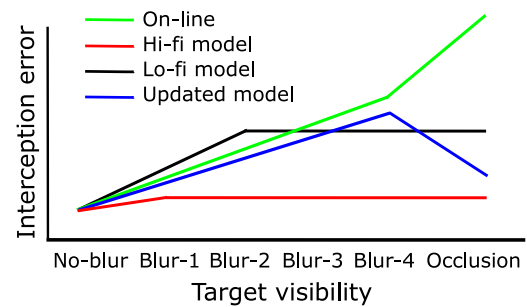

Figure 4. Four predictions about constant and variable interception error due to increasingly degraded target visibility: on-line control hypothesis (green), high-fidelity internal model (red), medium- or low-fidelity internal model (black), and continuously updated internal model (blue).

would decrease. We also anticipated that the target's positional uncertainty would increase with blur.

Each trial began with a fully visible target moving horizontally on the ground plane (refer to Figure 3). The target then appeared to move behind the translucent occluder (corresponding to the "blur point" in Figure 3). The participant's task was to walk to intercept the moving target. The initial conditions were such that the interception point was always behind the occluder; at slow target speeds the participant could turn onto a straight interception path before the target reached the occluder, but at high target speeds steering adjustments had to continue when the target was behind the occluder for interception to be successful.

According to the on-line control hypothesis, performance is dependent on current visual information about the target's bearing direction and its rate of change (i.e., target position and speed). This hypothesis predicts that as target blur increases, perceived speed will decrease, so the participant should turn too slowly and undershoot the interception point (interception error); if information is removed completely, performance should deteriorate further. These qualitative predictions are illustrated by the green curve in Figure 4.

To understand this prediction, first consider the possibility that the visual system recovers the target's speed in world coordinates. If the perceived distal speed is reduced with blur, the derived angular speed $\dot{\psi}_m$ will shift to lower values, including its null point (the perceived constant bearing). This would yield an inadequate turning response ($\ddot{\phi}$) according to Equation 1, resulting in undershooting.

Now consider the possibility that the visual system detects the target's proximal angular speed ($\dot{\psi}_m$) per se, and attempts to null its value according to Equation 1.

This situation is more subtle. If the participant initially lags behind the interception path, blurring the target will decrease the perceived $\dot{\psi}_m$, yielding a turning response ($\ddot{\phi}$) that is too low to catch up to the target, resulting in undershooting. If the participant initially leads the interception path, target blur will similarly decrease the perceived $\dot{\psi}_m$ and yield a low turning response back to the target, which in this case results in overshooting. Thus, constant interception error should increase with target blur, although the sign of the error will depend on initial conditions. If the angular speed can be exactly nulled however (a constant bearing), then interception should be accurate.

Finally, as the target's blur increases, so should uncertainty about its position (bearing direction ψ_m) and hence about whether $\dot{\psi}_m$ has been nulled, yielding an increase in variable error. In sum, the on-line hypothesis predicts that both constant and variable interception error should increase with target blur, with the greatest error when the target is completely occluded.

According to the model-based control hypothesis, an internal model of target motion is formed when the target is fully visible, and continues to mimic target motion and guide interception for some time after visual input is degraded or completely occluded. Unfortunately, the properties of such internal models are not well-specified in the literature, so it is difficult to operationalize the accuracy, duration, and decay rate of an internal model in order to make predictions about interception error. Consequently, we will consider a rather wide range of hypothetical internal models; the empirical results may allow us to distinguish among them.

First, at one end of the range, a high-fidelity internal model would be a highly accurate model that persists for some seconds after target occlusion. Although such a model could be considered a straw man, we deploy it to anchor the range of logically possible performance. A high-fidelity model would enable successful inter-

ception at a high level of performance after the target becomes blurred (red curve in Figure 4). This hypothesis assumes that the internal model is decoupled from the input when the information is degraded, so performance would not be impaired by the target blur, although performance would likely decay somewhat due to internal noise (e.g., the slight slope in the red curve in Figure 4). In addition, because the purpose of an internal model is to mimic the target's motion behind the occluder, adaptive steering adjustments would be expected to occur after the blur point.

