Exp Brain Res
DOI 10.1007/s00221-008-1522-6

RESEARCH ARTICLE

Testing the role of expansion in the prospective control of locomotion

Julien Bastin · David M. Jacobs · Antoine H. P. Morice · Cathy Craig · Gilles Montagne

Received: 2 November 2006 / Accepted: 25 July 2008

Abstract The constant bearing angle (CBA) strategy is a prospective strategy that permits the interception of moving objects. The purpose of the present study is to test this strategy. Participants were asked to walk through a virtual environment and to change, if necessary, their walking speed so as to intercept approaching targets. The targets followed either a rectilinear or a curvilinear trajectory and target size was manipulated both within trials (target size was gradually changed during the trial in order to bias expansion) and between trials (targets of different sizes were used). The curvature manipulation had a large effect on the kinematics of walking, which is in agreement with the CBA strategy. The target size manipulations also affected the kinematics of walking. Although these effects of target size are not predicted by the CBA strategy, quantitative comparisons of observed kinematics and the kinematics predicted by the CBA strategy showed good fits. Furthermore, predictions based on the CBA strategy were deemed superior to predictions based on a required velocity (V_{REQ}) model. The role of target size and expansion in the prospective control of walking is discussed.

Keywords Constant bearing angle model · Interception · Curved target trajectories · Prospective control · Expansion pattern

J. Bastin · D. M. Jacobs · A. H. P. Morice · C. Craig ·
G. Montagne (✉)
Faculté des Sciences du Sport,
Institut des Sciences du Mouvement, Etienne-Jules MAREY,
UMR 6233 Université de la Méditerranée and CNRS,
163 Avenue de Luminy, 13009 Marseille, France
e-mail: gilles.montagne@univmed.fr

J. Bastin
UFR STAPS Grenoble Université Joseph Fourier,
Grenoble, France

D. M. Jacobs
Facultad de Psicología,
Universidad Autonoma de Madrid, Madrid, Spain

C. Craig
School of Psychology, Queen's University, Belfast, UK

Introduction

Humans and animals often show high levels of performance in apparently complex perceptual-motor tasks. Consider the example of walking through a crowded environment toward a moving person. How does the perceptual-motor system cope with demanding requirements such as multiple collision avoidance and goal achievement? Several studies have addressed the control of heading tasks (e.g., Rushton et al. 1998; Fajen and Warren 2003; Wilkie and Wann 2005) and interceptive tasks (e.g., Chardenon et al. 2004; Fajen and Warren 2004; Michaels and Oudejans, 1992; McLeod et al. 2006). These studies have led to the formalization of control laws that explicitly relate informational variables to action parameters, offering in this way a framework to study perceptual-motor behavior.

A particularly interesting control law is the constant bearing angle (CBA) strategy. A bearing angle is the angle between the direction of motion of an observer and the line between the observer and a moving target. The CBA strategy holds that in order to intercept moving targets, observers adapt their forward speed so as to keep the bearing angle constant. One of the reasons that make the CBA strategy interesting is its apparent generality. Animal studies, for instance, indicate that fishes (Lanchester and Mark 1975; Rossel et al. 2002), dragonflies (Olberg et al.

2000), and bats (Ghose et al. 2006) use the strategy to intercept prey. Likewise, dogs seem to use the strategy to intercept Frisbees (Shaffer et al. 2004) and houseflies to chase other houseflies (Land and Collett 1974). Thus, the CBA strategy could act as a perceptual-motor principle relevant over a wide range of situations, but also for different species.

The present study investigates the use of the CBA strategy by human observers. Observers were asked to walk along a straight trajectory through a virtual environment and to adjust their walking speed in order to intercept approaching targets (see Fig. 1). The targets should be intercepted when they cross the participants' path of locomotion, which was indicated by a visible axis (i.e., the displacement axis). Support for the use of the CBA strategy in a similar virtual-reality environment has been reported by Chardenon et al. (2002) (see also Lenoir et al. 1999). As predicted by the CBA strategy, participants successfully intercepted targets under various changes in task constraints, including target speed, angle of approach and target trajectory (cf., Chardenon et al. 2005; Bastin et al. 2006b; Lenoir et al. 2002). Further support for the CBA strategy has been reported by Bastin et al. (2006b), who showed that the curvature of target paths affects the walking kinematics, as predicted by the CBA strategy. The use of virtual reality has shown that several perceptual variables, including proprioceptive ones, provide redundant perceptual degrees of freedom involved in the detection of the bearing angle (Chardenon et al. 2004; Bastin and Montagne 2005; Bastin et al. 2006a). Finally, the CBA strategy has been shown to operate equally well in more natural situations (e.g., in field studies; Lenoir et al. 2002).

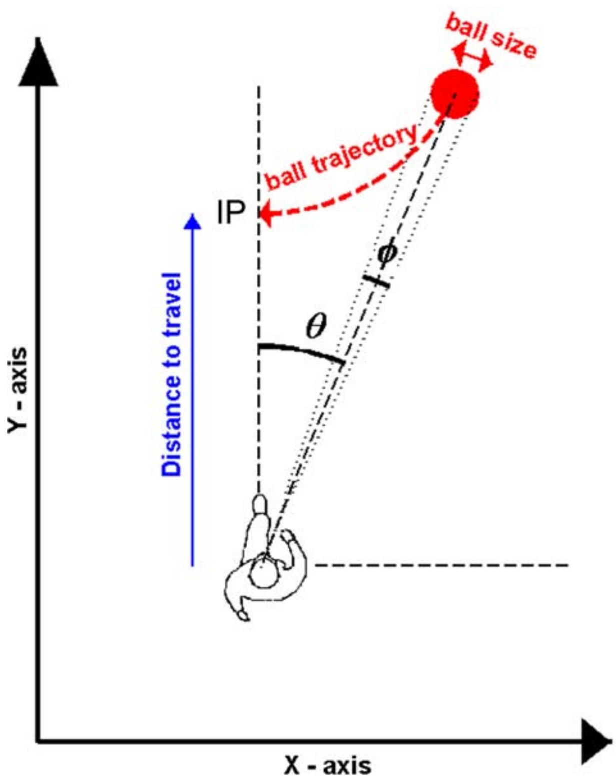


Fig. 1 Bird's-eye view of the experimental layout. Participants walked on a rectilinear path and aimed to intercept balls that travelled toward the interception point (IP). Optical angles of interest are the bearing angle, θ, and the angle subtended by the ball, ϕ

The present experiment is not concerned with the way in which the bearing angle is detected. It is nevertheless important to note that the bearing angle can be detected both through variables available in the optic flow (i.e., variables that require change in the ambient optic array) and through variables independent of the optic flow (i.e., variables that can also be defined for unchanging optic arrays). A flow variable that corresponds to the bearing angle is the angle between the focus of expansion and the optical direction of the target (e.g., Chardenon et al. 2004). Non-flow variables (both proprioceptive and visual) are available if the midline body axis is aligned with the direction of locomotion (as in the present study), in which case the bearing angle can be detected through the direction of the target in body-centered coordinates (Llewellyn 1971). Examples of empirical comparisons of flow and non-flow variables can be found in Rushton et al. (1998) and Warren et al. (2001).

