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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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► **To cite this version:**

Remy Casanova, Gwenaelle Ceyte, Reinoud J. Bootsma. Visual guidance of locomotor interception is based on nulling changes in target bearing (not egocentric target direction nor target-heading angle). Human Movement Science, 2022, 82, 10.1016/j.humov.2022.102929 . hal-03551910

**HAL Id: hal-03551910**

**<https://amu.hal.science/hal-03551910>**

Submitted on 23 Jun 2022

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3 **Visual guidance of locomotor interception is based on nulling changes in**  
4 **target bearing (not egocentric target direction nor target-heading angle)**  
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13 Remy Casanova, Gwenaëlle Ceyte, and Reinoud J. Bootsma\*

14 Aix Marseille Université, CNRS, Institut des Sciences du Mouvement, Marseille, France  
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23 \* Corresponding author:

24 Reinoud Bootsma

25 *Postal address:*

26 Institut des Sciences du Mouvement ISM - UMR 7287, Bât. FSS, 163 avenue de Luminy,  
27 13288 Marseille Cedex 9, France.

28  
29 *Email:*

30 reinoud.bootsma@univ-amu.fr

31  
32 *ORCID:*

33 <https://orcid.org/0000-0002-3719-7586>  
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39 **Keywords:** interception, steering, information, reversal movements, heuristics, dynamics,  
40 fractional order  
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44 **Declarations of interest: none**  
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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

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2 Notwithstanding extensive research, the information used in the visual guidance of locomotor  
3 interception<sup>1</sup> remains subject of debate. Identifying the information used requires specifying  
4 both the *what*, that is, the source(s) of information relied upon, and the *how*, that is, the  
5 particular manner of integration of the information into movement (Bootsma et al., 1997;  
6 Bootsma, 1998). For locomotor interception potential information sources identified typically  
7 include (changes in) egocentric target direction, target-heading angle and the target's bearing  
8 angle (see **Fig. 1** for definitions).  
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12 \*\*\*\*\* Figure 1 (definitions of angles here) \*\*\*\*\*  
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15 For operational reasons, we begin our examination of the relevant literature by focusing on  
16 egocentric target direction. Indeed, three different studies (Rushton et al., 1998; Fajen &  
17 Warren; 2004; Chardenon et al., 2004) all concluded that egocentric visual information plays  
18 a substantial role in the control of locomotor interception. Yet, all three studies suffer from  
19 methodological and/or conceptual shortcomings, thereby seriously weakening the case in  
20 favor of reliance on perceived egocentric target direction.  
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24 We note that Rushton et al.'s (1998) study primarily focused on visual guidance of (on foot)  
25 locomotion towards a *stationary* target. Egocentric target location, defined relative to the  
26 body's midline, was experimentally manipulated by having participants wear displacing prism  
27 glasses. In the environmental setting of a homogenous grass lawn, this condition gave rise to  
28 curved, rather than straight, locomotor paths to the target. With path curvature globally  
29 corresponding to the prism-induced constant heading error, Rushton et al. (1998) concluded  
30 that locomotion is guided by the target's egocentric direction rather than by global optic flow:  
31 participants steered by walking in the target's egocentric direction rather than by placing the  
32 global optic flow's focus of expansion (i.e., heading direction) on the target. While such  
33 predominance of egocentric target direction over global optic flow was later qualified as  
34 depending on the richness of the available flow (cf. Warren et al., 2001), the main point of  
35 interest for the present purposes is that Rushton et al.'s (1998) description of effects observed  
36 when locomoting to intercept a *moving* target was limited to the general statement that  
37 "results were similar to those for the previous static target set. The value of the [target-  
38 locomotor direction] error was found to remain approximately constant throughout the trial  
39 (...) as predicted by the perceived-direction model." (p. 1193), accompanied by the  
40 presentation of two exemplary trials (Fig. 4, p. 1194). From this figure's caption it appears  
41 that target motion was not experimentally controlled either in magnitude or in direction.  
42 Overall, Rushton et al.'s (1998) results with respect to locomoting to intercept a moving  
43 target, suggesting a pursuit-like interception strategy based on continuously steering in the  
44 egocentric target direction, should therefore be considered as preliminary at best and perhaps  
45 specific to the particular setting. We will come back to this in the general discussion.  
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58 <sup>1</sup> Locomotor interception is operationally defined as making contact with a moving target by means of whole-  
59 body displacement. Contrary to manual interception tasks (accomplished by hand displacement), locomotor  
60 interception tasks thus imply displacement of the point of observation.  
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1 In a systematic study of locomotor interception of uniformly moving targets Fajen and  
2 Warren (2004) demonstrated that freely walking participants did not implement a pursuit-like  
3 interception strategy. Rather, they systematically steered ahead of the moving target, with  
4 locomotor paths eventually straightening out, when time until interception was sufficiently  
5 long. In four experiments Fajen and Warren (2004) explored visual guidance of locomotor  
6 interception by the target's egocentric direction, local optic flow from the target, and global  
7 optic flow from the environment. Noteworthy in the present context, Fajen and Warren (2004)  
8 defined egocentric target direction as the target's eccentricity with respect to felt, that is,  
9 proprioceptively perceived direction of locomotion, thus adopting a definition different (see  
10 **Fig. 1A**) from that of Rushton et al. (1998).