Second, a medium- or low-fidelity model predicts that interception error should increase as visibility is degraded until it plateaus at some level (black curve in Figure 4). This hypothesis also assumes that the internal model is decoupled from the input when the quality of current information drops below that of the internal model. Thus, the interception error at the plateau would provide an estimate of the internal model's fidelity. At higher blur levels, adaptive steering adjustments would also be expected after the target goes behind the occluder.

Finally, an internal model may be continuously updated by the current visual input, regardless of the quality of information. Therefore, even though a high-fidelity model might be created when the target is clearly visible, after the target is blurred the model would be updated based on degraded information. This would lead to interception error that increases with target blur, much like the on-line control prediction, because both hypotheses depend on current visual input. If the target is completely occluded, however, the initial internal model would persist, so interception performance should rebound in the occlusion condition (blue curve in Figure 4) and adaptive steering adjustments should occur after occlusion. The interception error in the occlusion condition would thus provide an estimate of the fidelity of the internal model.

We tested these predictions in a locomotor interception task by manipulating target visibility and target speed, and measuring steering adjustments and final interception error. The results indicate that interception is strongly dependent on current visual information and deteriorates qualitatively with total occlusion, consistent with on-line control.

Methods

Participants

Ten volunteers (five females, five males) participated in this experiment. Their ages ranged from 20 to 29 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 after the experiment. Brown University's Institutional Review Board approved the research protocol.

Apparatus

The experiment was carried out in the Virtual Environment Navigation Lab (VENLab) at Brown University. Participants walked freely in a 12- × 12-m tracking area while viewing a virtual environment in a wireless 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 with 100% binocular overlap. 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 recorded and used to update the display with a latency of approximately 50 ms.

Displays

The virtual environment consisted of a ground plane (50 m^2) mapped with a random noise texture of grayscale squares and a black sky, with several vertical objects resting on the ground plane. The home pole was a blue granite-textured cylinder, 3.0-m tall with a radius of 0.2 m, located at the origin of the coordinate system ($x = 0$ m, $z = 0$ m); the orientation pole was a red granite-textured cylinder, 1.8-m tall with a radius of 0.2 m, at location ($x = 0$ m, $z = 5$ m); and the target was a green two-dimensional bar, 2.0-m tall and 0.2 m wide, that appeared at location ($x = -2.0$ m, $z = 8.80$ m; refer to Figure 3). The target moved rightward, on a path parallel to the x-axis. These initial conditions were mirrored left/right, and the data were collapsed. The target moved parallel to a vertical backdrop, a gray patch (400-m wide × 200-m tall) located 2 cm behind the target's path (at $z = 8.82$ m). After 2.5 s, the target arrived at the virtual occluder and was progressively blurred so that it appeared to be dynamically occluded by a translucent gray screen of varying opacity. The appearance of an occluder was actually created by manipulating the transparency of the target against the gray backdrop, and was otherwise invisible.

There were six levels of target visibility (see Figure 2). In the no-blur condition, the rectangular bar (0.2-m wide) remained fully visible, with no occlusion. In the

Blur-1 to Blur-4 conditions, the bar was progressively blurred in the horizontal (x_t) direction as it passed behind the occluder. In the occlusion condition, the bar was completely deleted by the occluder. To create different levels of blur, we used the OpenGL Shading Language to manipulate the target's width ($w_t = 0.4$, 0.6, 0.8, 1.0 m) and alpha value (α). The alpha value determined the transparency of the target against the gray backdrop, and ranged from 1 (completely opaque, no-blur condition) to 0 (completely transparent, occlusion condition). Specifically, α was computed as a normalized Gaussian function of horizontal position x_t that depended on target width w_t:

$$\alpha(x_t) = \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{1}{2}\left(\frac{x_t - c_t}{\sigma}\right)^2} \quad (2)$$

$$\sigma = \frac{w_t}{6} \quad (3)$$

where $x_t = 0$ m is the left edge of the target and c_t is the target's center (e.g., $c_t = 0.2$ m for the target width of 0.4 m). Thus, each target appeared increasingly transparent from its center to its left/right edges, and wider targets appeared more transparent overall.