The CBA strategy can be modeled by relating the participant's acceleration to the rate of change of the bearing angle, with a damping term allowing the system to match the required value smoothly and to avoid oscillations around the attractor state (Fajen and Warren 2003; Wann and Wilkie 2004; Bastin et al. 2006a, b:

$$\ddot{Y}(t) = k_1 \times \frac{1}{1 + 200 \times e^{-10\times t}} \dot{\theta}(t) + k_2 \times \dot{Y}(t) \qquad (1)$$

In this equation, $\dot{Y}$ and $\ddot{Y}$ are the participant's walking speed and acceleration, respectively, $\dot{\theta}$ is the rate of change of the bearing angle, k_1 is a parameter that modulates the strength of the coupling between the acceleration and the rate of change of the bearing angle, and k_2 is a parameter that modulates the strength of the damping term. The function $\frac{1}{1+200\times e^{-10\times t}}$ is an activation function, which is a function of time (t).

One of the characteristics of the CBA strategy is that it relies on a single optical component, namely, the rate of change in the bearing angle. This means that the current formulation of the CBA strategy predicts that the kinematics of interception should not be affected by other optical quantities, such as optical expansion. Testing the dependence of walking kinematics on manipulations of optical expansion therefore constitutes a critical test for the CBA strategy. This critical test is more relevant if one considers the potential generality of the CBA strategy on the one hand, and the general importance of optical expansion in the control of interceptive movements, which we address next, on the other hand.

Previous work on grasping, hitting and catching has demonstrated that optical expansion affects both the initiation of movements as well as the kinematics of the unfolding movements (Bootsma and van Wieringen 1990; Savelsbergh et al. 1991; Sun et al. 1992; Shankar and Ellard 2000; Michaels et al. 2001; Caljouw et al. 2004; Ellard 2004). The role of expansion has also been investigated in interceptive tasks that involve whole-body displacements. Fajen and Warren (2004), for example, showed that observers who navigate through a virtual-reality environment are able to intercept non-expanding moving targets (in their study a non-expanding post). This led them to conclude that expansion is not necessary for successful performance. Even though this result is of importance, biasing rather than removing expansion would be a more direct test of the role of expansion. Arguably, removing expansion forces participants to rely on informational variables that might still be available (e.g., the bearing angle). Biasing rather than removing expansion would allow the experimenter to test whether participants rely on expansion.

Chardenon et al. (2004) performed this kind of manipulation, in a virtual-reality set-up, in order to test if a CBA strategy was involved while intercepting a moving ball. In an over-expansion condition, the size of a simulated target (0.1 m diameter) was doubled during the approach (11 s duration), and in an under-expansion condition, the size of the simulated target was reduced by half during the approach. In a third condition, target size was not manipulated. The authors report a marginal effect of over-expansion on walking speed, most notably a slight increase during the last second of the interception task. It remains possible, however, that expansion manipulations of a larger magnitude, tested with a larger number of empirical conditions, do show important effects. The aim of the present study, then, is to determine to what extent the falsification of expansion affects the adjustments in walking speed made by participants in order to intercept targets. We also examine the effect of the curvature of the target trajectory on the regulation of behavior. Bastin et al. (2006b) showed that the changes in walking speed depend on the target trajectory curvature, inline with predictions that were made on the basis of the CBA strategy. Said differently, the present study should help us to understand how the CBA strategy and expansion cooperate as part of the control of goal directed displacements.

As a final test of the CBA strategy, we compare the fits obtained with Eq. 1 (the CBA strategy) with the fits obtained with a required velocity (V_{REQ}) model. The V_{REQ} model was originally proposed by Peper et al. (1994) to describe lateral hand movements in catching (cf. Bootsma et al. 1997; Montagne et al. 1999, 2000). The version of the model that we use is similar to the one described in Jacobs and Michaels (2006). However, we use the model to describe forward walking speed, whereas the above-mentioned studies used the model to describe lateral hand movements. The model, as applied to the case of forward walking speed, is described by the equation:

$$\ddot{Y} = c_1 \left(\frac{c_2 \dot{\theta}/\dot{\phi}}{\left(\dot{\phi}/\phi - \dot{\theta}/\theta\right)^{-1}} - \dot{Y} \right) \tag{2}$$

As in Eq. 1, $\dot{Y}$ and $\ddot{Y}$ are the speed and acceleration of the observer, ϕ is the angular size of the ball, and θ is the bearing angle (see also Fig. 1). The parameters c_1 and c_2 are calibration parameters. The compound variable $\dot{\theta}/\dot{\phi}$ is related to the distance from the observer at which the target will cross the displacement axis (cf., Michaels et al. 2006) and the compound variable $\left(\dot{\phi}/\phi - \dot{\theta}/\theta\right)^{-1}$ is related to the time at which the target will cross the displacement axis (cf., Bootsma and Peper 1992). This means that the ratio of these compound variables is related to the velocity required to reach the interception point at the same time as the target. Given that the model includes optical size (ϕ) and expansion ($\dot{\phi}$), we will compare a model that is sensitive to expansion manipulations (the V_{REQ} model) with a model that is not sensitive to expansion manipulations (the CBA strategy).

Method

Participants

Nine graduate students and faculty members (aged 26.8 ± 4.2 years) participated in the experiment on a voluntary basis. They all had normal or corrected-to-normal vision and their experience in target games varied. A local ethics committee approved the experimental protocol.

Apparatus and task

We used a virtual-reality set-up (see also de Rugy et al. 2000), where a virtual environment (generated with 2 PC Dell Workstations and projected with an Electrohome 7500 video projector) was coupled online to a treadmill (Gymrol, BRL 1800). The unidirectional treadmill used in the present study made displacements possible solely along a single direction; behavioral adaptations amount necessarily to displacement velocity changes. The visual scene was projected by a video-projector (whose refresh rate was set to 60 frames/s) onto a projection screen (2.3 m high × 3.0 m wide) 0.70 m in front of participants (providing a 118° × 130° field of view). Our virtual set-up allowed an end-to-end latency close to 30 ms. The treadmill was equipped with a 0.6 m wide and 1.80 m long moving belt that glided over a flat and rigid surface. The force that set the belt in motion was generated partly by the motor of the treadmill and partly by the participants. The part of the force that was generated by the treadmill was adjusted for each participant, before the experiment, so that the forces generated by the participant would result in a speed of the belt that was approximately equivalent to the speed that would have resulted if the same forces were generated by the participant while walking on a normal surface.

Participants were attached to the framework of the treadmill by means of a weight-lifting belt that was fixed to a rotating axis via a rigid rod on the back of the treadmill (Fig. 2). This construction allowed small vertical and sideward movements while participants walked on the treadmill. The speed of the treadmill, sampled with an optical encoder, was fed into a workstation that generated the simulated environment so that the changes in the visual scene were appropriate with regard to the walking speed. The visual scene (non-stereo images) was made up of a textured ground plane (bricks), a 0.1 m wide visual displacement axis, and a spherical moving target (Fig. 2). The ground plane was perfectly neutral and did not contain specific objects, making the future crossing distance of the target very difficult to anticipate.