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

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44 Indeed, Fajen and Warren (2004) did not consider the consequences of their environmental  
45 rotation and displacement manipulations in terms of their effects on another potentially  
46 pertinent source of information, namely changes in the target's bearing angle. In fact, in their  
47 2004 contribution Fajen and Warren regularly appear to consider target-heading angle and the  
48 target's bearing angle as referring to the same angular quantity ( $\beta$ , as defined in **Fig. 1B**),  
49 alternating use of both terms. However, as subsequently pointed out in Fajen and Warren  
50 (2007) and illustrated in **Figure 1B**, the target's bearing angle  $\theta$  is qualitatively different from  
51 the target-heading angle  $\beta$ , with  $\theta$  defined relative to an exocentric reference direction and  $\beta$   
52 defined relative to the agent's movement direction. Because continuous rotation and  
53 displacement of the environment with respect to the observer affect the pattern of change in  
54 the target's bearing angle in ways opposite to their influences on the pattern of change in the  
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1 optically-specified target-heading angle<sup>2</sup>, reliance on changes in the target's bearing angle can  
2 in fact explain the experimental effects of environmental motion reported by Fajen and  
3 Warren (2004).  
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5 A similar lack of distinction between target-heading angle  $\beta$  and the target's bearing angle  $\theta$   
6 is found in Chardenon et al.'s (2004) study of direction-constrained locomotor interception,  
7 with participants regulating walking velocity on a servo-controlled treadmill to intercept  
8 targets moving toward their locomotor axis from the right. Inappropriately referring to the  
9 target-heading angle as the target's bearing angle (see their Fig. 1C, p. 101), Chardenon et al.  
10 (2004) evaluated the effects of continuous lateral displacement of the ground surface on  
11 locomotor speed, using targets coming in from the right. A right-left sawtooth-shaped pattern  
12 of displacement of the ground surface during interception evoked changes in walking speed  
13 characterized by an acceleration followed by a deceleration; the inverse pattern was observed  
14 for a left-right ground surface displacement, with participants here first decelerating and  
15 subsequently accelerating their walking speed during interception. Lateral ground surface  
16 displacement thus clearly affected locomotor speed, the relevant action variable in direction-  
17 constrained locomotion (Bootsma et al., 2016). Like Fajen and Warren (2004), Chardenon et  
18 al. (2004) argued that the effects provoked by ground surface motion were opposite in  
19 direction to the effects predicted by reliance on changes in optically-specified target-heading  
20 angle (improperly denoted bearing angle) and could not, therefore, reflect an effect of  
21 manipulating this informational quantity. Analogous to Fajen and Warren (2004), this led  
22 them to conclude, by default, that participants must then have relied on egocentric target  
23 direction. Once again, however, we argue that, because continuous displacement of the  
24 environment with respect to the observer affects the pattern of change in the target's bearing  
25 angle  $\theta$  in ways opposite to its influence on the pattern of change in the target-heading angle  
26  $\beta_{os}$ , changes in the target's bearing angle can, in fact, explain the experimental effects  
27 reported by Chardenon et al. (2004)<sup>3</sup>.  
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38 Because the target's bearing angle is defined with respect to an exocentric reference direction,  
39 detection of changes in bearing angle does not require detection of heading direction. While  
40 the latter may be recovered from global optic flow or from felt displacement, the former may  
41 be recovered from local flow *around* the target, that is, from the relative motion of target with  
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46 <sup>2</sup> To illustrate this with an example, let us assume that an agent is currently on an interception course with a  
47 uniformly-moving target, coming in from the right. In this situation the target, situated on the right, does not  
48 visually move (both target-heading angle and bearing angle are constant). A continuous rightward displacement  
49 of the environment optically specifies a leftward component of self-motion, thereby reorienting the agent's  
50 optically-specified heading direction with respect to the environment leftward. With the target situated on the  
51 right, this leads to *opening of the target-heading angle*. Since the target's bearing angle is defined, at the point of  
52 observation, by the target's direction with respect to the environment, the same continuous rightward  
53 displacement of the environment results in a leftward displacement of target with respect to the environment,  
54 thereby moving it inward from its (initially stable) position on the right. This leads to *closing of the target's*  
55 *bearing angle*.  
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57 <sup>3</sup> As rightward displacement of the environment (here ground surface) leads to closing of the bearing angle for a  
58 target moving inward from the right (see footnote 1), reliance on changes in the target's bearing angle would  
59 bring the agent to accelerate. The opening of the target's bearing angle, induced by leftward displacement of the  
60 environment, would bring the agent to decelerate. These predictions perfectly correspond to the results reported  
61 by Chardenon et al. (2004).  
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1 respect to its visual surroundings provided by the environment (background and ground  
2 surface texture elements and/or objects). As Cutting et al. (1995) eloquently reported in their  
3 psychophysical study of information for avoiding (or provoking) collision with stationary and  
4 moving objects: “When observers are fixated on a stationary object, their ability to find their  
5 aimpoint is good and adequate to the task. When observers are fixated on a moving object, on  
6 the other hand, (...) generally they have no clue where they are going.” (p. 635).  
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9 We have so far argued that the results of the locomotor interception studies of Fajen and  
10 Warren (2004) and Chardenon et al. (2004) may be explained by participants’ reliance on  
11 changes in the target’s bearing angle and would therefore not require evoking, as both these  
12 studies did, the default option of reliance on changes in the target’s egocentric direction. What  
13 further evidence do we have that pleads in favor of visual guidance of locomotor interception  
14 by changes in the target’s bearing angle? As argued by Bootsma et al. (2016, cf. Ceyte et al.,  
15 2021), direct evidence for any interception strategy requires defining such strategies not in  
16 terms of rule-of-thumb heuristics (defining what one should be doing) but in terms of  
17 dynamics (defining how one might get there), that is, in terms of how the system evolves over  
18 time toward a steady-state regime. Adopting such a dynamical perspective leads one to focus  
19 on transients rather than on steady-state regimes only. Modeling the behavioral dynamics of  
20 steering control in locomotor interception in this spirit, Fajen and Warren (2007)  
21 demonstrated that, contrary to their 2004 assertions, a steering model based on nulling  
22 changes in target-heading angle could, in fact, not even adequately explain the interception  
23 behavior (observed in their 2004 study) under stable environmental conditions. This, perhaps  
24 surprising, inadequacy of the classical interception strategy (cf. Bootsma et al., 2016) notably  
25 came to the fore when the target moved outward from an initial location directly ahead of the  
26 walking participant. At the onset of such a trial the outward-moving target created an  
27 immediate behavioral lag, characterized by the opening of the target-heading angle  $\beta$ . Under  
28 this initial condition nulling changes in  $\beta$ , by nulling  $d\beta/dt$ , did not lead to the experimentally  
29 observed steering ahead of the target, as all that could be accomplished by such a  $d\beta/dt$ -  
30 nulling interception strategy was reducing the  $\beta$ -lag over time. Modeling an interception  
31 strategy based on nulling  $d\theta/dt$ , on the other hand, did systematically lead to the  
32 experimentally observed steering ahead of the target. Thus, Fajen and Warren (2007)  
33 concluded that the observed phenomena were only adequately captured by a strategy of  
34 nulling changes in the target’s bearing angle.  
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47 In Fajen and Warren’s (2004) study, the target could initially be located straight ahead of the  
48 participant (CENTER condition) or to the left or right (SIDE condition), with targets moving  
49 at constant speed along Approach, Cross and Retreat directions (see **Fig. 2A** for definitions).  
50 Using a simulated driving task, Ceyte et al. (2021) recently studied locomotor interception  
51 with CENTER ( $0^\circ$ ) and SIDE ( $23^\circ$ ) initial target eccentricity conditions complemented by a  
52 SIDE+ ( $32^\circ$ ) eccentricity condition and with target directions (Approach, Cross, Retreat)  
53 complemented with a more direct Approach+ condition. Notwithstanding the task differences  
54 (real walking vs. simulated driving, with the latter thus not including physical displacement),  
55 Ceyte et al.’s (2021) overall pattern of results revealed strong similarities with Fajen and  
56 Warren (2004)’s findings. Since under all three target eccentricity conditions participants  
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1 were again found to systematically steer ahead of the moving target, Ceyte et al.'s (2021)  
2 results provided complementary evidence for an interception strategy relying on nulling  
3 changes in the target's bearing angle (i.e., on nulling  $d\theta/dt$ ) and, at the same time, against  
4 reliance on changes in target-heading angle (i.e., on nulling  $d\beta/dt$ ), whether it be defined  
5 egocentrically or otherwise.  
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8 \*\*\*\*\* Figure 2 (experimental conditions) about here \*\*\*\*\*  
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10 In the present experimental contribution, we explored whether a manipulation akin to that  
11 used by Rushton et al. (1998) would affect interception behavior in the simulated locomotor  
12 interception-by-steering task developed by Ceyte et al.'s (2021). To this end we compared  
13 interception behavior under standard environmental conditions with interception behavior  
14 when the virtual environment and target had been rotated  $10^\circ$  to the left or to the right. Before  
15 proceeding with this experiment, however, we first ran a control experiment (including only  
16 CENTER and SIDE target eccentricities and Approach, Cross and Retreat target directions) to  
17 determine (i) whether Ceyte et al.'s (2021) SIDE+ target eccentricity and/or Approach+ target  
18 direction conditions had not influenced behavior under the other six combinations of Target  
19 Eccentricity and Target Direction conditions (used by Fajen & Warren, 2004, and in our Exp.  
20 2) and (ii) to explore whether a particular phenomenon, namely the coming to the fore of  
21 reversals in movement direction under specific combinations of target eccentricity and target  
22 direction conditions, could be replicated. As will be detailed further on, both these issues are  
23 relevant to operational predictions with respect to the effects of performing the simulated  
24 interception-by-steering task under a constant  $10^\circ$  visual scene (i.e., target + virtual  
25 environment) rotation.  
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## 36 **2. Experiment 1: CENTER and SIDE target eccentricities**