We measured the chromaticity and luminance of the target and background (occluder over sky) with a colorimeter (Cambridge ColorCal MKII, Kent, UK), in CIE 1931 coordinates. The (Weber) chromatic contrast for parameter y was 0.51 in the no-blur condition, 0.14, 0.10, 0.07, 0.05 in the Blur-1 to Blur-4 conditions, and 0.00 in the occlusion condition. On the other hand, the chromatic contrast for parameter x was −0.12 in the no-blur condition, and between 0.01 and 0 in all other conditions. The luminance contrast between the target and the background was −0.15 in the no-blur condition, 0.02, 0.03, 0.03, 0.06 in the Blur-1 to Blur-4 conditions, and 0.02 in the occlusion condition. Thus, the target and background had nearly the same luminance in all blur conditions, but their y chromatic contrast decreased with blur.

Design and procedure

Three target speeds (0.6, 0.8, or 1.0 m/s) were crossed with the six levels of visibility (no-blur, Blur-1–Blur-4, and occlusion), yielding a 3 (Speed) × 6 (Visibility) factorial design with a total of 18 conditions.

At the beginning of an experimental session, the HMD was set up and interocular distance was calibrated for the participant according to the procedure described in Fajen and Warren (2003). This was followed by 12 practice trials, two in each visibility condition with randomly assigned target speeds. The participant then performed 144 test trials, with eight repetitions in each of the 18 conditions. The order of

trials was randomized for each participant. An experimental session lasted about 1 hr.

The participant's task was to walk to intercept the moving target, without running. Participants were instructed that the target would be blurred or totally occluded on some trials, in which case they were to intercept the target as if it were fully visible. All instructions were prerecorded and delivered over headphones.

At the beginning of each trial, the home pole and orientation pole appeared. To establish the initial conditions, the participant was instructed to walk to and stand at the home pole, facing the orientation pole (5-m away). After 1.5 s, the orientation pole turned yellow and the participant walked straight toward it. After the participant walked 0.5 m, the home and orientation poles disappeared; after another 0.5 m, the target appeared (7.8-m ahead and 2.0 m to the left or right) and immediately started moving. When the participant arrived 0.4 m from the target's path (i.e., at a z value of 8.40 m), the target disappeared and the trial ended; the next trial began right away with the reappearance of the home and orientation poles.

The time series of head position was recorded by the tracking system. The x position at the end of the trial was taken to be the interception point; if the participant was on a direct interception path, the final x position would be very close to that of the target. Constant error was computed as the distance in x between the interception point and the midpoint of the target at the end of the trial; positive values indicate overshooting and negative values undershooting. The variable error was the mean of the within-subject standard deviation of constant errors in each condition. Before computing measures of the participant's path, we first filtered the time series of x and z position in each trial using a forward and backward fourth-order low-pass Butterworth filter with a cutoff frequency of 0.6 Hz, to reduce the effects of tracker noise and gait oscillation. Mean walking speed was computed by multiplying the displacement (in meters) on successive frames by 60, the number of frames recorded per second. Heading direction (ϕ) was computed with reference to the x-axis in each frame according to the following equation:

$$\phi_i = \operatorname{arc\,cot}\left(\frac{x_i - x_{i-1}}{z_i - z_{i-1}}\right) \quad (4)$$

where x_i and z_i are the head coordinates on the ith frame.