Participants walked on a rectilinear path through the virtual environment and they were instructed to intercept the targets that travelled toward them obliquely. The targets, which moved at eye height, were to be intercepted at the moment at which they crossed the displacement axis. Participants were informed about the possible need to regulate their walking speed. The targets always crossed the displacement axis 5 s after their appearance. The position at which the target crossed this axis was controlled by varying the distance of the position at which the target started (target offset). Qualitative visual feedback was given after each trial. A green square was displayed after successful trials and a red square after unsuccessful trials. A trial was considered to be successful if the target would have made contact with the participant's head.

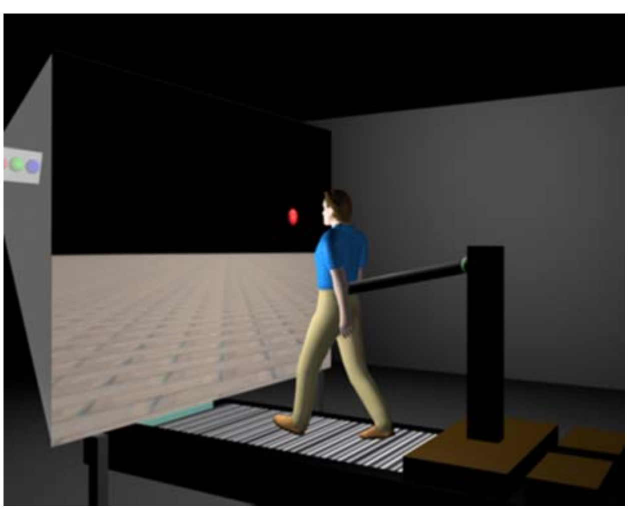


Fig. 2 Representation of the virtual reality set-up. Participants' walking speed on the treadmill was integrated and coupled to the projected visual scene, so that visual scene displacements were proportional to the participants' current speed

At the start of each trial, participants were required to stabilize their walking speed between 1.15 and 1.25 m s^{-1}. To help them to achieve this, a vertical white line of 0.2 m representing the current walking speed was shown within a rectangular zone representing a speed interval centered on 1.2 m s^{-1}. To satisfy the initial-speed requirement, the vertical line had to be kept within the prescribed rectangular zone. When the prescribed walking speed was maintained for at least 500 ms, the rectangle and vertical line disappeared and the trial began.

Independent variables

We manipulated the curvature of the target trajectory (3 levels), target size (2 levels), and optical expansion (3 levels). Three curvatures were used. The final positions of the targets were independent of this manipulation (Fig. 3). The target could move from the initial to the final position along trajectories with curvatures of 0.13, 0 and −0.13 m^{-1}. A curvature of 0 means that the target moved along a rectilinear path and a nonzero curvature means that the target moved along a segment of a circle with a radius of 1/curvature. Two target sizes were used: a small target (0.12 m diameter) and a large target (0.24 m diameter). The expansion of the moving targets was also manipulated (normal, over-, and under-expansion conditions). In the over- and under-expansion conditions, the target size was linearly increased or decreased during the trial so that the simulated target was either three times as big or three times as small at the end of the trial as compared to at the start of the trial (see Fig. 3).

Finally, three starting positions (target offsets) were used to vary the target arrival position along the displacement axis. These positions were computed on the basis of the participants' initial walking speed. If the participant had maintained his/her initial walking speed unchanged, the target would have crossed the axis of displacement 1 m in front of the participant (1 m condition), 1 meter behind the participant (−1 m condition), or coinciding with the location of the participant (0 m condition). Thus, these three different conditions forced the participant to produce

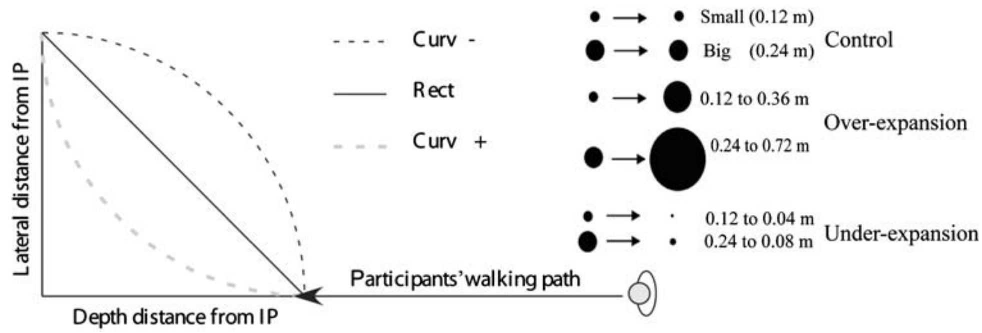


Fig. 3 Bird's-eye view of the task and the target trajectories (*left*) and a schematic representation of the size and expansion conditions (*right*). *IP* interception point, *Curv* − negative curvature, *Rect* rectilinear, *Curv* + positive curvature

different trajectories by accelerating, decelerating or maintaining a constant speed, respectively.

Procedure and design

The experiment consisted of 150 trials, of which 90 were experimental trials and 60 were control trials. The experimental trials were all performed in the 0 m target offset condition; we manipulated trajectory curvature (0.13, 0 and -0.13 m^{-1}), target size (0.12 and 0.24 m), and the expansion pattern (under expansion, no expansion and over expansion). These 18 experimental conditions were repeated five times each. The control trials were all performed with a fixed target size (0.12 m); we manipulated trajectory curvature (0.13, 0 and -0.13 m^{-1}) and target offset (+1 and −1 m). These six control conditions were repeated ten times each. The control trials were mixed with the experimental trials and the trial presentation was randomized. A training session consisting of 36 trials (3 target offsets × 3 curvatures × 4 repetitions) preceded the experiment to familiarize participants with the task. The whole experiment lasted approximately 45 min.

Data analysis

The analyses were based on the position-time series (sampled at 200 Hz) for each experimental trial of each participant. We used a forward and backward second order low-pass Butterworth filter with a cut off frequency of 10 Hz. The time series of these variables were averaged over intervals of 500 ms (i.e., corresponding approximately to one step; for a similar methodology, see Warren et al. 2001). All trials (successful or not) were used in the analyses, with data being synchronized at the moment at which the center of the target crossed the participants' axis of displacement. The analyses focused on the final spatial error and on the way the participant modified his/her walking speed over time. The final spatial error was calculated as the distance between the participant and the target's front edge at the moment at which the middle of the target crossed the displacement axis (i.e., at the end of the trial). The bearing angle was computed as the angle between the direction of locomotion and the line from the eye to the center of the target.[1]

The online modifications of walking speed were analyzed both with the CBA and V_{REQ} strategies. More specifically, we examined the quantitative fit between the data and the predictions of the concerned models (Eqs. 1, 2). To generate the predictions of the walking kinematics, both equations were solved for each trial of each participant using a Runge–Kutta procedure. The predictions were different for different trials, depending on the initial position and speed of the participant and on the experimental conditions concerning the trajectory of the target. The predicted and observed walking kinematics were compared using the sum of squared errors. The best-fitting parameters (k_1 and k_2 for the CBA model and c_1 and c_2 for the V_{REQ} model) were determined for each participant by comparing 100 combinations of parameter values (for a similar procedure, see Michaels et al. 2006) for the whole set of experimental trials (90 trials for each participant). The parameters k_1 and k_2 varied from -0.1 to -0.01 in increments of 0.01. The parameter c_1 varied from 0.0005 to 0.02 in increments of 0.002. The parameter c_2 varied from 5 to 27.5 in increments of 2.5. After computing the best-fitting parameters, the goodness-of-fit was accessed with squared Pearson product–moment correlations. Statistics were performed on the Fisher z-transformations of these correlation coefficients.