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38 Experiment 1 thus had two objectives. In the first place we sought to replicate the overall  
39 pattern of results reported by Ceyte et al. (2021) when using only CENTER and SIDE target  
40 eccentricities combined with only Approach, Cross and Retreat target directions. If similar  
41 results were observed in both cases, we may use the differential effects on interception  
42 behavior observed under Ceyte et al.'s (2021) SIDE and SIDE+ target eccentricity conditions  
43 for evaluating possible effects of the target + virtual environment rotation of Experiment 2. In  
44 the second place, we sought to replicate the direction reversal phenomenon observed by Ceyte  
45 et al. (2021) under the SIDE and SIDE+ eccentricities for the Cross and Retreat target  
46 directions. For reasons of clarity, we briefly describe this phenomenon here.  
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51 In their 2007 modeling study of their 2004 averaged behavioral data, Fajen and Warren  
52 reported one single observation that did not fit with interception behavior based on nulling  
53  $d\theta/dt$ : Under SIDE/Cross and SIDE/Retreat conditions locomotor paths revealed a slight S-  
54 shaped bend. Steering under these specific conditions was characterized by a discreet initial  
55 turn in the direction of the target followed by a reversal in movement direction (denoted RMD  
56 hereafter), so that the target was finally intercepted on the opposite side of the initial  
57 locomotor direction axis. Examining individual-trial (rather than overall-average) locomotor  
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1 paths, Ceyte et al. (2021) demonstrated that RMDs did indeed occur for the Cross and Retreat  
2 target directions under both the SIDE and SIDE+ target eccentricity conditions. Interestingly  
3 however, such RMDs were not observed on all trials of these particular conditions that  
4 revealed a considerable degree of between-trial variation in the moment of initiation of the  
5 first steering action. Trials with a RMD were in fact characterized by early initiation of the  
6 participant's first steering action, while trials without a RMD were characterized by later  
7 initiation of steering (see Ceyte et al., 2021, for details). The second objective of Experiment  
8 1 was therefore to seek to replicate Ceyte et al.'s (2021) specific pattern of results with  
9 respect to reversals in movement direction in the SIDE eccentricity condition.  
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## 15 **2.1. Materials and Methods**