Results

Sample interception paths appear in Figure 5 for the no-blur (black traces) and occlusion (red traces)
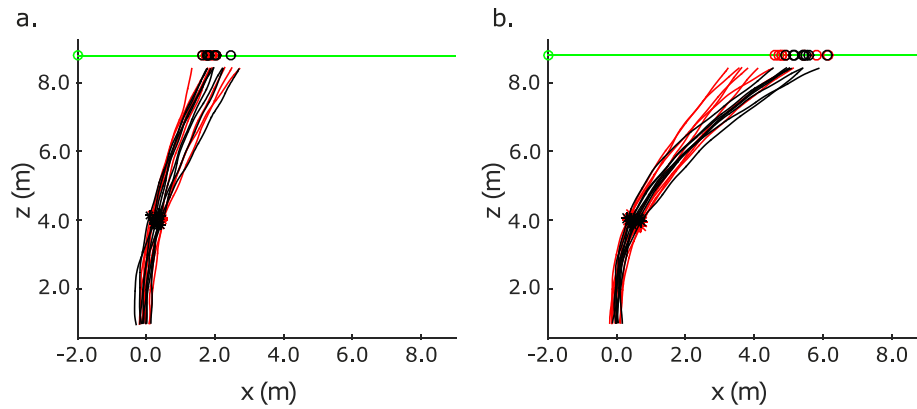
Figure 5. Sample interception paths from one participant, from no-blur (black traces) and occlusion (red traces) conditions, for target speeds of (a) 0.6 m/s and (b) 1.0 m/s. Black circles represent the target's final position in the no-blur condition, and red circles the same in the occlusion condition. Green circles and lines represent the target's starting position and path. Asterisks on participant paths indicate the blur point when the target went behind the occluder.

conditions. Note that participants turned onto an interception path before the slow target reached the occluder (Figure 5a), whereas they undershot the fast target in the occlusion condition (Figure 5b).

Constant error

The mean constant error in each condition appears in Figure 6a. At the slow target speed (0.6 m/s), constant errors were close to zero across levels of target visibility, indicating quite accurate interception. Evidently, participants had time to make an initial turn onto a straight interception path, and hence null change in the bearing direction, before the target reached the occluder (the blur point, asterisks in Figure 5a). At faster target speeds (0.8 and 1.0 m/s), however, constant errors were increasingly negative and exhibited more undershooting with greater blur. A two-way repeated-measures analysis of variance (ANOVA) indicated main effects of target speed, $F(2, 18) = 68.82$, $p < 0.01$, $\eta_p^2 = 0.88$; target visibility, $F(5, 45) = 9.70$, $p < 0.01$, $\eta_p^2 = 0.52$; and a significant interaction, $F(10, 90) = 28.14$, $p < 0.01$, $\eta_p^2 = 0.76$. The follow-up simple effect tests (with Sidak adjustment) revealed a main effect of target visibility in both the 0.8 m/s condition, $F(5, 5) = 6.97$, $p < 0.05$, and the 1.0 m/s condition, $F(5, 5) = 6.73$, $p < 0.05$, but not the 0.6 m/s condition, $F(5, 5) = 1.72$, $p = 0.28$. Thus, for the faster targets, undershooting increased monotonically as target visibility was degraded, with a large jump in the full occlusion condition. This finding is consistent with the expectation that reducing the target's spatial frequency and chromatic contrast would reduce perceived target speed.
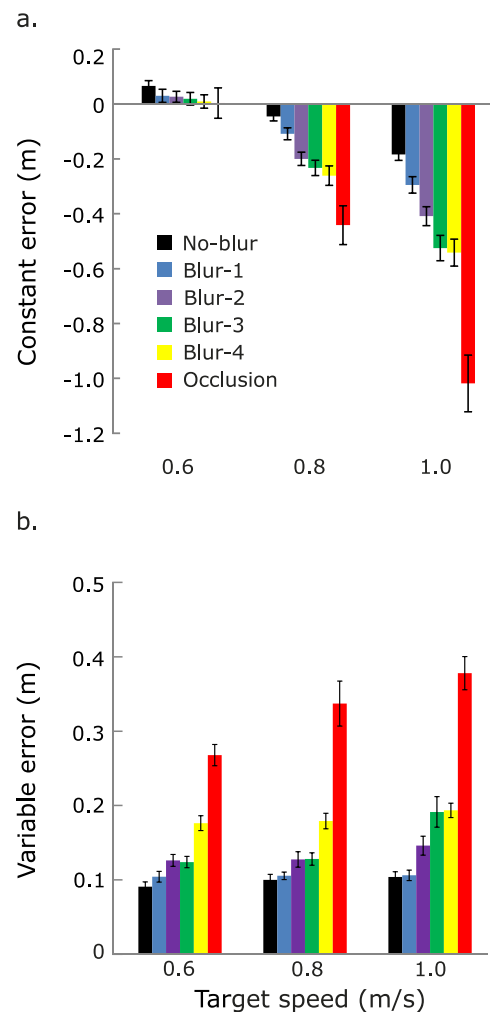