In addition to the previous trial-by-trial analyses, we performed analyses on averaged data. We first ran the analyses on data averaged over the five repetitions of identical trials (individual level of analysis) to remove the intra-participant variability within the experimental conditions. We also used the data for each experimental condition, obtained by averaging over the five repetitions and over the nine participants (group level analysis), to see to what extent the model fit was better when both the intra-participant and the inter-participants variability was removed within each experimental condition.

[1] One could also use the front or back edge of the target to compute the bearing angle. However, the alternative ways to compute the bearing angle would lead to similar results.

We submitted the resulting dependent variables to analyses of variance with individual repeated measures (ANOVA). In the case that the sphericity assumption was violated (using Mauchly's test), Huynh-Feldt adjustments of the *P* values are reported. The partial[2] effect size (η^2) is reported and post hoc comparisons were conducted with Tukey's HSD test.

Predictions

If participants rely on a CBA strategy, specific predictions can be made. Let us consider these predictions in the 0 m offset condition. Remember that no changes in walking speed are required in this condition. However, when the curvature of the target trajectory is positive, a constant walking speed would give rise to a decrease in bearing angle, and thus to a negative rate of change. A CBA strategy would therefore predict a corresponding increase in walking speed. This increase in walking speed, in turn, would result in an increase in bearing angle in the second part of the trial, which would go together with a decrease in walking speed in this second part of the trial. Following the same logic, the changes in walking speed produced in the negative curvature condition should mirror those exhibited in the positive curvature conditions. Finally, when the target path is rectilinear, a constant walking speed would lead to a constant bearing angle and, hence, the walking speed should remain unchanged.

The use of the CBA strategy also leads to specific predictions with regard to the manipulations of target size and expansion pattern; given that these manipulations are unrelated to bearing angle, they should not affect walking speed. Thus, if the CBA strategy is a general perceptual-motor principle, walking speed should not be affected, or be affected only minimally, by our manipulations of expansion pattern and target size. However, if an information variable based on target size or expansion interferes with the CBA strategy, further predictions can be made. A larger optical size or a larger optical expansion might be related to a nearer or faster approaching target, and thus lead to a decrease in walking speed. Likewise, a smaller optical size and a smaller optical expansion might go together with an increase in walking speed. Note that these qualitative predictions will be tested in addition to quantitative predictions based on the Eqs. 1 and 2.

[2] Partial η^2 have the advantage of being independent of the other effects involved and is considered as an alternative computation of the absolute eta square (Tabachnick and Fidell 1989). However, please note that partial η^2 values are not additive.

Results

Performance and final spatial error

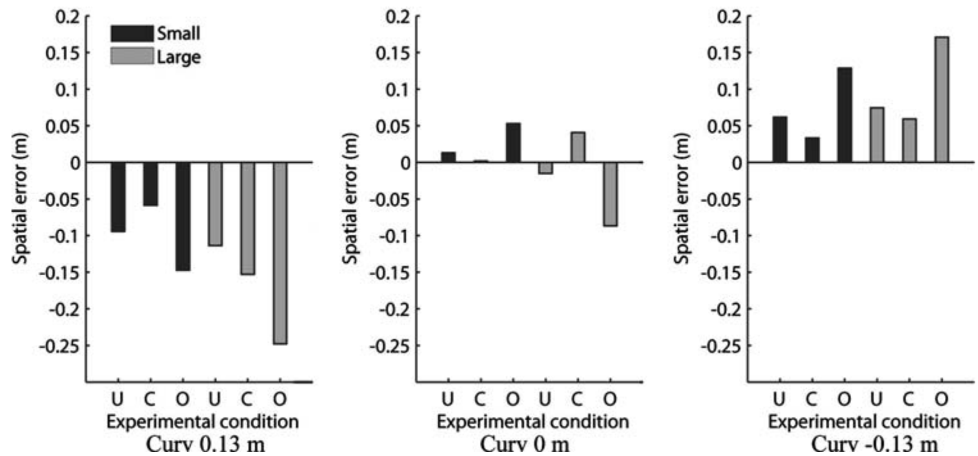
Participants were able to perform the task with a reasonable level of accuracy; their head would have contacted the ball in 64.3% (±32.5%) of the trials. Overall, the target's front edge passed very slightly behind the participants; the average signed spatial error was −1.55 cm. A three-way repeated measures analysis of variance with the factors trajectory curvature, target size, and expansion pattern was applied on the signed spatial error (see also Fig. 4). The analysis showed a significant main effect of curvature ($F_{(2,16)} = 12.3$, $P < 0.01$, $\eta^2 = 0.61$). *A posteriori* comparisons showed that participants walked farther and hence showed significantly more negative errors in the positive curvature condition as compared to the rectilinear and negative curvature conditions ($P < 0.01$).

Walking speed

A 3 trajectory curvature × target size × 3 expansion pattern × 10 time intervals repeated measures analysis of variance, with walking speed as dependent variable, revealed significant main effects of Curvature ($F_{(2,16)} = 63.9$, $P < 0.05$, $\eta^2 = 0.89$), target size ($F_{(1,8)} = 5.7$, $P < 0.05$, $\eta^2 = 0.42$), and expansion pattern ($F_{(2,16)} = 12.8$, $P < 0.05$, $\eta^2 = 0.62$). A significant interaction was also revealed between curvature and time intervals ($F_{(18,144)} = 53.7$, $P < 0.05$, $\eta^2 = 0.87$). Post hoc analyses revealed the following points (see also Fig. 5). No significant changes in walking speed were found in the rectilinear condition. Conversely, a positive curvature gave rise to a significant ($P < 0.01$) increase in walking speed from 2.5 to 3 s before the target crossed the participants' displacement axis and also a significant ($P < 0.01$) decrease in the last second of the trial. The results obtained with a negative curvature are the exact opposite of those obtained with a positive curvature. Taken together these results reveal that distinct walking-speed profiles were observed according to the target trajectory curvature. The analyses also revealed that the overall walking speed was significantly lower with a large target than with a small target (1.17 vs. 1.18 m s^{-1}). Finally, the overall walking speed was lower in the over-expansion condition (1.15 m s^{-1}) than in both the normal and the under-expansion conditions (1.18 and 1.19 m s^{-1}).