### 16 *2.1.1. Participants*

17 Five students from Aix Marseille University (3 women and 2 men, mean age  $22.4 \pm 0.9$  years)  
18 voluntarily took part in the experiment. None of them had participated in any other  
19 experiment using the same interception-by-steering task. Participants provided written  
20 consent prior to participation. The study was conducted according to University regulations  
21 and the Declaration of Helsinki.  
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### 26 *2.1.2. Task and procedure*

27 The experiment took place in a large virtual reality facility (<https://ism.univ-amu.fr/en/crvm>)  
28 comprising four projection surfaces, each served by two projectors: a  $3 \times 3$ -m floor and three  
29  $4$ -m high  $\times$   $3$ -m wide walls. The sidewalls were set at  $90^\circ$  angles with respect to the front  
30 wall. A basic driving simulator, comprising a seat, a set of (here non-operative) pedals and a  
31 steering wheel, was positioned in the middle of the floor surface. Stereopsis was ensured with  
32 passive Infitec filter technology. Participants' stereo glasses were equipped with a  
33 configuration of reflective markers. An eight-camera Advanced Realtime Tracking (ART,  
34 Weilheim, Germany) optical system enabled real-time motion capture of head position. The  
35 visual scene was refreshed at 60 Hz, taking into account the position and orientation of the  
36 participant's head relative to the virtual environment.  
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43 The visual scene consisted of a large grass-like flat plain, containing both fine and gross  
44 texture, bordered by distant mountains. The seated participant was instructed that on each trial  
45 the goal was to steer the "car" so as to intercept a horizontally-moving yellow cylinder ( $2$ -m  
46 radius,  $3$ -m high) by driving through it. Prior to trial onset, the participant, moving at a  
47 constant horizontal speed of  $20$  m/s, was to steer towards and subsequently align locomotor  
48 direction with a yellow line on the plain's ground. Alignment was considered as accomplished  
49 when the car's center (i.e., middle of the seat) attained a lateral distance of less than  $3$  cm with  
50 respect to the middle of the line while moving in a direction deviating less than  $0.1^\circ$  from the  
51 line orientation. This quite demanding requirement led participants to only minimally turn the  
52 steering wheel in the last stages of alignment. Once the alignment criteria were met, the  
53 yellow line disappeared and, at the same time, a red portal appeared  $40$  m ahead. Participants'  
54 instructions stipulated that they should refrain from further steering from the moment onward  
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1 that correct alignment had been achieved and until they passed through the portal. In fact,  
2 without the participants being aware of this, during that period the steering wheel was  
3 deactivated with wheel orientation recalibrated to zero, so that when the participant crossed  
4 the portal and the target appeared, they moved such that both  $\phi = 0^\circ$  and  $d\phi/dt = 0^\circ/s$ . A trial  
5 ended when the participant came within the target's circumference (successful interception)  
6 or when the participant reached a position further than 20 m in depth (Z-axis) beyond the  
7 current target position (missed trial).  
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10 In the experimental trials, targets were initially positioned at  $Z = 60$  m and  $X = 0.00$  m or  
11  $-25.35$  m, with initial participant position serving as the origin of the reference frame. Targets  
12 could thus appear at eccentricities of  $0^\circ$  (CENTER) and  $23^\circ$  (SIDE) to the left of the  
13 participant's initial locomotor direction (see **Fig. 2A**). Targets moved at 10 m/s along Retreat,  
14 Cross and Approach directions (oriented, respectively,  $+30^\circ$ ,  $0^\circ$ , and  $-30^\circ$  relative to the  
15 perpendicular with respect to the participant's initial locomotor direction). All initial  
16 conditions were also mirrored left/right and the data were subsequently collapsed for analysis.  
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21 The full set of 12 experimental conditions was presented in randomized order within a block  
22 of trials. Participants performed five blocks, for a total of 60 trials (10 per mirror-collapsed  
23 condition) and were invited to take a short break between blocks. Prior to the experiment  
24 proper participants performed 12 familiarization trials with stationary targets.  
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### 27 *2.1.3. Data acquisition and analysis*

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29 Participant position ( $x, z$ ) and locomotor orientation ( $\phi$ ) data were sampled at 100 Hz. These  
30 time series were subsequently filtered using a second-order Butterworth filter with a cut-off  
31 frequency of 8 Hz and collapsed over mirror conditions. Time derivatives were obtained using  
32 the Euler method. For each trial, the closest distance to the target was calculated,  
33 corresponding to zero at first contact with the target's circumference for successful  
34 interception trials and minimal Euclidean distance from the target's circumference for missed  
35 trials. Time to closest distance was defined as the time from onset of the trial until the  
36 moment the closest distance was reached.  
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41 The moment of initiation of the first steering action was determined for each trial as the time  
42 after trial onset at which the participant's rate of change in locomotor direction ( $d\phi/dt$ )  
43 exceeded 4 deg/s. A reversal in movement direction was defined as a lateral excursion of  
44 more than 0.05 m following initiation of the first steering action accompanied by a subsequent  
45 sign change in  $d\phi/dt$  leading to a movement in the opposite lateral direction. Pre-reversal  
46 excursion amplitude was defined as the largest initial lateral displacement before movement  
47 direction was reversed.  
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52 Moment of initiation of the first steering action was analyzed using a repeated-measures  
53 ANOVA with factors Eccentricity (CENTER, SIDE) and Direction (Approach, Cross,  
54 Retreat). More localized effects were evaluated using Chi-squared tests for frequency  
55 comparisons and Student t-tests for pre-reversal excursion amplitudes in trials with a reversal  
56 in movement direction and moment of initiation in trials with and trials without a reversal in  
57 movement direction. All tests were performed two-sided with significance level  $\alpha$  set to 0.05.  
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## 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  $\beta$ . 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  $\beta$  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  $\beta$  and the target's bearing angle  $\theta$ : the initial lag created under the CENTER eccentricity condition is visible as the early dip below zero (opening) of  $\beta$  for all three target directions. Participants' steering behavior then rapidly led them to lead the target, visible as the switch from negative to positive  $\beta$ -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  $0.85 \pm 0.36$  s and  $1.07 \pm 0.38$  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