Figure 6. (a) Constant error and (b) variable error of interception in each experimental condition. Error bars represent the SE.

Variable error

The mean variable error in each condition is presented in Figure 6b. Variable error increased with target blur at all target speeds, indicating greater variability in the interception point as target visibility was degraded, with a large jump in the full occlusion condition. A two-way repeated-measures ANOVA indicated main effects of target speed, $F(2, 18) = 3.69$, $p < 0.05$, $\eta_p^2 = 0.29$, and target visibility, $F(5, 45) = 40.36$, $p < 0.01$, $\eta_p^2 = 0.82$, but no interaction, $F(10, 90) = 1.39$, $p = 0.19$, $\eta_p^2 = 0.13$. This finding is consistent with the expectation that increasing target blur would increase positional uncertainty.

Final position, walking speed, and interception duration

To check that participants were responding differentially to the three target speeds and not simply taking similar paths on every trial, we analyzed the participant's final x position at the end of the trial, or interception point. The mean final x position in each condition appears in Figure 7a. A two-way repeated-measures ANOVA found main effects of target speed, $F(2, 18) = 237.37$, $p < 0.01$, $\eta_p^2 = 0.96$; target visibility, $F(5, 45) = 5.57$, $p < 0.01$, $\eta_p^2 = 0.38$; and a significant interaction, $F(10, 90) = 7.08$, $p < 0.01$, $\eta_p^2 = 0.44$. The main effect of speed confirms that participants turned farther to intercept faster targets, and that their responses were discriminable. The follow-up simple effect tests (with Sidak adjustment) showed a main effect of target visibility in the 0.8 m/s condition, $F(5, 5) = 5.21$, $p < 0.05$, but not in the two other speed conditions. This indicates that as visibility of the faster target was degraded participants tended to turn less in the direction of target motion, which contributed to the observed undershooting in this speed condition.

To examine the influence of target speed and visibility on walking speed, we measured the mean walking speed after the blur point (Figure 7b). A two-way repeated-measure ANOVA revealed main effects of target speed, $F(2, 18) = 81.39$, $p < 0.01$, $\eta_p^2 = 0.90$, and target visibility, $F(5, 45) = 11.33$, $p < 0.01$, $\eta_p^2 = 0.38$, as well as a significant interaction, $F(10, 90) = 4.81$, $p < 0.01$, $\eta_p^2 = 0.21$. The main effect of speed confirms that participants walked faster to intercept faster targets, again responding differentially. The follow-up simple effect tests (with Sidak adjustment) found a main effect of target visibility in the 1.0 m/s condition, $F(5, 5) = 11.75$, $p < 0.01$, but not in the two slower conditions. This finding indicates that participants walked more slowly as visibility of the faster target was degraded, which also contributed to the observed undershooting with the fast target.
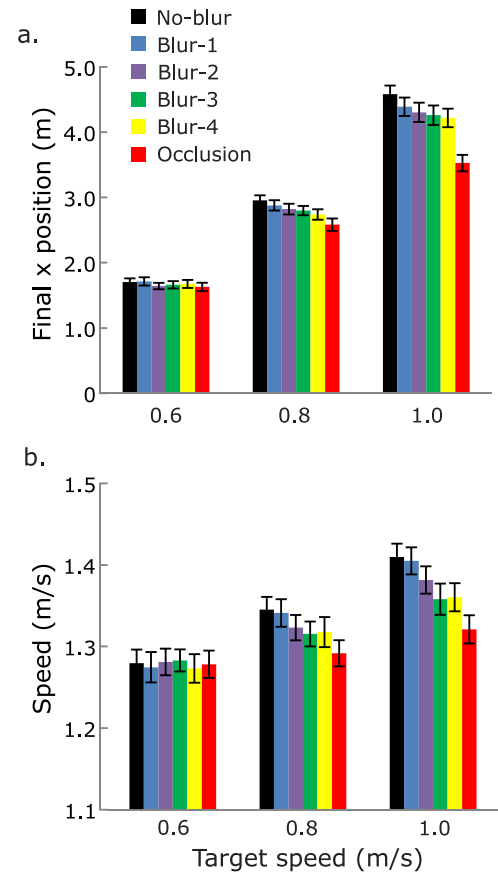

