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Visual guidance of locomotor interception is based on nulling changes in target bearing (not egocentric target direction nor target-heading angle)

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Highlights

- Interception behavior is only compatible with nulling changes in bearing angle
- Movement direction reversals reveal an early influence of initial target position
- Egocentric target direction does not play a consequential role

Abstract

In two experiments we studied how participants steer to intercept uniformly moving targets in a virtual driving task under hypotheses-differentiating conditions of initial target eccentricity and target motion. In line with our re-analysis of findings from earlier studies, in both experiments the observed interception behavior could not be understood as resulting from reliance on (changes in) egocentric target direction nor from reliance on (changes in) target-heading angle. The overall pattern of results observed was however compatible with a control strategy based on nulling changes in the target's bearing angle. The presence of reversals in movement direction under specific combinations of target eccentricity and motion conditions indicated that the information used was not purely rate-of-change (i.e., first-order) based but carried traces of an influence of initial target position. In Experiment 2 we explicitly tested the potential role of early reliance on perceived egocentric target direction by examining the effects of a 10° rotation of the visual scene (i.e., of both target and environment). While such a rotation gave rise to minor changes in the moment of initiation of the first steering action, contrary to predictions it did not affect the characteristics of the direction-reversal phenomenon. We conclude that the visual guidance of locomotor interception is best understood as resulting from nulling changes in the target's bearing angle, with such nulling perhaps best conceived as being fractional-order (rather integer-order) driven.

1. Introduction

Notwithstanding extensive research, the information used in the visual guidance of locomotor interception[1] remains subject of debate. Identifying the information used requires specifying both the *what*, that is, the source(s) of information relied upon, and the *how*, that is, the particular manner of integration of the information into movement (Bootsma et al., 1997; Bootsma, 1998). For locomotor interception potential information sources identified typically include (changes in) egocentric target direction, target-heading angle and the target's bearing angle (see **Fig. 1** for definitions).

***** Figure 1 (definitions of angles here) *****

For operational reasons, we begin our examination of the relevant literature by focusing on egocentric target direction. Indeed, three different studies (Rushton et al., 1998; Fajen & Warren; 2004; Chardenon et al., 2004) all concluded that egocentric visual information plays a substantial role in the control of locomotor interception. Yet, all three studies suffer from methodological and/or conceptual shortcomings, thereby seriously weakening the case in favor of reliance on perceived egocentric target direction.

We note that Rushton et al.'s (1998) study primarily focused on visual guidance of (on foot) locomotion towards a *stationary* target. Egocentric target location, defined relative to the body's midline, was experimentally manipulated by having participants wear displacing prism glasses. In the environmental setting of a homogenous grass lawn, this condition gave rise to curved, rather than straight, locomotor paths to the target. With path curvature globally corresponding to the prism-induced constant heading error, Rushton et al. (1998) concluded that locomotion is guided by the target's egocentric direction rather than by global optic flow: participants steered by walking in the target's egocentric direction rather than by placing the global optic flow's focus of expansion (i.e., heading direction) on the target. While such predominance of egocentric target direction over global optic flow was later qualified as depending on the richness of the available flow (cf. Warren et al., 2001), the main point of interest for the present purposes is that Rushton et al.'s (1998) description of effects observed when locomoting to intercept a *moving* target was limited to the general statement that "results were similar to those for the previous static target set. The value of the [target–locomotor direction] error was found to remain approximately constant throughout the trial (…) as predicted by the perceived-direction model." (p. 1193), accompanied by the presentation of two exemplary trials (Fig. 4, p. 1194). From this figure's caption it appears that target motion was not experimentally controlled either in magnitude or in direction. Overall, Rushton et al.'s (1998) results with respect to locomoting to intercept a moving target, suggesting a pursuit-like interception strategy based on continuously steering in the egocentric target direction, should therefore be considered as preliminary at best and perhaps specific to the particular setting. We will come back to this in the general discussion.

[1] Locomotor interception is operationally defined as making contact with a moving target by means of whole-body displacement. Contrary to manual interception tasks (accomplished by hand displacement), locomotor interception tasks thus imply displacement of the point of observation.

In a systematic study of locomotor interception of uniformly moving targets Fajen and Warren (2004) demonstrated that freely walking participants did not implement a pursuit-like interception strategy. Rather, they systematically steered ahead of the moving target, with locomotor paths eventually straightening out, when time until interception was sufficiently long. In four experiments Fajen and Warren (2004) explored visual guidance of locomotor interception by the target's egocentric direction, local optic flow from the target, and global optic flow from the environment. Noteworthy in the present context, Fajen and Warren (2004) defined egocentric target direction as the target's eccentricity with respect to felt, that is, proprioceptively perceived direction of locomotion, thus adopting a definition different (see **Fig. 1A**) from that of Rushton et al. (1998).

Experimental manipulation of local optic flow from the target, achieved by eliminating the target's optical expansion (Exp. 1) and by rotating a textured target around its vertical axis (Exp. 2), did not affect interception behavior to any significant degree and reliance on such uniquely target-centered local optic flow could therefore be ruled out. When participants were to intercept a moving target when this was the only element present in the display (i.e., in the absence of any environmental structure, No Room condition of Exp. 1), they necessarily relied on (changes in) the target's egocentric direction. Behavior under this extreme condition differed from that observed under a structured-environment condition, as revealed by smaller target-heading angles β over the course of interception under the former than under the latter condition. More subtle testing of the influence of environmental conditions was accomplished by rotating the environment around the observer (Exp. 3) and by laterally displacing the environment (Exp. 4) over the course of interception, thereby influencing optically-specified target-heading angle (β_{os}, see **Fig. 1A**). In both cases the reported effects on interception behavior were found to be opposite in direction to the effects predicted by reliance on changes β_{os}. As such effects could thus not be understood as resulting from visual guidance by changes in the optically-specified target-heading angle, by deduction these results led Fajen and Warren (2004) to conclude that participants must then have relied on changes in egocentric target direction, with environmental motion assumed to influence the perception of target motion. We would, however, like to point out that a different explanation is not only possible but, moreover, plausible.

Indeed, Fajen and Warren (2004) did not consider the consequences of their environmental rotation and displacement manipulations in terms of their effects on another potentially pertinent source of information, namely changes in the target's bearing angle. In fact, in their 2004 contribution Fajen and Warren regularly appear to consider target-heading angle and the target's bearing angle as referring to the same angular quantity (β, as defined in **Fig. 1B**), alternating use of both terms. However, as subsequently pointed out in Fajen and Warren (2007) and illustrated in **Figure 1B**, the target's bearing angle θ is qualitatively different from the target-heading angle β, with θ defined relative to an exocentric reference direction and β defined relative to the agent's movement direction. Because continuous rotation and displacement of the environment with respect to the observer affect the pattern of change in the target's bearing angle in ways opposite to their influences on the pattern of change in the

optically-specified target-heading angle[2], reliance on changes in the target's bearing angle can in fact explain the experimental effects of environmental motion reported by Fajen and Warren (2004).

A similar lack of distinction between target-heading angle β and the target's bearing angle θ is found in Chardenon et al.'s (2004) study of direction-constrained locomotor interception, with participants regulating walking velocity on a servo-controlled treadmill to intercept targets moving toward their locomotor axis from the right. Inappropriately referring to the target-heading angle as the target's bearing angle (see their Fig. 1C, p. 101), Chardenon et al. (2004) evaluated the effects of continuous lateral displacement of the ground surface on locomotor speed, using targets coming in from the right. A right-left sawtooth-shaped pattern of displacement of the ground surface during interception evoked changes in walking speed characterized by an acceleration followed by a deceleration; the inverse pattern was observed for a left-right ground surface displacement, with participants here first decelerating and subsequently accelerating their walking speed during interception. Lateral ground surface displacement thus clearly affected locomotor speed, the relevant action variable in direction-constrained locomotion (Bootsma et al., 2016). Like Fajen and Warren (2004), Chardenon et al. (2004) argued that the effects provoked by ground surface motion were opposite in direction to the effects predicted by reliance on changes in optically-specified target-heading angle (improperly denoted bearing angle) and could not, therefore, reflect an effect of manipulating this informational quantity. Analogous to Fajen and Warren (2004), this led them to conclude, by default, that participants must then have relied on egocentric target direction. Once again, however, we argue that, because continuous displacement of the environment with respect to the observer affects the pattern of change in the target's bearing angle θ in ways opposite to its influence on the pattern of change in the target-heading angle β_{os}, changes in the target's bearing angle can, in fact, explain the experimental effects reported by Chardenon et al. (2004)[3].

Because the target's bearing angle is defined with respect to an exocentric reference direction, detection of changes in bearing angle does not require detection of heading direction. While the latter may be recovered from global optic flow or from felt displacement, the former may be recovered from local flow *around* the target, that is, from the relative motion of target with

[2] To illustrate this with an example, let us assume that an agent is currently on an interception course with a uniformly-moving target, coming in from the right. In this situation the target, situated on the right, does not visually move (both target-heading angle and bearing angle are constant). A continuous rightward displacement of the environment optically specifies a leftward component of self-motion, thereby reorienting the agent's optically-specified heading direction with respect to the environment leftward. With the target situated on the right, this leads to *opening of the target-heading angle*. Since the target's bearing angle is defined, at the point of observation, by the target's direction with respect to the environment, the same continuous rightward displacement of the environment results in a leftward displacement of target with respect to the environment, thereby moving it inward from its (initially stable) position on the right. This leads to *closing of the target's bearing angle*.

[3] As rightward displacement of the environment (here ground surface) leads to closing of the bearing angle for a target moving inward from the right (see footnote 1), reliance on changes in the target's bearing angle would bring the agent to accelerate. The opening of the target's bearing angle, induced by leftward displacement of the environment, would bring the agent to decelerate. These predictions perfectly correspond to the results reported by Chardenon et al. (2004).

respect to its visual surroundings provided by the environment (background and ground surface texture elements and/or objects). As Cutting et al. (1995) eloquently reported in their psychophysical study of information for avoiding (or provoking) collision with stationary and moving objects: "When observers are fixated on a stationary object, their ability to find their aimpoint is good and adequate to the task. When observers are fixated on a moving object, on the other hand, (…) generally they have no clue where they are going." (p. 635).