1 amplitudes before heading direction was reversed ( $r(32) = -0.61, p = 0.001$ ). These findings  
2 thus closely corresponded to the pattern of results reported by Ceyte et al. (2021).  
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### 5 6 **2.3. Discussion**

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8 The goal of this preliminary experiment was to replicate Ceyte et al.'s (2021) study when  
9 target eccentricity was limited to two initial conditions (CENTER and SIDE) and target  
10 direction was limited to three conditions (Approach, Cross, and Retreat), as was the case in  
11 Fajen and Warren's (2004) study and implemented in our Experiment 2. The overall pattern  
12 of results from this preliminary replication experiment clearly corroborated Ceyte et al.'s  
13 (2021) findings, both qualitatively and quantitatively. First, the locomotor paths observed  
14 under the CENTER eccentricity condition once again systematically revealed steering ahead  
15 of the target, thereby anew demonstrating that steering behavior was generally compatible  
16 with a strategy of nulling changes in the target's bearing angle and not with a strategy of  
17 nulling changes in the target-heading angle (nor in egocentric target direction for that matter).  
18 Second, under the SIDE eccentricity conditions Cross and Retreat target directions gave rise  
19 to reversals in movement direction in, respectively, 46.0% and 22.0% of the trials. As these  
20 RMDs were associated with early initiation of the first steering action, these results confirm  
21 that the control of steering is not exclusively based on first-order (i.e., rate-of-change based)  
22 information, but that, at least early on, target position related information also plays a role (cf.  
23 Bootsma et al., 2016; Ceyte et al., 2021).  
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### 34 **3. Experiment 2: Rotation of the visual scene (target + virtual environment)**

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36 Using the  $2 \times 3$  target eccentricity and direction conditions design of Experiment 1, in  
37 Experiment 2 we explored the effects of a stepwise  $10^\circ$  rotation of the target and virtual  
38 environment (denoted TVE hereafter). This manipulation is akin to that of Rushton et al.  
39 (1998), while avoiding the flow-warping distortion effects of displacing prism glasses  
40 reported by Warren et al. (2001). To pinpoint the effect of such a TVE rotation on potential  
41 information sources for locomotor interception, we stipulate once more that these information  
42 sources differ in the reference they are defined by. The target's bearing angle ( $\theta$ ) is defined by  
43 its eccentricity at the point of observation with respect to an exocentric (environment-based)  
44 reference direction and is therefore not influenced by a given TVE rotation, as from the onset  
45 of a trial both the target and the environment are rotated in the same way (i.e., in the same  
46 direction and to the same extent). The optically-specified target-heading angle ( $\beta_{os}$ ) is defined  
47 by the target's eccentricity at the point of observation with respect to the agent's current  
48 direction of motion. Influencing target eccentricity and agent heading direction in the same  
49 way, a constant TVE Rotation therefore does not influence the target-heading angle  $\beta_{os}$  either.  
50 When the target's egocentric direction is defined relative to the body midline (Rushton et al.'s  
51 1998 definition), however, TVE rotation does affect this potential information source ( $\beta_{e1}$ ), as  
52 the body midline orientation remains identical while the target is displaced. For sake of  
53 completeness, we note that in our simulated interception-by-steering task, egocentric direction  
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1 as defined by felt locomotor displacement ( $\beta_{e2}$ , Fajen and Warren's 2004 definition) is simply  
2 not available. We also note that TVE rotation would not be expected to have any effect on  
3 interception behavior if participants would uniquely rely on the rate-of-change in any  
4 particular angle, either because they are simply not affected by the manipulation or because  
5 offset is constant (as for  $\beta_{e1}$ ).  
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7  
8 As can be seen from **Figure 2B**, by applying an outward 10° TVE rotation (referred to  
9 hereafter as R+), for the SIDE condition the target's initial egocentric eccentricity increases  
10 from 23° to 33°, corresponding closely to the target's true initial 32° eccentricity under the  
11 SIDE+ condition explored in Ceyte et al. (2021). A 10° TVE rotation in the same direction  
12 (R+) applied to the CENTER condition and an inward 10° TVE rotation (R-) applied to the  
13 SIDE condition give rise to quite similar (13° and 10°, respectively) new egocentric  
14 eccentricity conditions (see **Fig. 2B**), that we may refer to as an imaginary SIDE- condition.  
15 If early on participants were to rely on egocentric target direction in the control of their  
16 interception behavior, we can thus formulate a set of specific predictions with respect to the  
17 behavior expected under R+ and R- TVE rotation conditions compared to the R0 control  
18 condition, based on the differential results observed by Ceyte et al. (2021) under the true  
19 SIDE+, SIDE and CENTER eccentricity conditions. In formulating these predictions, we  
20 concentrate on the Cross and Retreat target directions exclusively.  
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#### 23 *Egocentric Target Direction predictions with respect to the first steering action*