Figure 7. (a) Mean interception point (final x position) and (b) mean walking speed after the blur point in each experimental condition. Error bars represent the *SE*.

Mean interception duration was 6.09 s ($SD = 0.71$) for target speed 0.6 m/s; 6.28 s ($SD = 0.82$) for 0.8 m/s; and 6.72 s ($SD = 1.11$) for 1.0 m/s. Because the target was blurred 2.5 s after it appeared, the occluded portion of a trial ranged from 3.6 to 4.2 s. A two-way repeated-measure ANOVA revealed only a significant main effect of target speed on interception duration, $F(2, 18) = 27.84$, $p < 0.01$, $\eta_p^2 = 0.76$, with no significant main effect of target visibility, nor an interaction. When intercepting the more blurred target, participants tended to undershoot more and walked at relatively lower speed, which might have resulted in similar interception duration across target visibility.

Steering adjustments

To investigate the influence of target speed and visibility on steering adjustments to intercept the target, we measured the participant's turning rate ($\dot{\phi}$, change in heading direction) before and after target occlusion. We first determined whether viewing the target's initial motion for 2.5 s was enough for participants to respond differentially to the target speeds, by measuring the
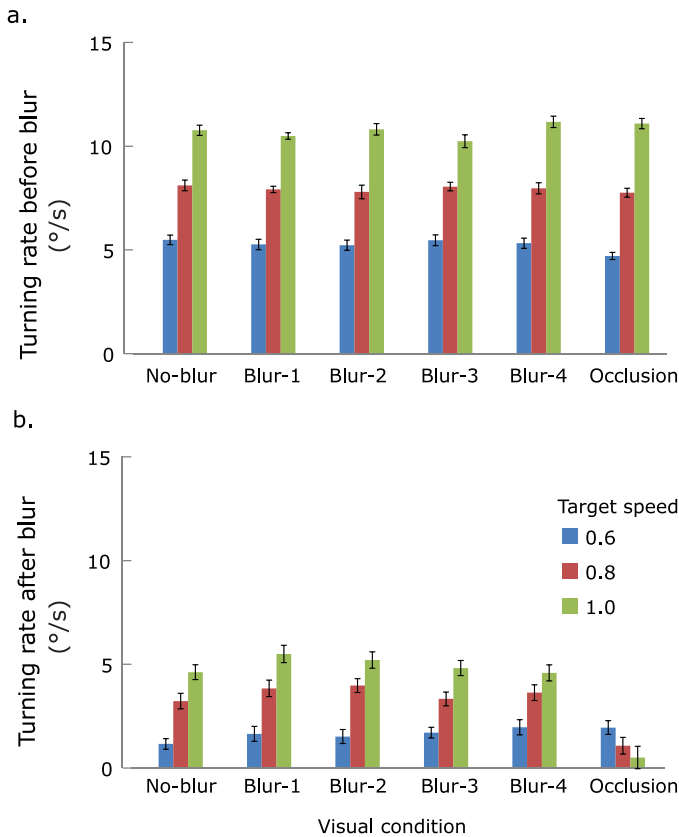
Figure 8. Turning rate before blur point (a) and after blur point (b). Positive values represent turning in the target movement direction. Error bars represent the *SE*.