Let us tentatively try to compare the size of the effects of curvature, target size, and expansion pattern. Note, in this regard that the speed curves shown in Fig. 5 are very different for the positive and negative curvature conditions (i.e., for the curves in the upper and lower panels, respectively). In comparison, the differences appear to be

Fig. 4 Mean spatial error (m) as a function of target trajectory conditions and target size conditions (small and large target). The *left* panel presents data for the positive curvature condition (Curv 0.13 m), the *middle* one for the rectilinear condition (Curv 0 m), and the *right* one for the negative curvature condition (Curv −0.13 m). *U* under-expansion condition, *C* control condition, *O* over-expansion condition



smaller for the different target sizes (i.e., for the curves in the left and right panels, respectively) and for the under and over-expansion conditions (i.e., for the curves marked with plus signs and squares, respectively). To affirm this, we calculated the average differences between the walking speeds in the different conditions, which correspond to the distance between the respective curves in Fig. 5. This average difference was 0.36 m s^{-1} for the positive and negative curvature conditions, which is significantly ($P < 0.01$) larger than the difference of 0.01 m s^{-1} observed with regard to the large and small targets, and the difference of 0.04 m s^{-1} observed with regard to the under and over-expansion conditions.

Bearing angle

In the previous analyses we analyzed walking speed and concluded that both the path curvature and the target size and expansion affect performance, although the effects of size and expansion seemed to be relatively small. We will now further support this conclusion with analyses on the time-evolution of the bearing angle. Remember that the CBA model holds that the bearing angle, θ, is kept constant, which is to say, that $\dot{\theta}$ is kept close to zero. Qualitative analyses revealed that $\dot{\theta}$ indeed remained close to zero for the zero-curvature condition and that $\dot{\theta}$ converged from about −3.5 and 3.5° s^{-1} to 0° s^{-1} during trials in the −0.13 and +0.13 m^{-1} curvature conditions, respectively. To further analyze this we performed a 3 curvature × 6 size-expansion × 9 time interval repeated measures analysis of variance on the individual mean values of $\dot{\theta}$.[3] All main effects were significant; $F_{(2,16)} = 14.1, P < 0.05, \eta^2 = 0.64$, for curvature, $F_{(5,40)} = 2.5$, $P < 0.05$, $\eta^2 = 0.24$, for size-expansion, and $F_{(8,64)} = 10.9, P < 0.05, \eta^2 = 0.58$, for time interval. Moreover, a significant interaction was found between the effects of curvature and time interval, $F_{(16,128)} = 40.4$, $P < 0.05$, $\eta^2 = 0.84$. The other interactions did not reach significance. Again, the significant effect of size and expansion is inconsistent with the CBA strategy. This makes the comparison of the quantitative predictions of the CBA and V_{REQ} models all the more interesting.

[3] The nine time-intervals correspond to the first 4.5 seconds of each trial. The tenth time-interval of the 5-second trials was excluded because it showed large and apparently uninteresting variation.

Behavioral strategy

Contrasting CBA and V_{REQ} predictions

We now address how well the different models predict the observed movement kinematics. Remember that we analyzed the results at three levels: the trial level (movement data without averaging), the individual level (movement data averaged over the five repetitions per individual), and the group level (movement data averaged over repetitions and individuals). Table 1 shows the correlations between the predicted and observed movement kinematics for the two models and for the different experimental conditions and levels of analysis. Note first that for the CBA model, the average squared correlations are 0.47, 0.59 and 0.72, respectively, for analyses at the trial level, the individual level, and the group level. For the V_{REQ} model, these squared correlations are 0.42, 0.48 and 0.60. This seems to indicate two trends. First and as expected, the more variation is averaged out at a level of analysis, the higher the correlations. Second and more interesting, the CBA model seems to explain more variance than the V_{REQ} model at all levels of analysis.

To further investigate and test these results we performed a repeated measures analysis of variance with the factors Model (CBA and V_{REQ}) and size-expansion (6 levels) on the squared correlations between predicted and observed kinematics at the individual level. Both main effects and the

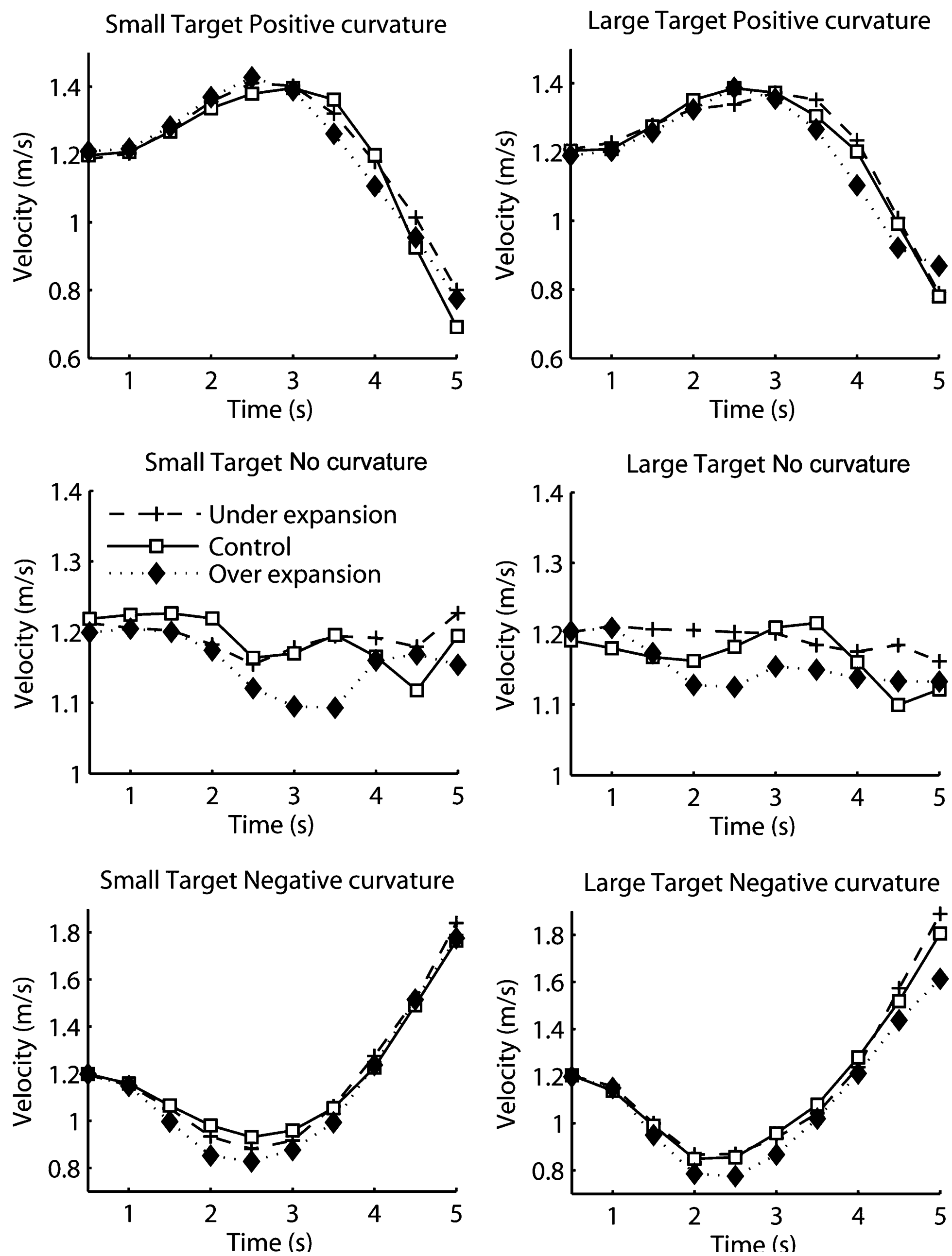


Fig. 5 Mean walking speed represented as a function of target size, expansion condition, and target trajectory. Note the scale differences across the target trajectory conditions. The target crossed the displacement axis after 5 s