We have so far argued that the results of the locomotor interception studies of Fajen and Warren (2004) and Chardenon et al. (2004) may be explained by participants' reliance on changes in the target's bearing angle and would therefore not require evoking, as both these studies did, the default option of reliance on changes in the target's egocentric direction. What further evidence do we have that pleads in favor of visual guidance of locomotor interception by changes in the target's bearing angle? As argued by Bootsma et al. (2016, cf. Ceyte et al., 2021), direct evidence for any interception strategy requires defining such strategies not in terms of rule-of-thumb heuristics (defining what one should be doing) but in terms of dynamics (defining how one might get there), that is, in terms of how the system evolves over time toward a steady-state regime. Adopting such a dynamical perspective leads one to focus on transients rather than on steady-state regimes only. Modeling the behavioral dynamics of steering control in locomotor interception in this spirit, Fajen and Warren (2007) demonstrated that, contrary to their 2004 assertions, a steering model based on nulling changes in target-heading angle could, in fact, not even adequately explain the interception behavior (observed in their 2004 study) under stable environmental conditions. This, perhaps surprising, inadequacy of the classical interception strategy (cf. Bootsma et al., 2016) notably came to the fore when the target moved outward from an initial location directly ahead of the walking participant. At the onset of such a trial the outward-moving target created an immediate behavioral lag, characterized by the opening of the target-heading angle β. Under this initial condition nulling changes in β, by nulling $d\beta/dt$, did not lead to the experimentally observed steering ahead of the target, as all that could be accomplished by such a $d\beta/dt$-nulling interception strategy was reducing the β-lag over time. Modeling an interception strategy based on nulling $d\theta/dt$, on the other hand, did systematically lead to the experimentally observed steering ahead of the target. Thus, Fajen and Warren (2007) concluded that the observed phenomena were only adequately captured by a strategy of nulling changes in the target's bearing angle.

In Fajen and Warren's (2004) study, the target could initially be located straight ahead of the participant (CENTER condition) or to the left or right (SIDE condition), with targets moving at constant speed along Approach, Cross and Retreat directions (see **Fig. 2A** for definitions). Using a simulated driving task, Ceyte et al. (2021) recently studied locomotor interception with CENTER (0°) and SIDE (23°) initial target eccentricity conditions complemented by a SIDE+ (32°) eccentricity condition and with target directions (Approach, Cross, Retreat) complemented with a more direct Approach+ condition. Notwithstanding the task differences (real walking vs. simulated driving, with the latter thus not including physical displacement), Ceyte et al.'s (2021) overall pattern of results revealed strong similarities with Fajen and Warren (2004)'s findings. Since under all three target eccentricity conditions participants

were again found to systematically steer ahead of the moving target, Ceyte et al.'s (2021) results provided complementary evidence for an interception strategy relying on nulling changes in the target's bearing angle (i.e., on nulling dθ/dt) and, at the same time, against reliance on changes in target-heading angle (i.e., on nulling dβ/dt), whether it be defined egocentrically or otherwise.

***** Figure 2 (experimental conditions) about here *****

In the present experimental contribution, we explored whether a manipulation akin to that used by Rushton et al. (1998) would affect interception behavior in the simulated locomotor interception-by-steering task developed by Ceyte et al.'s (2021). To this end we compared interception behavior under standard environmental conditions with interception behavior when the virtual environment and target had been rotated 10° to the left or to the right. Before proceeding with this experiment, however, we first ran a control experiment (including only CENTER and SIDE target eccentricities and Approach, Cross and Retreat target directions) to determine (i) whether Ceyte et al.'s (2021) SIDE+ target eccentricity and/or Approach+ target direction conditions had not influenced behavior under the other six combinations of Target Eccentricity and Target Direction conditions (used by Fajen & Warren, 2004, and in our Exp. 2) and (ii) to explore whether a particular phenomenon, namely the coming to the fore of reversals in movement direction under specific combinations of target eccentricity and target direction conditions, could be replicated. As will be detailed further on, both these issues are relevant to operational predictions with respect to the effects of performing the simulated interception-by-steering task under a constant 10° visual scene (i.e., target + virtual environment) rotation.

2. Experiment 1: CENTER and SIDE target eccentricities

Experiment 1 thus had two objectives. In the first place we sought to replicate the overall pattern of results reported by Ceyte et al. (2021) when using only CENTER and SIDE target eccentricities combined with only Approach, Cross and Retreat target directions. If similar results were observed in both cases, we may use the differential effects on interception behavior observed under Ceyte et al.'s (2021) SIDE and SIDE+ target eccentricity conditions for evaluating possible effects of the target + virtual environment rotation of Experiment 2. In the second place, we sought to replicate the direction reversal phenomenon observed by Ceyte et al. (2021) under the SIDE and SIDE+ eccentricities for the Cross and Retreat target directions. For reasons of clarity, we briefly describe this phenomenon here.

In their 2007 modeling study of their 2004 averaged behavioral data, Fajen and Warren reported one single observation that did not fit with interception behavior based on nulling dθ/dt: Under SIDE/Cross and SIDE/Retreat conditions locomotor paths revealed a slight S-shaped bend. Steering under these specific conditions was characterized by a discreet initial turn in the direction of the target followed by a reversal in movement direction (denoted RMD hereafter), so that the target was finally intercepted on the opposite side of the initial locomotor direction axis. Examining individual-trial (rather than overall-average) locomotor

paths, Ceyte et al. (2021) demonstrated that RMDs did indeed occur for the Cross and Retreat target directions under both the SIDE and SIDE+ target eccentricity conditions. Interestingly however, such RMDs were not observed on all trials of these particular conditions that revealed a considerable degree of between-trial variation in the moment of initiation of the first steering action. Trials with a RMD were in fact characterized by early initiation of the participant's first steering action, while trials without a RMD were characterized by later initiation of steering (see Ceyte et al., 2021, for details). The second objective of Experiment 1 was therefore to seek to replicate Ceyte et al.'s (2021) specific pattern of results with respect to reversals in movement direction in the SIDE eccentricity condition.

2.1. Materials and Methods

2.1.1. Participants

Five students from Aix Marseille University (3 women and 2 men, mean age 22.4 ± 0.9 years) voluntarily took part in the experiment. None of them had participated in any other experiment using the same interception-by-steering task. Participants provided written consent prior to participation. The study was conducted according to University regulations and the Declaration of Helsinki.

2.1.2. Task and procedure

The experiment took place in a large virtual reality facility (https://ism.univ-amu.fr/en/crvm) comprising four projection surfaces, each served by two projectors: a 3 × 3-m floor and three 4-m high × 3-m wide walls. The sidewalls were set at 90° angles with respect to the front wall. A basic driving simulator, comprising a seat, a set of (here non-operative) pedals and a steering wheel, was positioned in the middle of the floor surface. Stereopsis was ensured with passive Infitec filter technology. Participants' stereo glasses were equipped with a configuration of reflective markers. An eight-camera Advanced Realtime Tracking (ART, Weilheim, Germany) optical system enabled real-time motion capture of head position. The visual scene was refreshed at 60 Hz, taking into account the position and orientation of the participant's head relative to the virtual environment.

The visual scene consisted of a large grass-like flat plain, containing both fine and gross texture, bordered by distant mountains. The seated participant was instructed that on each trial the goal was to steer the "car" so as to intercept a horizontally-moving yellow cylinder (2-m radius, 3-m high) by driving through it. Prior to trial onset, the participant, moving at a constant horizontal speed of 20 m/s, was to steer towards and subsequently align locomotor direction with a yellow line on the plain's ground. Alignment was considered as accomplished when the car's center (i.e., middle of the seat) attained a lateral distance of less than 3 cm with respect to the middle of the line while moving in a direction deviating less than 0.1° from the line orientation. This quite demanding requirement led participants to only minimally turn the steering wheel in the last stages of alignment. Once the alignment criteria were met, the yellow line disappeared and, at the same time, a red portal appeared 40 m ahead. Participants' instructions stipulated that they should refrain from further steering from the moment onward

that correct alignment had been achieved and until they passed through the portal. In fact, without the participants being aware of this, during that period the steering wheel was deactivated with wheel orientation recalibrated to zero, so that when the participant crossed the portal and the target appeared, they moved such that both $\phi = 0°$ and $d\phi/dt = 0$ °/s. A trial ended when the participant came within the target's circumference (successful interception) or when the participant reached a position further than 20 m in depth (Z-axis) beyond the current target position (missed trial).

In the experimental trials, targets were initially positioned at Z = 60 m and X = 0.00 m or −25.35 m, with initial participant position serving as the origin of the reference frame. Targets could thus appear at eccentricities of 0° (CENTER) and 23° (SIDE) to the left of the participant's initial locomotor direction (see **Fig. 2A**). Targets moved at 10 m/s along Retreat, Cross and Approach directions (oriented, respectively, +30°, 0°, and −30° relative to the perpendicular with respect to the participant's initial locomotor direction). All initial conditions were also mirrored left/right and the data were subsequently collapsed for analysis.

The full set of 12 experimental conditions was presented in randomized order within a block of trials. Participants performed five blocks, for a total of 60 trials (10 per mirror-collapsed condition) and were invited to take a short break between blocks. Prior to the experiment proper participants performed 12 familiarization trials with stationary targets.

2.1.3. Data acquisition and analysis

Participant position (x, z) and locomotor orientation (ϕ) data were sampled at 100 Hz. These time series were subsequently filtered using a second-order Butterworth filter with a cut-off frequency of 8 Hz and collapsed over mirror conditions. Time derivatives were obtained using the Euler method. For each trial, the closest distance to the target was calculated, corresponding to zero at first contact with the target's circumference for successful interception trials and minimal Euclidean distance from the target's circumference for missed trials. Time to closest distance was defined as the time from onset of the trial until the moment the closest distance was reached.

The moment of initiation of the first steering action was determined for each trial as the time after trial onset at which the participant's rate of change in locomotor direction ($d\phi/dt$) exceeded 4 deg/s. A reversal in movement direction was defined as a lateral excursion of more than 0.05 m following initiation of the first steering action accompanied by a subsequent sign change in $d\phi/dt$ leading to a movement in the opposite lateral direction. Pre-reversal excursion amplitude was defined as the largest initial lateral displacement before movement direction was reversed.