mean turning rate before the blur point on each trial (Figure 8a). Participants turned more with faster targets in all visibility conditions. A two-way repeated-measures ANOVA found a main effect of target speed, $F(2, 18) = 431.49$, $p < 0.01$, $\eta_p^2 = 0.98$, but no effect of target visibility, $F(5, 45) = 0.58$, $p = 0.71$, $\eta_p^2 = 0.06$, nor an interaction, $F(10, 90) = 1.23$, $p = 0.29$, $\eta_p^2 = 0.12$. The results indicate that viewing the target for 2.5 s was sufficient for participants to distinguish the target speeds and adjust their heading adaptively.

Second, to determine whether participants also made adaptive steering adjustments when the target was behind the occluder, we measured the mean turning rate after the blur point on each trial (Figure 8b). Participants turned more with faster targets in the five blur conditions, but not in the full occlusion condition. A two-way repeated-measures ANOVA found main effects of target speed, $F(2, 18) = 56.39$, $p < 0.01$, $\eta_p^2 = 0.86$; target visibility, $F(5, 45) = 4.02$, $p < 0.01$, $\eta_p^2 = 0.31$; and a significant interaction, $F(10, 90) = 11.40$, $p < 0.01$, $\eta_p^2 = 0.56$. The follow-up simple effect tests (with Sidak adjustment) revealed a significant effect of target speed in each of the five blur conditions (all $ps < 0.01$), but not in the occlusion condition, $F(2, 8) = 2.00$, $p = 0.19$. The results indicate that participants adjusted their

heading direction after the blur point as long as the target was minimally visible. However, they did not make adaptive steering adjustments after the target was totally occluded, but continued to walk in approximately the same direction on a tangent path (Figure 5b).

Discussion

In the current study, we found that degrading target visibility impaired both the accuracy and precision of locomotor interception—that is, greater target blur led to more undershooting and higher variability in interception, while total occlusion resulted in qualitatively worse performance (constant errors up to −1.0 m and variable errors up to 0.4 m). Most revealing, participants did not make appropriate steering adjustments for higher target speeds after the target was completely occluded, but continued to walk in approximately the same direction.

These results show that interception is strongly dependent on current visual information. If interception were guided by an internal model of target motion that persists after information is degraded or withdrawn, error would either remain low (red curve in Figure 4) or plateau at a level that reflects the model's fidelity (black curve). On the contrary, we find that interception error increases monotonically as target visibility is reduced. This finding implies that interception is either controlled on-line (green curve) or guided by a continuously updated internal model (blue curve). But we also find that interception error jumps and steering adjustments cease in the full occlusion condition, contrary to a persisting internal model of target motion. These findings are consistent with on-line control.

The results bear on the issue of whether interception is actively controlled during full occlusion. Analysis of turning rate revealed that the majority of steering adjustments occurred before the blur point in all conditions, with faster targets yielding higher turning rates (Figure 8). After the blur point, participants continued to adjust their heading in accordance with the target's speed in all conditions except full occlusion (Figure 8b). This implies that, although the target's visibility was degraded, some visual information was still available, enabling participants to steer adaptively. However, when the target was completely occluded they failed to make adaptive adjustments and kept walking on an approximately straight tangent path. This behavior accounts for the greater undershooting of the faster targets (0.8 and 1.0 m/s) in the occlusion condition. The absence of adaptive adjustments during full occlusion indicates that behavior was not guided by

an internal model that simulated or predicted the target's motion behind the occluder.