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29 In Ceyte et al.'s (2021) study and replicated in Exp. 1, the earliest steering initiation was  
30 observed under the CENTER eccentricity condition, with moments of initiation around 0.5 s  
31 for all target directions. Ceyte et al. (2021) also observed that, for each target direction,  
32 steering was initiated earlier under the SIDE+ than under the SIDE eccentricity condition (see  
33 their Table 1). Under the SIDE eccentricity of Experiment 2 the increased egocentric target  
34 direction of the R+ condition should (in comparison to the SIDE R0 control condition)  
35 therefore lead to earlier initiation. By extrapolation, the decreased egocentric target direction  
36 of the SIDE R- condition should (in comparison to the SIDE R0 control condition) therefore  
37 lead to later initiation. With the SIDE R- condition closely resembling the CENTER R+  
38 condition in terms of initial egocentric target direction (together forming the imaginary SIDE-  
39 eccentricity), the CENTER R+ condition should (compared to the CENTER R0 condition)  
40 lead to later initiation, with moments of initiation for the two conditions of the imaginary  
41 SIDE- eccentricity condition being value-wise close together.  
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#### 44 *Egocentric Target Direction predictions with respect to reversals in movement direction*

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49 In Ceyte et al.'s (2021) study, a larger proportion of trials with a RMD were observed under  
50 the SIDE+ than under the SIDE eccentricity conditions. Under the SIDE eccentricity of  
51 Experiment 2, the increased egocentric target direction of the R+ condition should (in  
52 comparison to the R0 control condition) therefore also lead to an increase in the proportion of  
53 trials with a RMD. By extrapolation, the decreased egocentric target direction of the R-  
54 condition should then lead to a smaller proportion of trials with a RMD and, by the same  
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1 token, a comparable proportion of trials with a RMD should come to the fore under the  
2 CENTER R+ condition.  
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### 5 **3.1.Method**

#### 6 *3.1.1. Participants*

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9 Sixteen students from Aix Marseille University (8 women and 8 men, mean age  $24.3 \pm 2.0$   
10 years) voluntarily took part in the experiment. None of them had participated in any other  
11 experiment using the same interception task. Participants provided written consent prior to  
12 participation. The study was conducted according to University regulations and the  
13 Declaration of Helsinki.  
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#### 16 *3.1.2. Task and procedure*

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19 Apart from the addition of constant TVE rotation conditions, the task and procedure were  
20 identical to that described for Experiment 1, including CENTER and SIDE initial target  
21 eccentricities and Approach, Cross and Retreat target directions. These experimental  
22 conditions were combined with a TVE Rotation condition in which the target + virtual  
23 environment were rotated. While all of the participants performed the task under the control  
24 condition of  $0^\circ$  TVE rotation (R0), eight of them also performed all six combinations of  
25 Target Eccentricity (CENTER, SIDE) and Target Direction (Approach, Cross, Retreat) under  
26 a  $10^\circ$  leftward TVE rotation; the other eight participants performed the same six combinations  
27 of Target Eccentricity and Target Direction under a  $10^\circ$  rightward TVE rotation. As can be  
28 seen from **Figure 2B**, leftward rotation increased egocentric eccentricity for the left SIDE  
29 condition, with the rightward-moving targets thereby constituting the six R+ rotation  
30 conditions for the  $10^\circ$ -leftward rotation participant group. Note that for this participant group,  
31 the (mirror) leftward-moving trajectories (where the same leftward rotation decreased  
32 egocentric eccentricity for the right SIDE condition) constituted the six R- rotation  
33 conditions. Conversely, for the  $10^\circ$ -rightward rotation participant group, the leftward-moving  
34 trajectories constituted the R+ rotation conditions and the rightward-moving trajectories  
35 constituted the R- rotation conditions.  
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44 In the leftward-rotation group, half of the participants first performed the task under the no-  
45 rotation conditions and then under leftward-rotation conditions, while the other half first  
46 performed the task under the leftward-rotation conditions and then under the no-rotation  
47 conditions. The same procedure was applied to the rightward-rotation group.  
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50 The (mirrored) set of 12 combinations of Target Eccentricity (CENTER, SIDE) and Target  
51 Direction (Approach, Cross, Retreat) was again presented in randomized order within a block  
52 of trials. Participants performed five blocks under both the no-rotation and (participant-group  
53 specific) rotation conditions, for a total of 120 trials and were invited to take a short break  
54 between blocks. Prior to the experiment proper participants performed 12 familiarization trials  
55 with stationary targets.  
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1 For analysis, data were collapsed over groups, giving rise to 10 trials per Target Eccentricity  
2 and Target Direction combination under the R0 rotation condition and five trials per  
3 participant per Target Eccentricity and Target Direction combination under both the R+  
4 condition and the R- rotation condition.  
5

### 6 3.1.3. Data acquisition and analysis

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8 Data acquisition and analysis was identical to that described for Experiment 1, except that  
9 statistical analysis now included three factors: TVE Rotation (R0, R+, R-), Target  
10 Eccentricity (SIDE, CENTER) and Target Direction (Approach, Cross, Retreat).  
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## 15 3.2. Results

### 16 3.2.1. Interception performance

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18 Participants intercepted the targets in 89.0%, 90.2% and 89.4% of the trials under the R0, R+  
19 and R- conditions, respectively. As in Experiment 1, success rate was close to maximum for  
20 the Cross and Retreat target directions under both the CENTER and SIDE eccentricities and  
21 lower under de Approach target direction, especially under the SIDE eccentricity (see **Table**  
22 **2**). TVE rotation did not affect performance to any noticeable extent. Even on the 204 missed  
23 trials (out of the total of 1920 trials) participants generally came close to the target (overall  
24 median closest distance 0.06 m). Subsequent analyses were based on all trials.  
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### 29 3.2.2. Interception Paths