interaction were significant; $F_{(1,26)} = 43.64$, $P < 0.05$, $\eta^2 = 0.63$, for Model, $F_{(5,130)} = 17.85$, $P < 0.05$, $\eta^2 = 0.40$, for size-expansion, and $F_{(5,130)} = 10.75$, $P < 0.05$, $\eta^2 = 0.29$, for the interaction. The main effect of Model indicates that the CBA model explains more variance than the V_{REQ} model. The main effect of size-expansion and the interaction are more clearly illustrated in Fig. 6. The figure presents the average squared correlations for the CBA and V_{REQ} models for each expansion condition. For the V_{REQ} model, the squared correlations are higher for the under-expansion condition (black bars) and control condition (gray bars) than for the over-expansion condition (white bars). The predictions of the CBA model do not seem to be as much affected by the expansion condition. The post hoc results of our analysis of variance, also shown in the figure, confirm these findings.

To summarize, the predictions of the CBA model seem to be better than the predictions of the tested version of the V_{REQ} model and, in addition, the predictions of the CBA model seem to be more robust over the different expansion conditions than the V_{REQ} model. Because our analyses at the trial and group levels led to very similar results, we omit the description of these analyses. Remember, however, that the CBA model explains as much as 72% of the variance in walking speed at the group level (look back to Table 1). We want to note that this percentage increases to

Table 1 Coefficient of determination (r^2) expressing the quantitative fit of both models (Eqs. 1 and 2) to the observed kinematics in each experimental condition and for each level of analysis, and the average best-fitting parameters of the CBA model (k_1 and k_2) and V_{REQ} model (c_1 and c_2)

Experimental conditions			Trial level		Individual level		Group level	
			r^2		r^2		r^2	
Trajectory	Target size	Expansion	CBA	V_{REQ}	CBA	V_{REQ}	CBA	V_{REQ}
Curv 0 m	Small	Under	0.30	0.24	0.43	0.38	0.52	0.52
Curv 0 m	Small	Control	0.27	0.22	0.38	0.27	0.53	0.54
Curv 0 m	Small	Over	0.20	0.16	0.29	0.20	0.57	0.50
Curv 0 m	Large	Under	0.30	0.25	0.36	0.30	0.53	0.56
Curv 0 m	Large	Control	0.24	0.19	0.32	0.23	0.48	0.50
Curv 0 m	Large	Over	0.22	0.18	0.21	0.17	0.61	0.70
Curv 0.13 m	Small	Under	0.63	0.66	0.77	0.72	0.89	0.78
Curv 0.13 m	Small	Control	0.60	0.68	0.77	0.77	0.91	0.86
Curv 0.13 m	Small	Over	0.61	0.58	0.79	0.70	0.84	0.71
Curv 0.13 m	Large	Under	0.64	0.68	0.76	0.76	0.94	0.88
Curv 0.13 m	Large	Control	0.58	0.54	0.73	0.65	0.88	0.72
Curv 0.13 m	Large	Over	0.51	0.28	0.62	0.30	0.78	0.36
Curv −0.13 m	Small	Under	0.61	0.71	0.70	0.75	0.72	0.81
Curv −0.13 m	Small	Control	0.58	0.56	0.73	0.63	0.76	0.60
Curv −0.13 m	Small	Over	0.54	0.39	0.66	0.42	0.76	0.41
Curv −0.13 m	Large	Under	0.56	0.57	0.66	0.62	0.69	0.57
Curv −0.13 m	Large	Control	0.56	0.40	0.69	0.44	0.69	0.40
Curv −0.13 m	Large	Over	0.54	0.33	0.67	0.36	0.80	0.34
Mean			0.47	0.42	0.59	0.48	0.72	0.60
Standard-deviation			0.16	0.20	0.19	0.22	0.15	0.17
Mean k_1			−0.064 (0.0083)		−0.068 (0.0092)		−0.063	
Mean k_2			−0.037 (0.0082)		−0.038 (0.011)		−0.040	
Mean c_1				0.011 (0.0025)		0.011 (0.0025)		0.011
Mean c_2				14.7 (1.4)		13.3 (2.0)		15

Standard deviations of the calibration parameters are shown between brackets

81% if we limit the analyses to the conditions with positive and negative curvature, which are the conditions in which the model predicts notable changes in walking speed.

Discussion

The aim of the present study was to test the CBA strategy. The CBA strategy allows the control of walking speed in order to intercept moving targets. We manipulated the curvature of the target trajectory and the expansion pattern of the targets. If a CBA strategy dominates the control process, the observed walking kinematics should be identical for the different target size and expansion conditions. On the other hand, the use of a CBA strategy would give rise to different walking kinematics for targets that follow trajectories with different curvature (cf., Bastin et al. 2006b).

Effect of curvature

The curvature of the target trajectory affected the final spatial error, which was more negative in the positive curvature condition than in the two other curvature conditions. Said differently, on average the targets crossed the displacement axis slightly behind the participants in the positive curvature condition but not in the other curvature conditions. More importantly, a second set of analyses showed that the curvature of the target trajectory also affected the kinematics of the unfolding movements. Recall that for a displacement at constant speed, a positive curvature goes together with a decrease in the bearing angle which, according to a CBA strategy, should lead to an increase in walking speed. This increase in walking speed should then give rise to an increase in the bearing angle in the second part of the trial, which should be compensated for by an ensuing decrease in walking speed

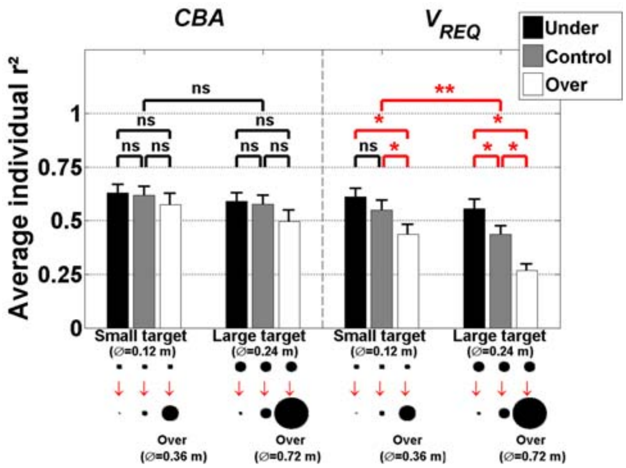


Fig. 6 Average individual values ($n = 9$) of the coefficient of determination (r^2) obtained from comparisons between individual walking-speed profiles and the numerical simulation of the CBA and V_{REQ} models for the different target size and expansion conditions. The *vertical bars* depict the standard errors of individual means. The star symbol (*asterisk*) indicates a statistical difference (post hoc Tukey's HSD test, $P < 0.05$), whereas *ns* indicates the absence of a statistical difference ($P > 0.05$)

close to target contact. Again according to a CBA strategy, a negative curvature should give rise to the opposite effects on walking speed. The speed modifications recorded in our experiment match these predictions, and they thereby provide empirical support for the CBA strategy. Furthermore, these findings are in agreement with previously obtained results (Bastin et al. 2006b).