Moment of initiation of the first steering action was analyzed using a repeated-measures ANOVA with factors Eccentricity (CENTER, SIDE) and Direction (Approach, Cross, Retreat). More localized effects were evaluated using Chi-squared tests for frequency comparisons and Student t-tests for pre-reversal excursion amplitudes in trials with a reversal in movement direction and moment of initiation in trials with and trials without a reversal in movement direction. All tests were performed two-sided with significance level α set to 0.05.

2.2. Results

2.2.1. Interception performance

Overall, participants intercepted the target in 89.3% of the trials. Close to maximum performance was observed for the Cross and Retreat target directions under both the SIDE and CENTER eccentricity conditions. For the Approach target direction success rate was 80.0% for the SIDE and 64.0% for the CENTER eccentricity conditions (see **Table 1**). Even when a target was missed, participants generally came close, as attested to by the overall 0.06-m median closest distance to the target circumference for the 32 missed trials. Subsequent analyses were based on all trials.

***** Table 1 about here *****

2.2.2. Interception paths

The (time-averaged) mean interception paths followed by the participants are presented in **Figure 3** for the six combinations of Target Eccentricity and Target Direction. Inspection of the path shapes observed in the present study revealed strong similarities to those of Ceyte et al. (2021) for the corresponding conditions (i.e., CENTER and SIDE eccentricities combined with Approach, Cross and Retreat target directions). Under the CENTER conditions interception paths were once again characterized by an early, relatively sharp initial turn followed by a straightening out of the interception path, with the latter being most clearly visible for the Retreat and Cross target directions. We again emphasize that, because CENTER conditions caused participants to initially lag the target, the straightening out of the path cannot be accounted for by the interception strategy of nulling changes in target-heading angle β. As pointed out by Fajen and Warren (2007) and Ceyte et al. (2021), such a $d\beta/dt$-nulling strategy cannot explain the sign change in β that necessarily accompanies the change from the initial lag situation (target to the right of participant heading direction, see **Fig. 3**) to the later lead situation (target to the left of participant heading direction). This is even more clearly visible in **Figure 4**, presenting the evolution over time of target-heading angle β and the target's bearing angle θ: the initial lag created under the CENTER eccentricity condition is visible as the early dip below zero (opening) of β for all three target directions. Participants' steering behavior then rapidly led them to lead the target, visible as the switch from negative to positive β-values within the first seconds after trial onset Under the SIDE conditions participants more gradually turned towards the final interception locations, on the left for the Approach direction and on the right for the Cross and Retreat direction. We note that this pattern of results can be understood as resulting from an interception strategy based on nulling changes in the target's bearing angle.

***** Fig. 3 (Exp. 1 - mean paths) about here *****

The overall pattern of results thus also closely corresponded to that of Fajen and Warren (2004), with one main difference: As in Ceyte et al. (2021), we did not find a clearly visible S-shaped bend in the initial part of the average interception paths for the Cross and Retreat target directions under the SIDE eccentricity condition, but (again as in Ceyte et al., 2021),

we did observe —as detailed further on— the expected reversals in movement direction at the level of individual trials.

***** Fig. 4 (Exp. 1 – angles over time) about here *****

2.2.3. Moment of initiation of the first steering action

A repeated-measures ANOVA with the factors Eccentricity (CENTER, SIDE) and Direction (Retreat, Cross, Approach) revealed a significant main effect of Eccentricity ($F(1, 4) = 296.00$. $p < 0.001$, $\eta^2_p = 0.99$). Similar to Ceyte et al.'s (2021) findings, the earliest steering actions were observed under the CENTER condition where participants initiated steering about 0.5 s after the target appeared for all target directions. Steering initiation occurred later under the SIDE condition, after 0.76, 0.99 and 1.00 s on the average for the Approach, Cross and Retreat Target Directions, respectively (see **Table 1**).

2.2.4. Reversals in movement direction

Overall, a reversal in movement direction (RMD) was detected in 36 (i.e.,12.0%) of the total of 300 trials. This low overall percentage of trials with a RMD was expected, as trials with a RMD were hypothesized to occur under the SIDE/Cross and SIDE/Retreat target conditions only (i.e., two out of six conditions). In line with this hypothesis and again corroborating Ceyte et al.'s (2021) findings, the presence of RMD trials was not randomly distributed over the experimental conditions ($\chi^2(5) = 112.76$, $p < 0.0001$). Indeed, as expected, the grand majority ($n = 34$) of RMD trials occurred under the SIDE/Cross ($n = 23$; 46.0%) and SIDE/Retreat ($n = 11$; 22.0%) conditions. The remaining two RMD trials were observed under the SIDE-Approach condition; no RMD trials were observed under the CENTER eccentricity condition. RMD trials were detected for all participants (n = 5 to 9 range), indicating that their coming to the fore was not participant-specific. Performance on the task was not noticeably affected by the presence of a RMD, as demonstrated by the overall 91.7% success rate of trials with a RMD.

Figure 5 presents all individual trial paths for each of the Cross and Retreat target directions under the CENTER and SIDE eccentricity conditions. Zooming in on lateral displacement, this figure brings out the co-existence of trials with and without a RMD within the same subset of experimental conditions (i.e., Cross and Retreat target directions under the SIDE eccentricity conditions).

***** Figure 5 (Exp. 1 - individual paths) about here *****

Finally, for the Cross and Retreat target directions under the SIDE eccentricity condition, comparison of the trials with a RMD and the trials without a RMD revealed that the former were consistently initiated earlier than the latter ($M \pm SD$ respectively 0.85 ± 0.36 s and 1.07 ± 0.38 s, $t(98) = 2.84$, $p = 0.0055$). Moreover, within the set of trials with a RMD, the pre-reversal excursion amplitude was negatively correlated with the moment of initiation of the first steering action, indicating that earlier initiation was accompanied by larger excursion

amplitudes before heading direction was reversed ($r(32) = –0.61$, $p = 0.001$). These findings thus closely corresponded to the pattern of results reported by Ceyte et al. (2021).

2.3. Discussion

The goal of this preliminary experiment was to replicate Ceyte et al.'s (2021) study when target eccentricity was limited to two initial conditions (CENTER and SIDE) and target direction was limited to three conditions (Approach, Cross, and Retreat), as was the case in Fajen and Warren's (2004) study and implemented in our Experiment 2. The overall pattern of results from this preliminary replication experiment clearly corroborated Ceyte et al.'s (2021) findings, both qualitatively and quantitatively. First, the locomotor paths observed under the CENTER eccentricity condition once again systematically revealed steering ahead of the target, thereby anew demonstrating that steering behavior was generally compatible with a strategy of nulling changes in the target's bearing angle and not with a strategy of nulling changes in the target-heading angle (nor in egocentric target direction for that matter). Second, under the SIDE eccentricity conditions Cross and Retreat target directions gave rise to reversals in movement direction in, respectively, 46.0% and 22.0% of the trials. As these RMDs were associated with early initiation of the first steering action, these results confirm that the control of steering is not exclusively based on first-order (i.e., rate-of-change based) information, but that, at least early on, target position related information also plays a role (cf. Bootsma et al., 2016; Ceyte et al., 2021).

3. Experiment 2: Rotation of the visual scene (target + virtual environment)

Using the 2 × 3 target eccentricity and direction conditions design of Experiment 1, in Experiment 2 we explored the effects of a stepwise 10° rotation of the target and virtual environment (denoted TVE hereafter). This manipulation is akin to that of Rushton et al. (1998), while avoiding the flow-warping distortion effects of displacing prism glasses reported by Warren et al. (2001). To pinpoint the effect of such a TVE rotation on potential information sources for locomotor interception, we stipulate once more that these information sources differ in the reference they are defined by. The target's bearing angle (θ) is defined by its eccentricity at the point of observation with respect to an exocentric (environment-based) reference direction and is therefore not influenced by a given TVE rotation, as from the onset of a trial both the target and the environment are rotated in the same way (i.e., in the same direction and to the same extent). The optically-specified target-heading angle (β_{os}) is defined by the target's eccentricity at the point of observation with respect to the agent's current direction of motion. Influencing target eccentricity and agent heading direction in the same way, a constant TVE Rotation therefore does not influence the target-heading angle β_{os} either. When the target's egocentric direction is defined relative to the body midline (Rushton et al.'s 1998 definition), however, TVE rotation does affect this potential information source (β_{e1}), as the body midline orientation remains identical while the target is displaced. For sake of completeness, we note that in our simulated interception-by-steering task, egocentric direction

as defined by felt locomotor displacement (β_{e2}, Fajen and Warren's 2004 definition) is simply not available. We also note that TVE rotation would not be expected to have any effect on interception behavior if participants would uniquely rely on the rate-of-change in any particular angle, either because they are simply not affected by the manipulation or because offset is constant (as for β_{e1}).

As can be seen from **Figure 2B**, by applying an outward 10° TVE rotation (referred to hereafter as R+), for the SIDE condition the target's initial egocentric eccentricity increases from 23° to 33°, corresponding closely to the target's true initial 32° eccentricity under the SIDE+ condition explored in Ceyte et al. (2021). A 10° TVE rotation in the same direction (R+) applied to the CENTER condition and an inward 10° TVE rotation (R–) applied to the SIDE condition give rise to quite similar (13° and 10°, respectively) new egocentric eccentricity conditions (see **Fig. 2B**), that we may refer to as an imaginary SIDE– condition. If early on participants were to rely on egocentric target direction in the control of their interception behavior, we can thus formulate a set of specific predictions with respect to the behavior expected under R+ and R– TVE rotation conditions compared to the R0 control condition, based on the differential results observed by Ceyte et al. (2021) under the true SIDE+, SIDE and CENTER eccentricity conditions. In formulating these predictions, we concentrate on the Cross and Retreat target directions exclusively.

Egocentric Target Direction predictions with respect to the first steering action

In Ceyte et al.'s (2021) study and replicated in Exp. 1, the earliest steering initiation was observed under the CENTER eccentricity condition, with moments of initiation around 0.5 s for all target directions. Ceyte et al. (2021) also observed that, for each target direction, steering was initiated earlier under the SIDE+ than under the SIDE eccentricity condition (see their Table 1). Under the SIDE eccentricity of Experiment 2 the increased egocentric target direction of the R+ condition should (in comparison to the SIDE R0 control condition) therefore lead to earlier initiation. By extrapolation, the decreased egocentric target direction of the SIDE R– condition should (in comparison to the SIDE R0 control condition) therefore lead to later initiation. With the SIDE R– condition closely resembling the CENTER R+ condition in terms of initial egocentric target direction (together forming the imaginary SIDE– eccentricity), the CENTER R+ condition should (compared to the CENTER R0 condition) lead to later initiation, with moments of initiation for the two conditions of the imaginary SIDE– eccentricity condition being value-wise close together.