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31 As shown in **Figure 6**, the average interception paths for the R0 condition were very similar  
32 to those observed in Experiment 1 (cf. Ceyte et al., 2021, and Fajen & Warren, 2004). TVE  
33 rotation did not affect mean paths to any remarkable degree; still, relative to the R0 condition,  
34 under the Retreat and Cross target direction conditions average paths were shifted slightly to  
35 the left for the R+ condition and to right left for the R- condition. Time until closest distance  
36 (TCD; see Table 2) was reached was not affected by TVE rotation conditions.  
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41 \*\*\*\*\* Figure 6 (mean interception paths) about here \*\*\*\*\*  
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### 43 3.2.3. Moment of initiation

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45 As in Experiment 1, the earliest steering actions were observed under the CENTER condition  
46 where participants initiated steering around 0.5 s after the target appeared for all target  
47 directions under all TVE Rotation conditions (see **Table 2**). A repeated-measures ANOVA  
48 with the factors TVE Rotation (R0, R+, R-), Eccentricity (CENTER, SIDE), and Direction  
49 (Approach, Cross, Retreat,) revealed significant main effects for all three factors (Rotation:  
50  $F(2,30) = 5.49, p < 0.009, \eta^2_p = 0.27$ ; Eccentricity:  $F(1,15) = 171.44, p < 0.001, \eta^2_p = 0.92$ ;  
51 Direction  $F(2,30) = 46.79, p < 0.001, \eta^2_p = 0.76$ ), as well as significant two-way interactions  
52 (Rotation  $\times$  Eccentricity,  $F(2,30) = 4.36, p < 0.022, \eta^2_p = 0.23$ , Eccentricity  $\times$  Direction,  
53  $F(2,30) = 45.08, p < 0.001, \eta^2_p = 0.75$ , and Rotation  $\times$  Direction,  $F(4,60) = 3.08, p < 0.023,$   
54  $\eta^2_p = 0.17$ ) and a three-way interaction between the factors Rotation, Eccentricity, and  
55 Direction ( $F(4,60) = 3.55, p < 0.012, \eta^2_p = 0.19$ ). Post-hoc Newman-Keuls analysis of the  
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1 overarching triple interaction confirmed that under the CENTER Eccentricity, moments of  
2 initiation did not significantly vary over Rotation and Direction conditions. While under the  
3 SIDE Eccentricity, moments of initiation observed for the Approach direction did not  
4 significantly vary over Rotation conditions either, an effect of Rotation was found for the  
5 Cross and Retreat target directions: moments of initiation were significantly later ( $p$ 's < 0.01)  
6 under the R+ condition than under the R- condition (Cross: 1.37 s  $\pm$  0.28 s and 1.19 s  $\pm$  0.23  
7 s, respectively; Retreat: 1.24 s  $\pm$  0.37 s and 1.13 s  $\pm$  0.34 s, respectively). Significant  
8 differences involving R0 were only observed for the Cross target direction, where steering  
9 actions were initiated significantly later ( $p$  < 0.001) under the R+ condition than under the R0  
10 condition (1.25 s  $\pm$  0.24 s). This pattern of results does not fit with predictions based on early  
11 reliance on egocentric target direction, as, for instance, earlier (rather than later, as found)  
12 moments of initiation were then expected under the SIDE/R+ conditions than under the  
13 SIDE/R0 conditions.  
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19 \*\*\*\*\* Table 2 about here \*\*\*\*\*  
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#### 21 3.2.4. Reversals in movement direction 22

23 Trials with a RMD were detected in 184 (i.e., 9.6%) of the total of 1920 trials. As expected,  
24 the grand majority ( $n$  = 152) of these RMD trials was observed under the SIDE eccentricity  
25 condition for the Cross ( $n$  = 92, 28.8%) and Retreat ( $n$  = 60, 18.8%) target directions. The  
26 other 32 RMD trials were distributed over the remaining conditions, occurring only rarely in  
27 each (see **Table 3**). Although two participants did not reveal any trials with a RMD under the  
28 R0 Rotation condition<sup>4</sup>, all participants revealed RMD trials under the R+ and R- Rotation  
29 conditions. The presence of RMD was thus once again not participant-specific. The presence  
30 of a RMD did not noticeably degrade performance, as interception was achieved in 94.1% of  
31 the RMD trials.  
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37 \*\*\*\*\* Table 3 about here \*\*\*\*\*  
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39 Overall, contrary to egocentric direction-based predictions, no effect of Rotation condition on  
40 the frequency of RMD trials observed for the Cross and Retreat directions could be  
41 demonstrated (R0: 82 of total 320 trials = 25.6%; R+: 43 of total 160 trials = 26.9%; R-: 27 of  
42 total 160 trials = 16.9%;  $\chi^2(2) = 4.12, p = 0.1275$ ). As in Experiment 1 and in Ceyte et al.  
43 (2021), however, more RMD trials were observed for the Cross direction ( $n$  = 92) than for the  
44 Retreat direction ( $n$  = 60;  $\chi^2(1) = 6.74, p = 0.0009$ ). Moreover, RMD trials for the Cross and  
45 Retreat directions were, once again, initiated (0.93 s  $\pm$  0.34 s) significantly earlier ( $t(638) =$   
46 10.33,  $p < 0.0001$ ) than NoRMD trials (1.31 s  $\pm$  0.41 s). Finally, for the RMD trials maximal  
47 pre-reversal excursion amplitude was negatively related to the first moment steering action  
48 ( $r(150) = -0.51, p < 0.0001$ ).  
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57 <sup>4</sup> We note that the two participants that did not reveal RMD trials under the R0 (control) condition were found to  
58 initiate their first steering action significantly later than all other participants together (0.87 s  $\pm$  0.42 s versus  
59 0.76 s  $\pm$  0.40 s;  $t(958) = 2.76, p = 0.0029$ ). Later initiation is generally associated with less RMD trials.  
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### 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