Effects of target size and expansion pattern

The speed of self motion was slightly affected by the manipulations of target size and expansion pattern. The large target and the over-expansion condition gave rise to a lower overall speed than the small target and the under-expansion condition. These effects are in line with the results of de Rugy et al. (2001) and Sun et al. (1992). Recall, however, that Chardenon et al. (2004) and de Rugy et al. (2001) reported an influence of target expansion on walking speed only at the final part of the unfolding movement. Our results indicate effects of target size and expansion from the beginning to the end of the trials, which is to say that we did not find an interaction between the effects of time intervals and expansion conditions on walking speed. The effects of the different target sizes and expansion conditions seem to be in agreement with the general literature on target size and expansion. A larger optical size or a larger optical expansion might be related to closer objects or faster approaching objects, and might thereby lead to a reduction in walking speed. Nevertheless, the target size and expansion conditions are unrelated to bearing angle and the effects on walking speed induced by them are therefore inconsistent with current formulations of the CBA strategy.

It is interesting to relate our results to the detection thresholds of expansion and contraction (i.e., $\dot{\phi}$). Lee (1976) suggested that these thresholds are about 1/12 and $-1/12°\ s^{-1}$, respectively. Figure 7 shows the evolution of $\dot{\phi}$ in our experiment. In the control and over-expansion conditions, $\dot{\phi}$ mostly evolved above the threshold of $1/12°\ s^{-1}$. In the under-expansion condition, in contrast, $\dot{\phi}$ partly evolved in the below-threshold region between $-1/12$ and $1/12°\ s^{-1}$. This might explain why, in our study, the effects of under expansion were less pronounced than the effects of over expansion.

To summarize, we have reported findings that support a CBA strategy—the effects of curvature—and findings that are inconsistent with a CBA strategy—the effects of target size and expansion. Relevant in this regard is that the walking speed seemed to be more affected by the curvature manipulations than by the expansion manipulations. Also

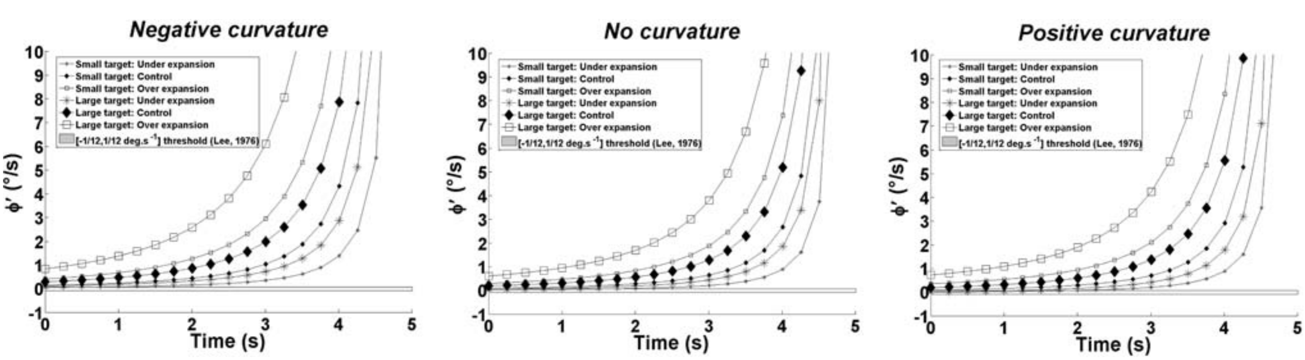


Fig. 7 Visual expansion and contraction of the target ($\dot{\phi}$, in $°\ s^{-1}$) plotted as a function of time for an agent moving at a constant velocity of $1.2\ m\ s^{-1}$ in the under-expansion (*eight headed star*), control (*diamond*), and over-expansion (*square*) conditions, for the two target sizes (*small* and *big symbols*), and for the negative, rectilinear, and positive curvature conditions (from *left* to *right*, respectively). The gray area depicts the [–1/12 to $1/12°\ s^{-1}$] interval reported by Lee (1976) to be the below-threshold interval for perceiving the contraction/expansion of an object

relevant is that even though a CBA strategy does not account for effects of target size and expansion, it explained a large amount of variance in walking speed. In the positive and negative curvature conditions, for instance, 81% of the variance in the averaged walking kinematics was explained by the CBA strategy, despite the effects of target size and expansion pattern. Also, the CBA predictions were found to be superior to the predictions of a required velocity (V_{REQ}) model. We therefore conclude that the CBA strategy is the best explanation for our results available at present. At the same time we conclude that improvements in CBA models are possible.

How might CBA or similar models be improved to account for effects of target size and expansion? Remember that our formulation of a CBA model (Eq. 1) is based on a single optical variable, $\dot{\theta}$. It is also possible to use different candidate variables in equations that are otherwise similar to Eq. 1. Among such candidate variables might, for instance, be the higher order variables $\dot{\theta}/\dot{\phi}$ and $\dot{\theta}/\dot{\phi} \times \theta/\phi$, in which ϕ and $\dot{\phi}$ are the optical angle subtended by the target and its rate of change. These compound variables have been suggested to be implicated in the guidance of lateral interception (Jacobs and Michaels 2006; Michaels et al. 2006; see also the here-discussed V_{REQ} model) and in the perception of the arrival position of targets in football (Craig et al. 2006). Hence, one possible way to adapt CBA models would be to try to identify a candidate optical variable that is sufficiently similar to the rate of change in the bearing angle so that it accounts for curvature effects while at the same time being to some extent related to the optical size of targets and changes therein so that it accounts for effects of target size and expansion.

A final observation relevant in this regard is that movements in ecologically relevant situations are not generally constrained to a single axis of displacement. This means that CBA strategies should be embedded in a more general context of strategies that also control the direction of motion. To give an example, a constant bearing angle is not a sufficient condition for interception if the direction of movement of the target and the one who intercepts might be parallel. In such more general situations, more general control mechanisms should also achieve that one approaches the target. Variables such as optical expansion seem to be of primary importance for such more general mechanisms (Lenoir et al. 1999; Fajen and Warren 2004). The suggestion that we want to conclude with here, then, is that effects of target size and expansion pattern as observed in the present study might be due to control mechanisms that usually function in more general task situations. More complete explanations of the results that we obtained might hence require a further understanding of the control of interception in more general situations.