Egocentric Target Direction predictions with respect to reversals in movement direction

In Ceyte et al.'s (2021) study, a larger proportion of trials with a RMD were observed under the SIDE+ than under the SIDE eccentricity conditions. Under the SIDE eccentricity of Experiment 2, the increased egocentric target direction of the R+ condition should (in comparison to the R0 control condition) therefore also lead to an increase in the proportion of trials with a RMD. By extrapolation, the decreased egocentric target direction of the R– condition should then lead to a smaller proportion of trials with a RMD and, by the same

token, a comparable proportion of trials with a RMD should come to the fore under the CENTER R+ condition.

3.1.Method

3.1.1. Participants

Sixteen students from Aix Marseille University (8 women and 8 men, mean age 24.3 ± 2.0 years) voluntarily took part in the experiment. None of them had participated in any other experiment using the same interception task. Participants provided written consent prior to participation. The study was conducted according to University regulations and the Declaration of Helsinki.

3.1.2. Task and procedure

Apart from the addition of constant TVE rotation conditions, the task and procedure were identical to that described for Experiment 1, including CENTER and SIDE initial target eccentricities and Approach, Cross and Retreat target directions. These experimental conditions were combined with a TVE Rotation condition in which the target + virtual environment were rotated. While all of the participants performed the task under the control condition of 0° TVE rotation (R0), eight of them also performed all six combinations of Target Eccentricity (CENTER, SIDE) and Target Direction (Approach, Cross, Retreat) under a 10° leftward TVE rotation; the other eight participants performed the same six combinations of Target Eccentricity and Target Direction under a 10° rightward TVE rotation. As can be seen from **Figure 2B**, leftward rotation increased egocentric eccentricity for the left SIDE condition, with the rightward-moving targets thereby constituting the six R+ rotation conditions for the 10°-leftward rotation participant group. Note that for this participant group, the (mirror) leftward-moving trajectories (where the same leftward rotation decreased egocentric eccentricity for the right SIDE condition) constituted the six R– rotation conditions. Conversely, for the 10°-rightward rotation participant group, the leftward-moving trajectories constituted the R+ rotation conditions and the rightward-moving trajectories constituted the R– rotation conditions.

In the leftward-rotation group, half of the participants first performed the task under the no-rotation conditions and then under leftward-rotation conditions, while the other half first performed the task under the leftward-rotation conditions and then under the no-rotation conditions. The same procedure was applied to the rightward-rotation group.

The (mirrored) set of 12 combinations of Target Eccentricity (CENTER, SIDE) and Target Direction (Approach, Cross, Retreat) was again presented in randomized order within a block of trials. Participants performed five blocks under both the no-rotation and (participant-group specific) rotation conditions, for a total of 120 trials and were invited to take a short break between blocks. Prior to the experiment proper participants performed 12 familiarization trials with stationary targets.

For analysis, data were collapsed over groups, giving rise to 10 trials per Target Eccentricity and Target Direction combination under the R0 rotation condition and five trials per participant per Target Eccentricity and Target Direction combination under both the R+ condition and the R– rotation condition.

3.1.3. Data acquisition and analysis

Data acquisition and analysis was identical to that described for Experiment 1, except that statistical analysis now included three factors: TVE Rotation (R0, R+, R–), Target Eccentricity (SIDE, CENTER) and Target Direction (Approach, Cross, Retreat).

3.2. Results

3.2.1. Interception performance

Participants intercepted the targets in 89.0%, 90.2% and 89.4% of the trials under the R0, R+ and R– conditions, respectively. As in Experiment 1, success rate was close to maximum for the Cross and Retreat target directions under both the CENTER and SIDE eccentricities and lower under de Approach target direction, especially under the SIDE eccentricity (see **Table 2**). TVE rotation did not affect performance to any noticeable extent. Even on the 204 missed trials (out of the total of 1920 trials) participants generally came close to the target (overall median closest distance 0.06 m). Subsequent analyses were based on all trials.

3.2.2. Interception Paths

As shown in **Figure 6**, the average interception paths for the R0 condition were very similar to those observed in Experiment 1 (cf. Ceyte et al., 2021, and Fajen & Warren, 2004). TVE rotation did not affect mean paths to any remarkable degree; still, relative to the R0 condition, under the Retreat and Cross target direction conditions average paths were shifted slightly to the left for the R+ condition and to right left for the R– condition. Time until closest distance (TCD; see Table 2) was reached was not affected by TVE rotation conditions.

***** Figure 6 (mean interception paths) about here *****

3.2.3. Moment of initiation

As in Experiment 1, the earliest steering actions were observed under the CENTER condition where participants initiated steering around 0.5 s after the target appeared for all target directions under all TVE Rotation conditions (see **Table 2**). A repeated-measures ANOVA with the factors TVE Rotation (R0, R+, R–), Eccentricity (CENTER, SIDE), and Direction (Approach, Cross, Retreat,) revealed significant main effects for all three factors (Rotation: $F(2,30) = 5.49$, $p < 0.009$, $\eta^2_p = 0.27$; Eccentricity: $F(1,15) = 171.44$, $p < 0.001$, $\eta^2_p = 0.92$; Direction $F(2,30) = 46.79$, $p < 0.001$, $\eta^2_p = 0.76$), as well as significant two-way interactions (Rotation × Eccentricity, $F(2,30) = 4.36$, $p < 0.022$, $\eta^2_p = 0.23$, Eccentricity × Direction, $F(2,30) = 45.08$, $p < 0.001$, $\eta^2_p = 0.75$, and Rotation × Direction, $F(4,60) = 3.08$, $p < 0.023$, $\eta^2_p = 0.17$) and a three-way interaction between the factors Rotation, Eccentricity, and Direction ($F(4,60) = 3.55$, $p < 0.012$, $\eta^2_p = 0.19$). Post-hoc Newman-Keuls analysis of the

overarching triple interaction confirmed that under the CENTER Eccentricity, moments of initiation did not significantly vary over Rotation and Direction conditions. While under the SIDE Eccentricity, moments of initiation observed for the Approach direction did not significantly vary over Rotation conditions either, an effect of Rotation was found for the Cross and Retreat target directions: moments of initiation were significantly later (p's < 0.01) under the R+ condition than under the R– condition (Cross: 1.37 s ± 0.28 s and 1.19 s ± 0.23 s, respectively; Retreat: 1.24 s ± 0.37 s and 1.13 s ± 0.34 s, respectively). Significant differences involving R0 were only observed for the Cross target direction, where steering actions were initiated significantly later ($p < 0.001$) under the R+ condition than under the R0 condition (1.25 s ± 0.24 s). This pattern of results does not fit with predictions based on early reliance on egocentric target direction, as, for instance, earlier (rather than later, as found) moments of initiation were then expected under the SIDE/R+ conditions than under the SIDE/R0 conditions.

***** Table 2 about here *****

3.2.4. Reversals in movement direction

Trials with a RMD were detected in 184 (i.e., 9.6%) of the total of 1920 trials. As expected, the grand majority ($n = 152$) of these RMD trials was observed under the SIDE eccentricity condition for the Cross ($n = 92$, 28.8%) and Retreat ($n = 60$, 18.8%) target directions. The other 32 RMD trials were distributed over the remaining conditions, occurring only rarely in each (see **Table 3**). Although two participants did not reveal any trials with a RMD under the R0 Rotation condition[4], all participants revealed RMD trials under the R+ and R– Rotation conditions. The presence of RMD was thus once again not participant-specific. The presence of a RMD did not noticeably degrade performance, as interception was achieved in 94.1% of the RMD trials.

***** Table 3 about here *****

Overall, contrary to egocentric direction-based predictions, no effect of Rotation condition on the frequency of RMD trials observed for the Cross and Retreat directions could be demonstrated (R0: 82 of total 320 trials = 25.6%; R+: 43 of total 160 trials = 26.9%; R–: 27 of total 160 trials =16.9%; $\chi^2(2) = 4.12$, $p = 0.1275$). As in Experiment 1 and in Ceyte et al. (2021), however, more RMD trials were observed for the Cross direction (n = 92) than for the Retreat direction ($n = 60$; $\chi^2(1) = 6.74$, $p = 0.0009$). Moreover, RMD trials for the Cross and Retreat directions were, once again, initiated (0.93 s ± 0.34 s) significantly earlier ($t(638) = 10.33$, $p < 0.0001$) than NoRMD trials (1.31 s ± 0.41 s). Finally, for the RMD trials maximal pre-reversal excursion amplitude was negatively related to the first moment steering action ($r(150) = –0.51$, $p < 0.0001$).

[4] We note that the two participants that did not reveal RMD trials under the R0 (control) condition were found to initiate their first steering action significantly later than all other participants together (0.87 s ± 0.42 s versus 0.76 s ± 0.40 s; $t(958) = 2.76$, $p = 0.0029$). Later initiation is generally associated with less RMD trials.

3.3. Discussion

Experiment 2 once more closely replicated the pattern of results of Ceyte et al. (2021). Most importantly, as expected RMDs were again almost exclusively observed for the Cross and Retreat target directions under the SIDE eccentricity conditions and such RMDs occurred on trials with an early initiation of the first steering action. The observed effects of TVE rotation did not, however, support the hypothesis of an early reliance on egocentric target direction. Let us consider these effects in the light of our egocentric target direction-based predictions.