On the other hand, participants accurately intercepted the slow target (0.6 m/s) regardless of its visibility, with little constant error. This result confirms that participants understood the task and walked to the center of the target even at the highest blur levels. A possible explanation for this level of accuracy is that interception of the slow target required smaller adjustments in walking direction and speed, so the participant could null the target's angular velocity before it reached the occluder. Specifically, the mean turning rate after the blur point was close to zero in all blur conditions (Figure 8b), demonstrating that participants nearly completed the turn onto an interception path before the blur point. Walking speed was also the lowest for the slow target, with a mean speed of 1.28 m/s, implying that interception did not demand a large increase from the preferred walking speed of about 1.2 m/s (see Fajen & Warren, 2003, about the preferred walking speed). These observations account for the interception accuracy with the slow target.

Thus, we find that, in general, removal of current visual information qualitatively impairs interception accuracy and precision. These results are consistent with previous research on blind walking (Farrell & Thomson, 1999; Thomson, 1983) and driving after information is withdrawn (Cloete & Wallis, 2009; Hildreth et al., 2000; Wallis et al., 2002; Wallis et al., 2007). In those studies, the environment was static and visual information was either clearly available or totally eliminated. Here we also tested intermediate levels of target visibility, and found that greater target blur led to increasingly impaired performance. The results indicate a strong dependence on current visual information in a dynamic environment, as expected by on-line control.

Previous studies of manual actions such as catching and reaching also investigated the effects of complete visual occlusion in a dynamic environment. Generally speaking, these studies indicate that performance can be maintained with very brief target occlusion, but longer durations of occlusion lead to significantly degraded performance (Bennett, Ashford, & Elliott, 2003; Bennett, Elliott, Weeks, & Keil, 2003; Elliott, Chua, & Pollock, 1994; Elliott, Pollock, Lyons, & Chua, 1995; Lyons, Fontaine, & Elliott, 1997; Sharp & Whiting, 1974; Whiting & Sharp, 1974). In addition, visual occlusion during catching leads to changes in movement patterns (Dessing, Oostwoud-Wijdenes, Peper, & Beek, 2009; Mazyn, Savelsbergh, Montagne, & Lenoir, 2007; Tijtgat, Bennett, Savelsbergh, De Clercq, & Lenoir, 2011). For example, when Mazyn et al. (2007) withdrew visual information at the onset of hand movement to catch an approaching ball, participants delayed movement initiation to keep the ball

visible longer, and compensated with a faster movement speed and a larger hand aperture. Such findings imply that actors depend heavily on current visual information and will adapt their movements to prolong it, consistent with on-line control.

A general problem with the model-based control hypothesis is that the scope and properties of internal world models are rather unconstrained and seldom well-specified. Without clearly defining the characteristics of an internal model, such as accuracy, duration, and decay rate, the hypothesis is not only untestable but verges on vacuous (Haselager, de Groot, & van Rappard, 2003). We thus posited a range of internal models of varying fidelity and attempted to evaluate them against interception performance.

To account for the present data, one might assume an internal model that is continuously updated by incoming information (regardless of its quality), and rapidly decays when the information is withdrawn. This kind of internal model is heavily dependent on current information. In normal circumstances with available information, on-line control (CBS) has proven sufficient to account for successful locomotor interception (e.g., Bastin et al., 2006; Fajen & Warren, 2004, 2007; Morice, Francois, Jacobs, & Montagne, 2010). Given Oscam's razor, this appears preferable to an account based on such an internal model, until empirical evidence can be offered to specify such a model. In the absence of current information, a simple mapping or heuristic may also be preferable (for a discussion, see Zhao & Warren, 2015).

In summary, degrading target visibility increasingly impaired interception accuracy and precision, while total occlusion abolished adaptive steering adjustments, leading to a qualitative increase in error. The results are inconsistent with an internal world model that guides behavior in the absence of input, and strongly imply that locomotor interception is normally controlled by current information, consistent with on-line control.

Keywords: locomotor interception, action control, on-line control, model-based control

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