References

Bastin J, Montagne G (2005) The perceptual support of goal-directed displacement is context-dependent. Neurosci Lett 376:121–126

Bastin J, Calvin S, Montagne G (2006a) Muscular proprioception contributes to the control of interceptive actions. J Exp Psychol Hum Percept Perform 32:964–972

Bastin J, Craig C, Montagne G (2006b) Prospective strategies underlie the control of interceptive actions. Hum Mov Sci 376:121–126

Bootsma RJ, van Wieringen PCW (1990) Timing an attacking forehand drive in table tennis. J Exp Psychol Hum Percept Perform 16:21–29

Bootsma RJ, Peper CE (1992) Predictive visual information sources for the regulation of action with special emphasis on catching and hitting. In: Proteau L, Elliott (eds) Vision and motor control. North-Holland, Amsterdam, pp 285–314

Bootsma RJ, Fayt V, Zaal FTJM, Laurent M (1997) On the information-based regulation of movement: what Wann (1996) may want to consider. J Exp Psych Hum Percept Perform 23:1282–1289

Caljouw SR, van der Kamp J, Savelsbergh GJP (2004) Catching optical information for the regulation of timing. Exp Brain Res 155:427–438

Chardenon A, Montagne G, Buekers MJ, Laurent M (2002) The visual control of ball interception during human locomotion. Neurosci Lett 334:13–16

Chardenon A, Montagne G, Laurent M, Bootsma RJ (2004) The perceptual control of goal-directed locomotion: a common control architecture for interception and navigation? Exp Brain Res 158:100–108

Chardenon A, Montagne G, Laurent M, Bootsma RJ (2005) A robust solution for dealing with environmental changes in intercepting moving balls. J Motor Behav 37:52–64

Craig CM, Berton E, Rao G, Fernandez L, Bootsma RJ (2006) Judging where a ball will go: the case of curved free-kicks in football. Naturwissenschaften 93:97–101

Ellard CG (2004) Visually guided locomotion in the gerbil: a comparison of open- and closed-loop control. Behav Brain Res 149:41–48

Fajen BR, Warren WH (2003) Behavioral dynamics of steering, obstacle avoidance, and route selection. J Exp Psychol Hum Percept Perform 29:343–362

Fajen BR, Warren WH (2004) Visual guidance of intercepting a moving target on foot. Perception 33:689–715

Ghose K, Horiuchi TK, Krishnaprasad PS, Moss CF (2006) Echolocating bats use a nearly time-optimal strategy to intercept prey. PLoS Biol 4:e108

Jacobs DM, Michaels CF (2006) Lateral interception I: operative optical variables, attunement, and calibration. J Exp Psychol Hum Percept Perform 32:443–458

Lanchester BS, Mark RF (1975) Pursuit and prediction in the tracking of moving food by a teleost fish (Acanthaluteres spilomelanurus). J Exp Biol 63:627–645

Land MF, Collett TS (1974) Chasing behaviour of houseflies (fannia canicularis). A description and analysis. J Comp Physiol 89:331–357

Lee DN (1976) A theory of visual control of braking based on information about time-to-collision. Perception 5:437–459

Lenoir M, Musch E, Janssens M, Thiery E, Uyttenhove J (1999) Intercepting moving objects during self-motion. J Motor Behav 31:55–67

Lenoir M, Musch E, Thiery E, Savelsbergh GJP (2002) Rate of change of angular bearing as the relevant property in a horizontal interception task during locomotion. J Motor Behav 34:385–401

Llewellyn KR (1971) The visual guidance of locomotion. J Exp Psychol 91:245–261
McLeod P, Reed N, Dienes Z (2006) The generalized optic acceleration cancellation theory of catching. J Exp Psychol Hum Percept Perform 32:139–148
Michaels CF, Oudejans RR (1992) The optics and actions of catching fly balls: zeroing out optical acceleration. Ecol Psyc 4:199–222
Michaels CF, Zeinstra EB, Oudejans RR (2001) Information and action in punching a falling ball. Q J Exp Psychol A 54:69–93
Michaels CF, Jacobs DM, Bongers RM (2006) Lateral interception II: predicting hand movements. J Exp Psychol Hum Percept Perform 32:459–472
Montagne G, Laurent M, Durey A, Bootsma R (1999) Movement reversals in ball catching. Exp Brain Res 129:87–92
Montagne G, Fraisse F, Ripoll H, Laurent M (2000) Perception-action coupling in interceptive tasks: First order time-to-contact as an input variable. Hum Mov Sci 19:59–72
Olberg RM, Worthington AH, Venator KR (2000) Prey pursuit and interception in dragonflies[A]. J Comp Physiol 186:155–162
Peper CE, Bootsma RJ, Mestre DR, Bakker FC (1994) Catching balls: how to get the hand to the right place at the right time. J Exp Psych Hum Percept Perform 20:591–612
Rossel S, Corlija J, Schuster S (2002) Predicting three-dimensional target motion: how archer fish determine where to catch their dislodged prey. J Exp Biol 205:3321–3326
de Rugy A, Montagne G, Buekers MJ, Laurent M (2000) The study of locomotor pointing in virtual reality: the validation of a test set-up. Behav Res Methods Instr Comp 32:215–220
de Rugy A, Montagne G, Buekers MJ, Laurent M (2001) Spatially constrained locomotion under informational conflict. Behav Brain Res 123:11–15
Rushton SK, Harris JM, Lloyd MR, Wann JP (1998) Guidance of locomotion on foot uses perceived target location rather than optic flow. Curr Biol 8:1191–1194
Savelsbergh GJP, Whiting HTA, Bootsma RJ (1991) Grasping Tau. J Exp Psychol Hum Percept Perform 17:315–322
Shaffer DM, Krauchunas SM, Eddy M, McBeath MK (2004) How dogs navigate to catch frisbees. Psychol Sci 15:437–441
Shankar S, Ellard C (2000) Visually guided locomotion and computation of time-to-collision in the mongolian gerbil (Meriones unguiculatus): the effects of frontal and visual cortical lesions. Behav Brain Res 108:21–37
Sun HJ, Carey DP, Goodale MA (1992) A mammalian model of optic-flow utilization in the control of locomotion. Exp Brain Res 91:171–175
Tabachnik BG, Fidell LS (1989) Using multivariate statistics. Harper Row, New York
Wann JP, Wilkie RM (2004) How do we control high speed steering? Optic flow and beyond. SA Beardsley, Kluwer Academic Publishers, Dordrecht
Warren WH, Kay BA, Zosh WD, Duchon AP, Sahuc S (2001) Optic flow is used to control human walking. Nature Neurosci 4:213–216
Wilkie RM, Wann JP (2005) The role of visual and nonvisual information in the control of locomotion. J Exp Psychol Hum Percept Perform 31:901–911