The first set of predictions concerned the moment of initiation of the first steering action, under the SIDE and under the CENTER target eccentricities. Under the SIDE eccentricity conditions, the first steering action was expected to occur earlier under R+ (resembling Ceyte et al.'s SIDE+ condition) and later under R– rotation conditions, compared to the R0 control condition. While a statistically significant difference with R0 was only found under the R+ rotation condition for the Cross target direction, the difference between R+ and R– rotation conditions did reach significance for both the Cross and Retreat target directions. Yet, initiation of the first steering action occurred later (rather than earlier) under the R+ than under the R0 and R– rotation conditions. Under the CENTER eccentricity conditions, compared to the R0 control condition, the first steering action was expected to occur later under the R+ rotation condition and, value-wise, be close to that observed under the SIDE/R– condition, as this combination constituted the (imaginary) SIDE– eccentricity condition. No such an effect was observed, with moment of initiation of the first steering action systematically being close to 0.5 s under all CENTER eccentricity conditions. The second set of predictions concerned the presence and proportions of trials with a RMD. Under the SIDE eccentricity conditions, for both the Cross and Retreat target directions the proportion of trials with a RMD was expected to be higher under R+ (resembling Ceyte et al.'s SIDE+ condition) and lower under R– rotation conditions, compared to the R0 control condition. Moreover, under the CENTER eccentricity conditions, the presence of trials with a RMD was expected to emerge under the R+ rotation condition with a proportion close to that that observed under the SIDE/R– condition, as this combination constituted the (imaginary) SIDE– eccentricity condition. None of these predicted effects with respect to RMDs were observed.

4. General Discussion

The present contribution explored the visual guidance of locomotor interception by firstly addressing the question whether egocentric target direction plays a consequential role therein, as asserted by Rushton et al. (1998), Fajen and Warren (2004) and Chardenon et al. (2004). To this end, we began by examining the evidence presented in each of these studies, leading us to consider that methodological and/or conceptual shortcomings seriously undermined their conclusions. In short, Rushton et al.'s (1998) displacing-prism-glasses study, suggesting pursuit-like behavior based on egocentric target direction, was rather limited in scope, performed in a poorly-structured environmental with uncontrolled (but apparently very low

speed) target motion. The two other studies (Fajen & Warren, 2004; Chardenon et al., 2004), evaluating the effects of moving the (virtual) environment during interception, concluded in favor of reliance on changes in egocentric target direction *by default*, because the observed phenomena could not be explained by the only alternative (reliance on changes in target-heading angle) considered. Distinguishing the effects predicted by reliance on changes in the target's bearing angle from those predicted by reliance on changes in the target-heading angle, we showed that the phenomena observed in both studies could in fact be explained by reliance on changes in the target's bearing angle.

With Rushton et al.'s (1998) study thus being the only one to provide at least a pointer towards a potential role of egocentric target direction in locomotor interception, in the present contribution we called upon an experimental manipulation akin to theirs. To this end we explored the effects on interception behavior of a constant rotation of the visual scene, that is of both the (virtual) environment and the target. We did this in the framework of an experimental situation (targets moving uniformly from SIDE and CENTER initial eccentricities) also allowing distinctive patterns of behavior to emerge when participants relied on (changes in) the target-heading angle β or on (changes in) the target's bearing angle θ. While an interception strategy based on $d\theta/dt$-nulling is capable of explaining almost all aspects of observed locomotor behavior, Ceyte et al.'s (2021) study pinpointed a phenomenon that was not compatible with such full reliance on the rate of change in the target's bearing angle: under SIDE eccentricity conditions, participants regularly, although not consistently, first steered in the direction of the target, before reversing direction and steering onto an interception course. Such reversals in movement direction (RMD) were observed for the Cross and Retreat target directions, where the target was captured on the side opposite to initial target position, defined with respect to initial participant heading. Indeed, under these conditions the moment of initiation of the first steering action appeared to determine whether a RMD occurred or not, with early initiation being associated with the presence of RMDs. Moreover, when a RMD was observed, the amplitude of the initial movement in the direction of the target was larger the earlier the first steering action had been initiated. Finally, Ceyte et al. (2021) demonstrated that a larger initial target eccentricity gave rise to a higher proportion of trials with a RMD. In each of the two experiments reported in the present study we fully replicated Ceyte et al.'s above-described pattern of results for the CENTER and SIDE eccentricity conditions. We thus confirmed the selective appearance of trials with a RMD for specific combinations of initial target eccentricity and target motion direction. Moreover, we confirmed the co-existence of trials with a RMD and trials without a RMD under these specific initial conditions, with RMDs appearing only for trials with an early initiation of the first steering action. These RMD related results were observed for (almost) all participants and were thus not participant-specific. For uniformly-moving targets this direction-reversal phenomenon indicates that the information used cannot be purely first-order (i.e., rate-of-change based). It therefore echoes the angle-of-approach effect observed in direction-constrained manual (Arzamarski et al., 2007; Dessing and Craig, 2010; Dessing et al., 2005; 2009; Jacobs and Michaels, 2006; Ledouit et al., 2013; Michaels et al., 2006; Montagne et al., 1999; Peper et al., 1994) and locomotor (Bootsma et al., 2016) interception, also indicating

that the information used cannot be purely first-order but carries traces of an influence of initial target position.

While clearly not being able to explain the generally observed behavioral patterns of locomotor interception, egocentric target direction might therefore play a role early on, when the agent discovers the target. The predictions tested with respect to the effects on interception behavior that such an early role of egocentric target direction would evoke concerned both the timing of the moment of initiation of the first steering actions and the characteristics of RMDs. The results clearly did not comply with these predictions. Predicted to be earlier, initiation under the augmented (R+) SIDE target eccentricity was in fact found to be later relative to its R0 control. None of the other predictions bore out either, whether they concerned the initiation of first steering action when initial target direction (R+) was affected under the CENTER or the proportion of trials with a RMD under R+ and R– rotation conditions. How, then, should we interpret the overall pattern of result?

As argued by Bootsma et al. (2016), in the direction-constrained paradigm reasoning on the basis of the target's bearing angle allows one to consider (full or partial) reliance on zeroth-order (i.e., position-related) information in the control of locomotion, while reasoning on the basis of target-heading angle does not. The angle-of-approach effect observed in their study led Bootsma et al. (2016) to suggest that both first- and zeroth-order bearing angle information (i.e., $d\theta/dt$ and θ) played a role in intercepting rectilinearly moving targets. Rather than resorting to some unprincipled combination of two information sources, Bootsma et al. (2016) proposed reliance on fractional-order information $d\theta^{\alpha}/dt^{\alpha}$, with α slightly below 1 for (quasi) uniformly moving targets. Because fractional-order change is not locally defined, but integrates recent history, acting as "shadows on the walls" as Podlubny (2002) put it, the initial target position θ plays a role early on. We might thus speculate that, being the first available information, egocentric target position could perhaps simply serve to determine the environmental reference providing θ_0, but further work is needed on this subject.

However all this may be, the two experiments of the present contribution once again confirmed that in a structured environment locomotor interception is not guided by (i) a strategy based on nulling egocentric target direction (i.e., β_{e1}-nulling), as suggested by Rushton et al. (1998), (ii) a strategy based on nulling changes in egocentric target direction (i.e., $d\beta_{e2}/dt$-nulling), as suggested by Fajen and Warren (2004; also see Rushton & Allison, 2013), or (iii) a strategy based on nulling optically-specified changes in target-heading angle (i.e., $d\beta_{os}/dt$-nulling, as suggested by Zhao et al. (2019, 2021). The general results are, however, once again compatible with a strategy of nulling changes in the target's bearing angle (with the caveat that such change-nulling is based on $d\theta^{\alpha}/dt^{\alpha}$ rather than on conventional $d\theta/dt$-nulling).

Change in bearing angle is specified by local flow *around* the target. This can be most simply illustrated in the situation of a structured background against which the target is seen: the target's bearing angle is constant if the target does not move relative to the background. Change in the target's bearing angle is thus specified by relative motion between the target

and its (surrounding) background[5]. But even when the background is not sufficiently structured, changes in the target's bearing angle can be recovered from local target motion with respect to a structured ground plane or local motion parallax of ground surface elements around the target (cf. Cutting et al., 1995). It is thus only in the situation of an absence of any useful environmental structure that the strategy of nulling changes in the target's bearing angle cannot be used. The agent, then, cannot but revert to a strategy based on (changes in) egocentric target direction, as this is the only information available. This was most likely the case in Rushton et al.'s (1998) study, where uncontrolled (and apparently low) target speed evoked pursuit-like interception behavior.

Finally, the present work leads us launch a plea in favor of a clear distinction and systematic labeling of potential information sources. Neither Fajen and Warren (2004) nor Chardenon et al. (2004) clearly distinguished target-heading angle β from the target's bearing angle θ, resulting in the erroneous default-based conclusion in favor of egocentric target direction. In fact, the literature on direction-constrained locomotor interception has almost systematically referred to the target's bearing angle when, in fact, the work focused on the target-heading angle (Bastin et al., 2006, 2008; Chardenon et al., 2002, 2004, 2005; Chohan, 2006, 2008; Francois et al., 2011; Lenoir et al., 1999a, 1999b, 2002; Morice et al., 2010; also see Louveton et al., 2010, 2012)[6]. The confusion between potential information sources, due to non-systematic distinction and labeling, is quite wide-spread throughout the animal literature as well; as an example, Kane et al. (2014) refer to target-heading angle as bearing angle and to bearing angle as absolute target direction. Our plea in favor of a clear distinction and systematic labelling of potential information sources not only applies to reporting of one's own work, but also to interpreting and reporting results of other studies.

[5] Lenoir et al.'s (1999b) results with respect to a background effect on interception behavior might in this light be re-interpreted as relating to the detection of changes in the target's bearing angle (facilitated in the presence of a textured background) than rather than as relating to perceived target speed, because perceived target speed is not a pertinent variable in the framework of the proposed locomotor interception control strategy.

[6] Present contribution author RB co-authored several of these studies, at the time simply having been unaware of the distinction. In direction-constrained locomotor interception paradigms used in those studies the two angles indeed typically covary and the research focused on the interception control strategy of striving to null the rate of angular change. Confounding target-heading angle with the target's bearing angle in a direction-constrained paradigm is then not necessarily harmful … unless, of course, experimental manipulations involve displacement of the environment, as in Chardenon et al. (2004).

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6. Figure legends

Figure 1: Definition of variables in a plan view of an agent moving through an environment containing a target moving in the same plane. Instantaneous velocity vectors are represented by arrows (red for agent, green for target). (**A**) From left to right: egocentric target direction defined relative to the body midline (A-P) orientation (dashed line, β_{e1}, Rushton et al., 1998), egocentric target direction defined relative to felt (proprioceptively perceived) locomotor direction (β_{e2}, Fajen & Warren, 2007), and target direction defined relative to optically-specified heading direction (β_{os}). (**B**) Agent heading ϕ and target bearing θ are defined with respect to an exocentric reference direction (dashed blue line). Target-heading angle β is defined by the eccentricity of the target with respect to the agent's direction of locomotion so that $\beta = \phi - \theta$. Uniform target movement is defined by invariance of the target's velocity vector in both orientation and magnitude.

Figure 2: Plan view of the initial conditions of the experiments. (**A**) Experiment 1: the target appeared at CENTER (0°) or SIDE (23°) eccentricities with respect to the participant's initial heading direction. Under both eccentricity conditions, the target moved at 10 m/s along Cross (Cr), Retreat (Re), or Approach (Ap,) directions, corresponding to orientations of 0°, +30° and –30°, respectively, with respect to the direction orthogonal to the participant's initial heading direction. (**B**) Experiment 2: Initial target eccentricities and target directions used were identical to those of Exp. 1, but now combined with 0°, 10° outward and 10° inward rotations of the visual scene (target + virtual environment). For rightward moving targets these rotations give rise to, respectively, no change in egocentric target direction (R0, gray), a leftward direction shift increasing egocentric target eccentricity for the left SIDE condition (R+, green) and a rightward shift decreasing egocentric target eccentricity for the left SIDE condition (R–, red). Conditions were mirrored for leftward moving targets (not shown here).

Figure 3: Experiment 1: Overall average locomotor paths (in black) under the CENTER and SIDE eccentricity conditions for the Approach, Cross, and Retreat target directions. Grey outline dots and attached line segments indicate initial target positions and subsequent target trajectories.

Figure 4: Experiment 1: Evolution over time, up to 0.5 s before interception, of the target's bearing angle (θ, black lines) and the target-heading angle (β, grey lines) under the CENTER and SIDE eccentricity conditions for the Approach, Cross, and Retreat target directions. Note the early dip below zero in the target-heading angle β under the CENTER eccentricity condition. The subsequent change from an early lag (negative β, indicating steering behind the target) to a later lead (positive β, indicating steering ahead of the target) in locomotor direction is not compatible with a strategy of nulling $d\beta/dt$.

Figure 5: Experiment 1: Locomotor paths (zoomed-in view) of all individual trials (thin lines) under the CENTER and SIDE eccentricity conditions for the Cross and Retreat target directions. Trials with a reversal in movement direction (RMD trials) are depicted in light red and trials without a reversal in movement direction (NoRMD trials) in light blue. Red circles indicate pre-reversal excursion amplitudes. Fat lines represent time-averaged averaged locomotor paths for RMD trials (red), for NoRMD trials RMD (blue), and for all trials (black). Note that RMD trials occurred regularly under the two depicted SIDE eccentricity conditions (right panels) while being absent under the corresponding CENTER eccentricity conditions (left panels).

Figure 6: Experiment 2: Overall average locomotor paths under the CENTER and SIDE eccentricity conditions for the Approach, Cross, and Retreat target directions. Rotation conditions of the Target + Virtual Environment are presented with R0 in black, R+ in green and R– in red. Grey outline dots and

attached line segments indicate initial target positions and subsequent target trajectories. The slight shifts between the paths reflect minor differences in the moments of initiation of the first steering action.

Table 1: Means and between-participant standard deviations (*M* ± *SD*) for Experiment 1 of Success Rate (SR), Time until Closest Distance (TCD) and Moment of Initiation of first steering action (MoI) for the Approach, Cross and Retreat target directions under the CENTER and SIDE target eccentricity conditions.

		SR (%)	TCD (s)	MoI (s)
CENTER	Approach	80.0 ± 17.3	2.80 ± 0.05	0.48 ± 0.04
	Cross	100.0	3.71 ± 0.04	0.48 ± 0.04
	Retreat	100.0	4.72 ± 0.03	0.49 ± 0.05
SIDE	Approach	64.0 ± 15.2	2.35 ± 0.00	0.76 ± 0.16
	Cross	96.0 ± 5.5	2.94 ± 0.01	0.99 ± 0.17
	Retreat	96.0 ± 8.9	3.94 ± 0.01	1.00 ± 0.16

Table 2: Means and between-participant standard deviations (*M* ± *SD*) for Experiment 2 of Success Rate (SR), Time until Closest Distance (TCD) and Moment of Initiation of first steering action (MoI) under the R0, R+, and R– rotation conditions for the Approach, Cross and Retreat target directions under the CENTER and SIDE target eccentricity conditions.

		SR (%)			TCD (s)			MoI (s)		
		R0	R+	R–	R0	R+	R–	R0	R+	R–
CENTER	Approach	81.9 ± 18.7	77.5 ± 21.8	87.5 ± 19.2	2.78 ± 0.05	2.79 ± 0.06	2.76 ± 0.05	0.50 ± 0.04	0.50 ± 0.05	0.50 ± 0.05
	Cross	95.6 ± 7.3	100.0	93.8 ± 12.0	3.69 ± 0.05	3.71 ± 0.04	3.68 ± 0.09	0.49 ± 0.04	0.50 ± 0.04	0.50 ± 0.04
	Retreat	98.1 ± 5.4	100.0	100.0	4.72 ± 0.03	4.73 ± 0.04	4.72 ± 0.04	0.50 ± 0.04	0.51 ± 0.05	0.51 ± 0.06
SIDE	Approach	68.1 ± 12.2	71.3 ± 19.3	66.3 ± 22.8	2.35 ± 0.00	2.36 ± 0.01	2.36 ± 0.00	0.74 ± 0.10	0.77 ± 0.09	0.81 ± 0.10
	Cross	92.5 ± 7.8	95.0 ± 11.6	92.5 ± 12.4	2.94 ± 0.01	2.94 ± 0.01	2.93 ± 0.00	1.25 ± 0.24	1.37 ± 0.28	1.19 ± 0.23
	Retreat	97.5 ± 5.8	97.5 ± 6.8	96.3 ± 8.1	3.96 ± 0.01	3.96 ± 0.03	3.95 ± 0.01	1.16 ± 0.28	1.24 ± 0.37	1.13 ± 0.34

Table 3: Repartitioning (number and percentage, as total number of trials differed over rotation conditions) of trials with a RMD for Experiment 2 over the R0, R+, and R– rotation conditions for the Approach, Cross and Retreat target directions under the CENTER and SIDE target eccentricity conditions. Percentage RMD trials in SIDE/Cross and SIDE/Retreat conditions are highlighted in boldface.

	Approach			Cross			Retreat		
	R0	R+	R–	R0	R+	R–	R0	R+	R–
Total trials per condition	160	80	80	160	80	80	160	80	80
CENTER	0 0.0%	2 2.5%	0 0.0%	3 1.9%	1 1.3%	2 2.5%	1 0.6%	5 6.3%	0 0.0%
SIDE	5 3.1%	5 6.3%	8 10.0%	52 **32.5%**	25 **31.3%**	15 **18.8%**	30 **18.8%**	18 **22.5%**	12 **15.0%**

Figure 1

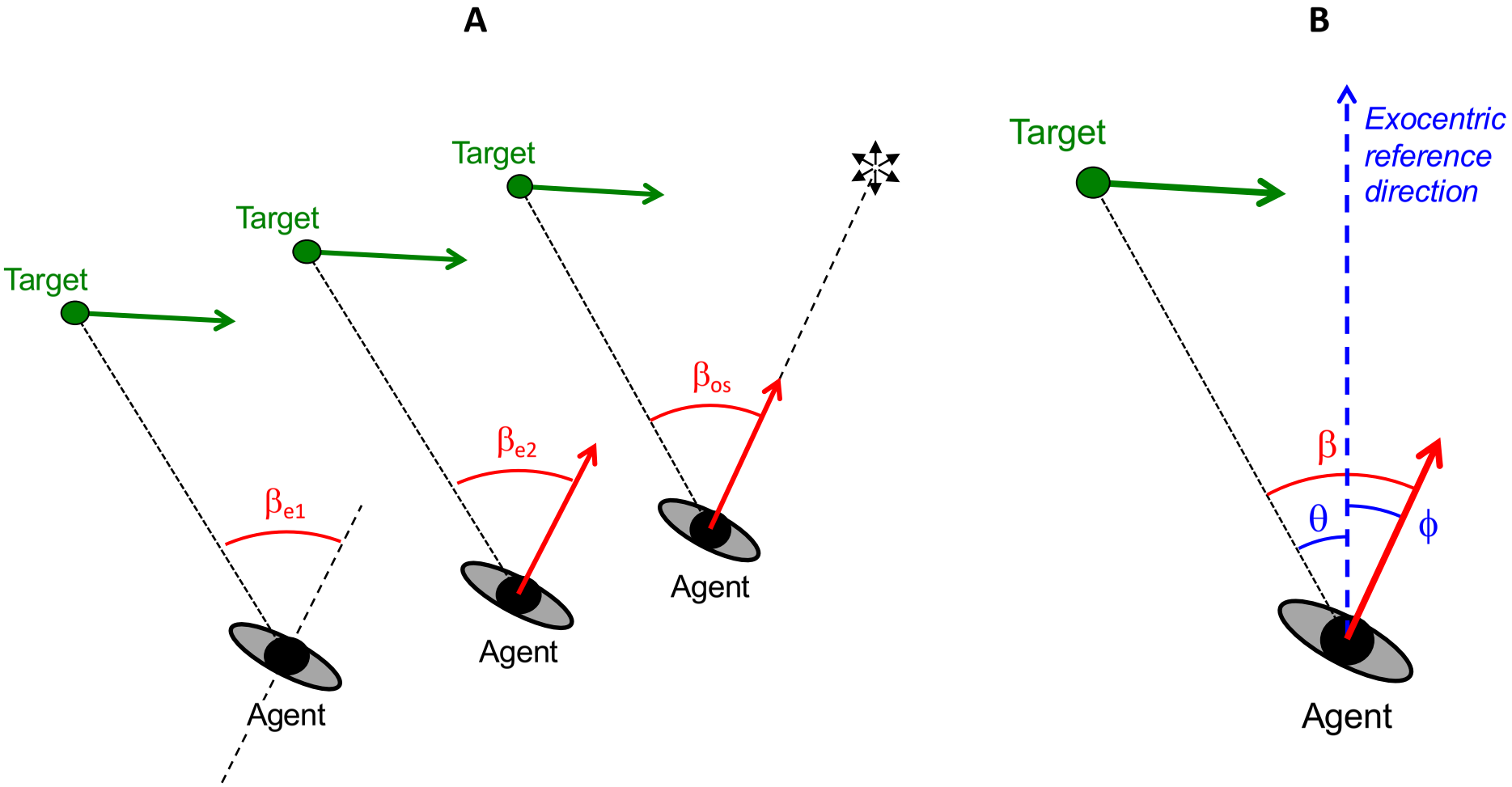

A
Target
Target
Target
Agent
Agent
Agent
β_{e1}
β_{e2}
β_{os}
B
Target
Exocentric
reference
direction
Agent
β
θ
ϕ

Figure 2

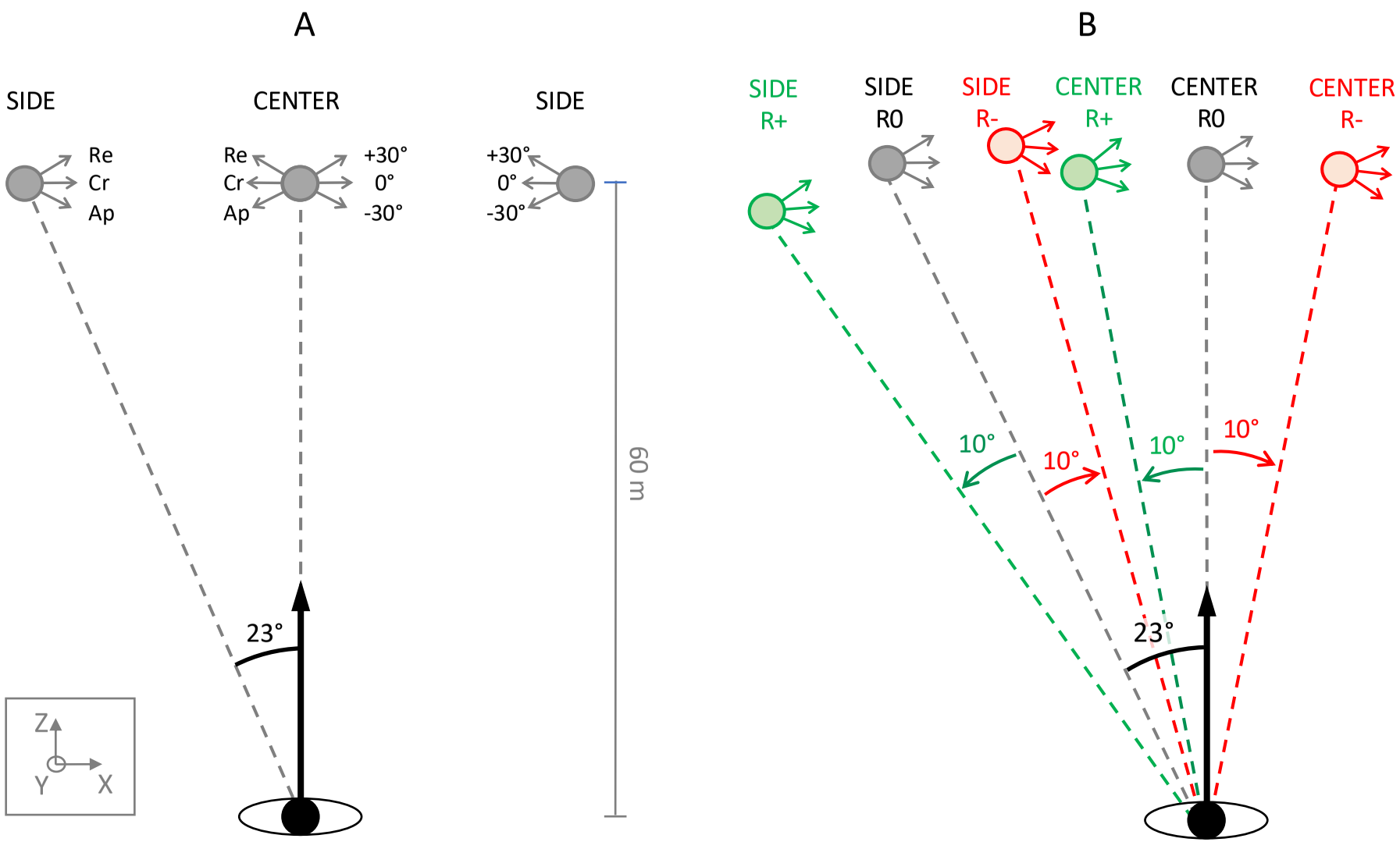

A
SIDE
CENTER
SIDE
Re
Cr
Ap
Re
Cr
Ap
+30°
0°
-30°
+30°
0°
-30°
60 m
23°
Z
Y
X
B
SIDE
R+
SIDE
R0
SIDE
R-
CENTER
R+
CENTER
R0
CENTER
R-
10°
10°
10°
10°
23°

Figure 3

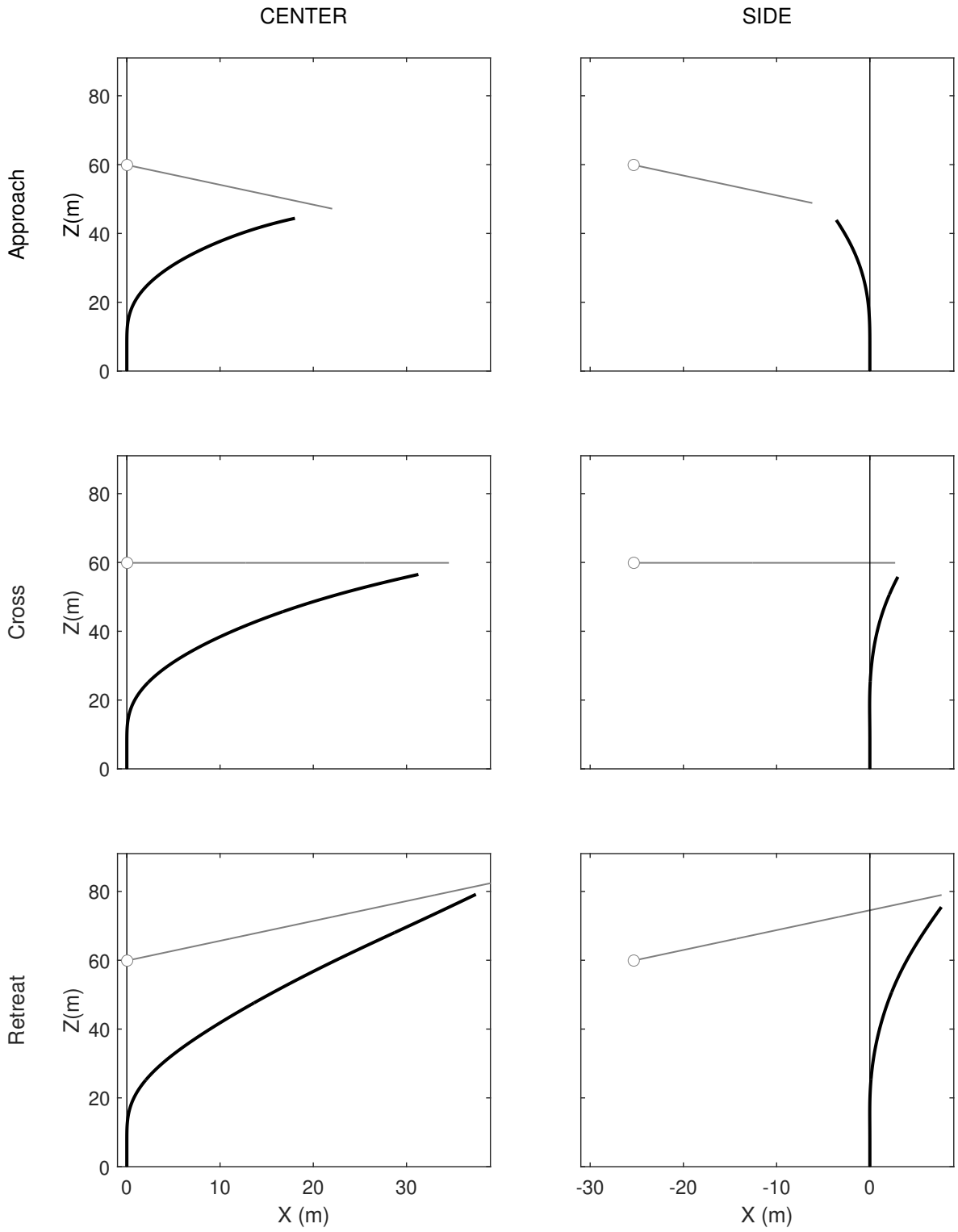

CENTER
SIDE
Approach
Cross
Retreat
Z(m)
X (m)
0
20
40
60
80
0
10
20
30
-30
-20
-10
0

Figure 4

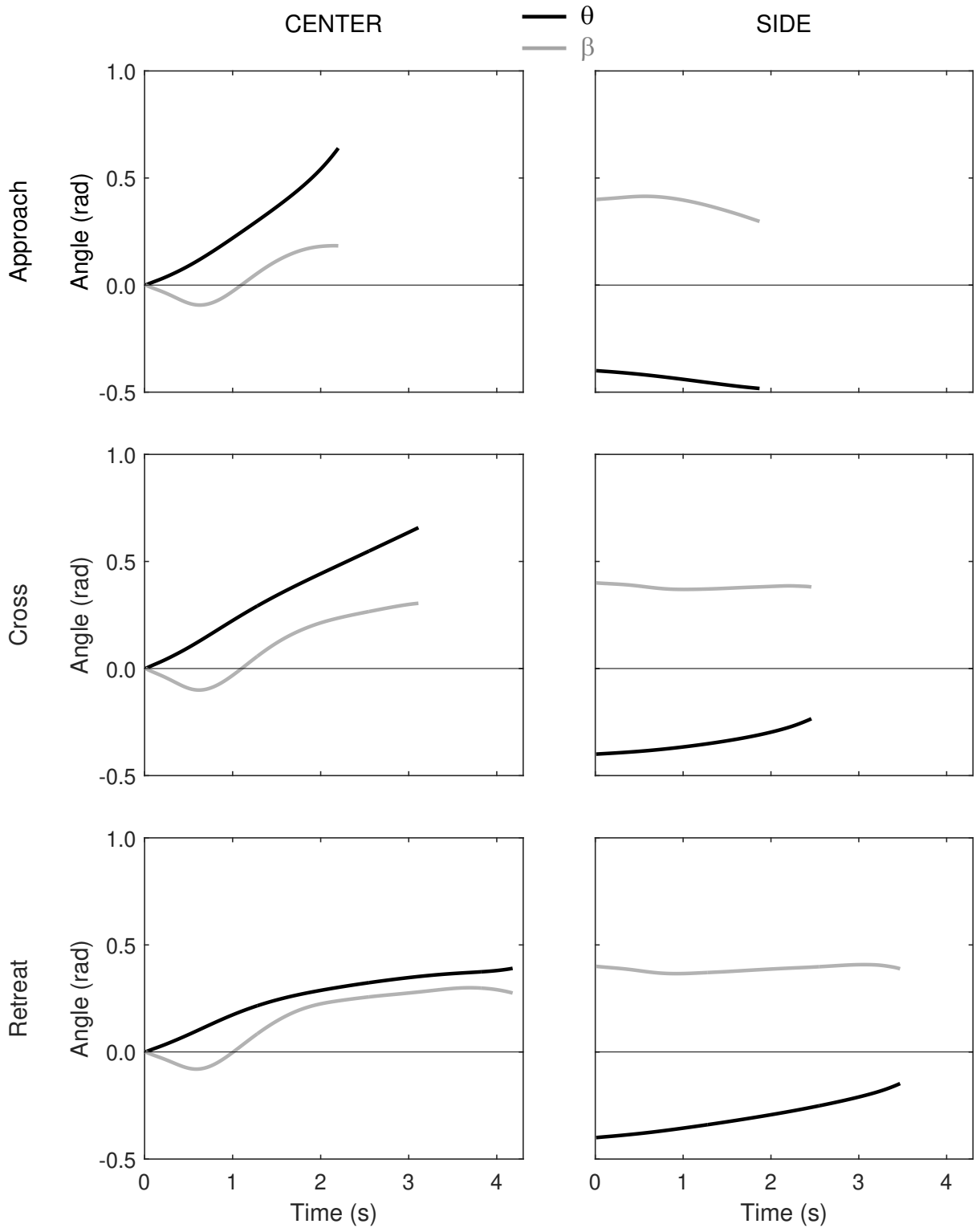

CENTER
SIDE
θ
β
Approach
Cross
Retreat
Angle (rad)
1.0
0.5
0.0
-0.5
0
1
2
3
4
Time (s)

Figure 5

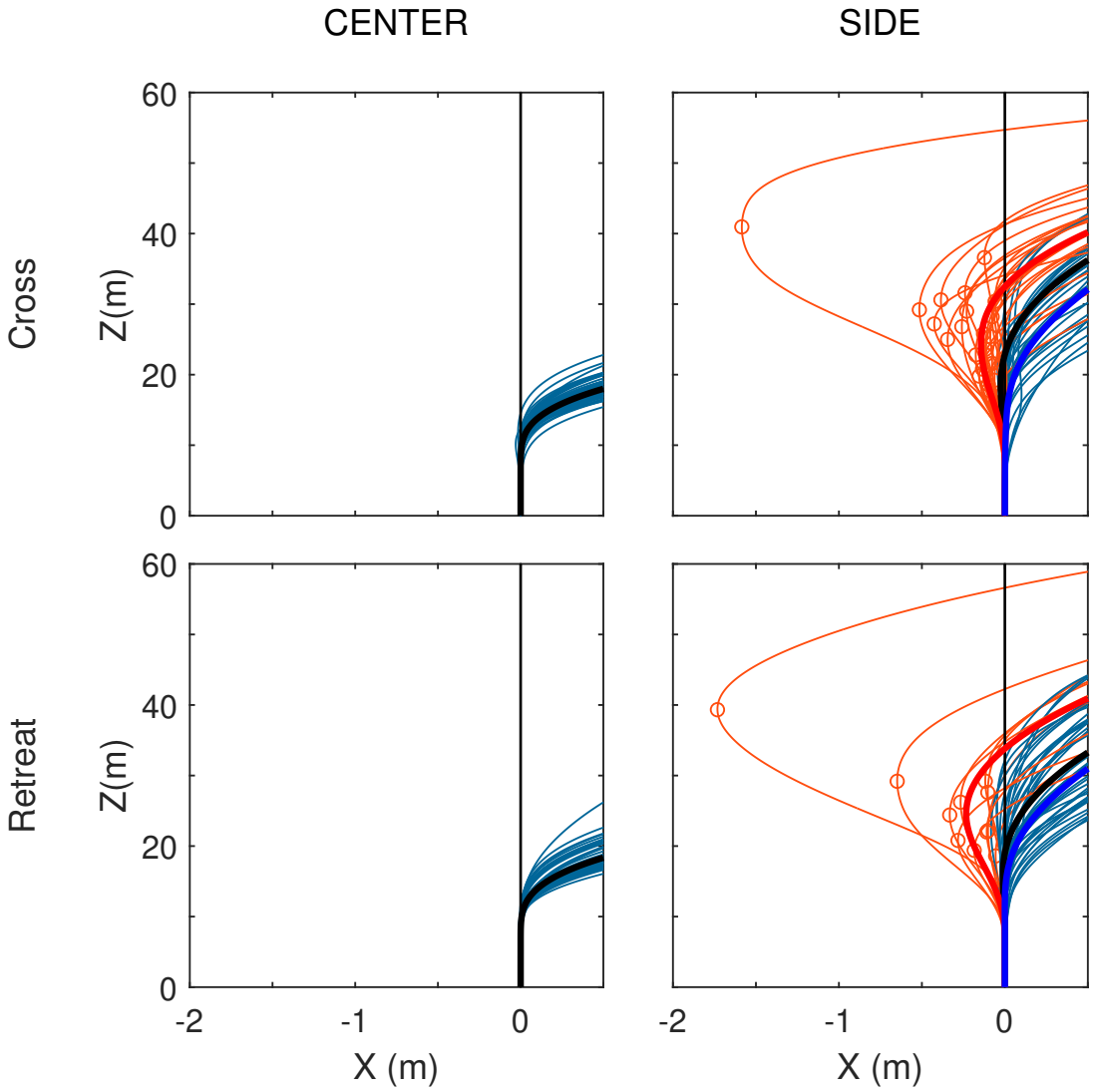
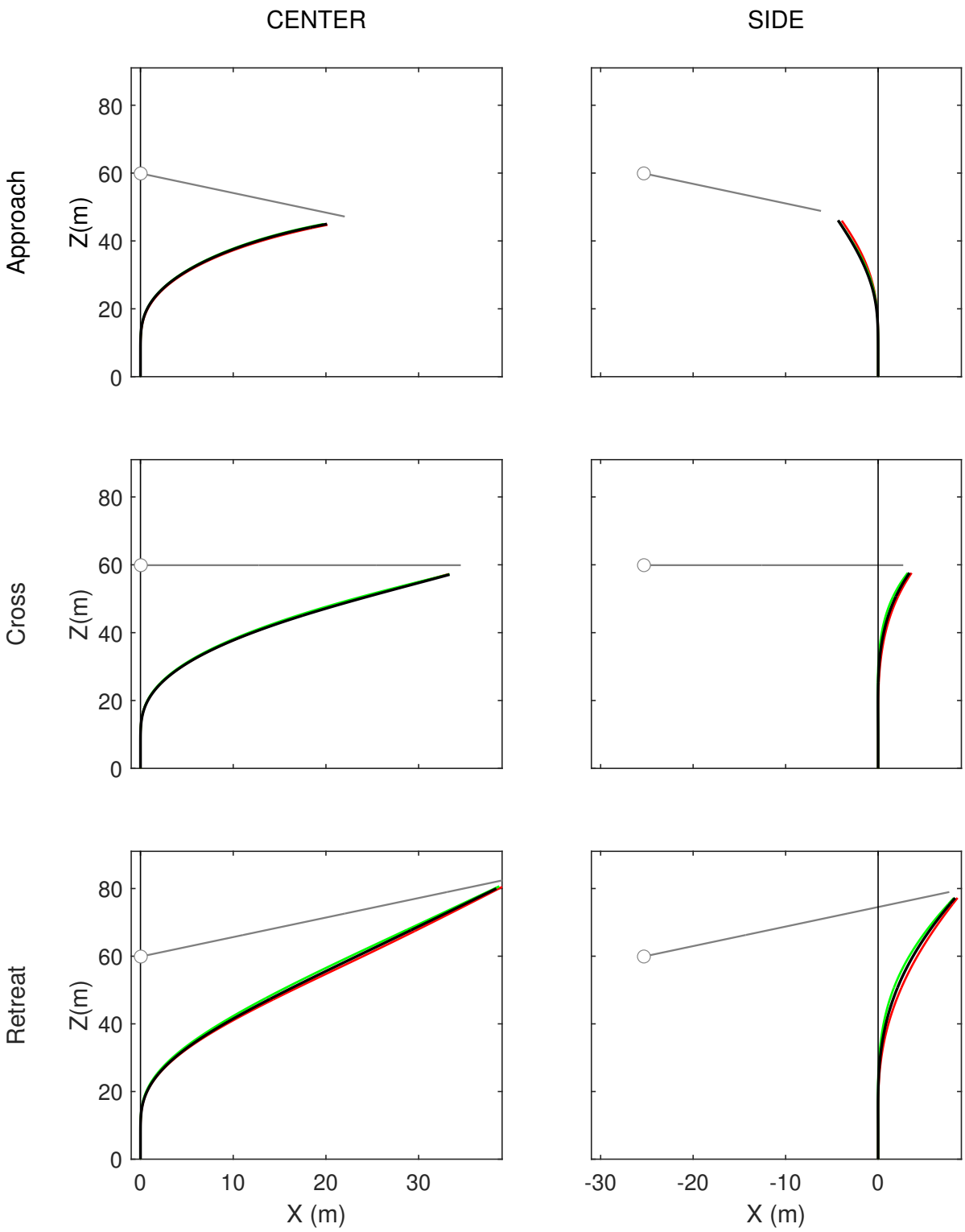


Figure 6


CENTER
SIDE
Approach
Cross
Retreat
Z(m)
0
20
40
60
80
0
10
20
30
-30
-20
-10
0
X (m)