1 speed) target motion. The two other studies (Fajen & Warren, 2004; Chardenon et al., 2004),  
2 evaluating the effects of moving the (virtual) environment during interception, concluded in  
3 favor of reliance on changes in egocentric target direction *by default*, because the observed  
4 phenomena could not be explained by the only alternative (reliance on changes in target-  
5 heading angle) considered. Distinguishing the effects predicted by reliance on changes in the  
6 target's bearing angle from those predicted by reliance on changes in the target-heading angle,  
7 we showed that the phenomena observed in both studies could in fact be explained by reliance  
8 on changes in the target's bearing angle.  
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11 With Rushton et al.'s (1998) study thus being the only one to provide at least a pointer  
12 towards a potential role of egocentric target direction in locomotor interception, in the present  
13 contribution we called upon an experimental manipulation akin to theirs. To this end we  
14 explored the effects on interception behavior of a constant rotation of the visual scene, that is  
15 of both the (virtual) environment and the target. We did this in the framework of an  
16 experimental situation (targets moving uniformly from SIDE and CENTER initial  
17 eccentricities) also allowing distinctive patterns of behavior to emerge when participants  
18 relied on (changes in) the target-heading angle  $\beta$  or on (changes in) the target's bearing angle  
19  $\theta$ . While an interception strategy based on  $d\theta/dt$ -nulling is capable of explaining almost all  
20 aspects of observed locomotor behavior, Ceyte et al.'s (2021) study pinpointed a phenomenon  
21 that was not compatible with such full reliance on the rate of change in the target's bearing  
22 angle: under SIDE eccentricity conditions, participants regularly, although not consistently,  
23 first steered in the direction of the target, before reversing direction and steering onto an  
24 interception course. Such reversals in movement direction (RMD) were observed for the  
25 Cross and Retreat target directions, where the target was captured on the side opposite to  
26 initial target position, defined with respect to initial participant heading. Indeed, under these  
27 conditions the moment of initiation of the first steering action appeared to determine whether  
28 a RMD occurred or not, with early initiation being associated with the presence of RMDs.  
29 Moreover, when a RMD was observed, the amplitude of the initial movement in the direction  
30 of the target was larger the earlier the first steering action had been initiated. Finally, Ceyte et  
31 al. (2021) demonstrated that a larger initial target eccentricity gave rise to a higher proportion  
32 of trials with a RMD. In each of the two experiments reported in the present study we fully  
33 replicated Ceyte et al.'s above-described pattern of results for the CENTER and SIDE  
34 eccentricity conditions. We thus confirmed the selective appearance of trials with a RMD for  
35 specific combinations of initial target eccentricity and target motion direction. Moreover, we  
36 confirmed the co-existence of trials with a RMD and trials without a RMD under these  
37 specific initial conditions, with RMDs appearing only for trials with an early initiation of the  
38 first steering action. These RMD related results were observed for (almost) all participants  
39 and were thus not participant-specific. For uniformly-moving targets this direction-reversal  
40 phenomenon indicates that the information used cannot be purely first-order (i.e., rate-of-  
41 change based). It therefore echoes the angle-of-approach effect observed in direction-  
42 constrained manual (Arzamarski et al., 2007; Dessing and Craig, 2010; Dessing et al., 2005;  
43 2009; Jacobs and Michaels, 2006; Ledouit et al., 2013; Michaels et al., 2006; Montagne et al.,  
44 1999; Peper et al., 1994) and locomotor (Bootsma et al., 2016) interception, also indicating  
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1 that the information used cannot be purely first-order but carries traces of an influence of  
2 initial target position.

3 While clearly not being able to explain the generally observed behavioral patterns of  
4 locomotor interception, egocentric target direction might therefore play a role early on, when  
5 the agent discovers the target. The predictions tested with respect to the effects on  
6 interception behavior that such an early role of egocentric target direction would evoke  
7 concerned both the timing of the moment of initiation of the first steering actions and the  
8 characteristics of RMDs. The results clearly did not comply with these predictions. Predicted  
9 to be earlier, initiation under the augmented (R+) SIDE target eccentricity was in fact found to  
10 be later relative to its R0 control. None of the other predictions bore out either, whether they  
11 concerned the initiation of first steering action when initial target direction (R+) was affected  
12 under the CENTER or the proportion of trials with a RMD under R+ and R- rotation  
13 conditions. How, then, should we interpret the overall pattern of result?  
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19 As argued by Bootsma et al. (2016), in the direction-constrained paradigm reasoning on the  
20 basis of the target's bearing angle allows one to consider (full or partial) reliance on zeroth-  
21 order (i.e., position-related) information in the control of locomotion, while reasoning on the  
22 basis of target-heading angle does not. The angle-of-approach effect observed in their study  
23 led Bootsma et al. (2016) to suggest that both first- and zeroth-order bearing angle  
24 information (i.e.,  $d\theta/dt$  and  $\theta$ ) played a role in intercepting rectilinearly moving targets.  
25 Rather than resorting to some unprincipled combination of two information sources, Bootsma  
26 et al. (2016) proposed reliance on fractional-order information  $d\theta^\alpha/dt^\alpha$ , with  $\alpha$  slightly below  
27 1 for (quasi) uniformly moving targets. Because fractional-order change is not locally defined,  
28 but integrates recent history, acting as "shadows on the walls" as Podlubny (2002) put it, the  
29 initial target position  $\theta$  plays a role early on. We might thus speculate that, being the first  
30 available information, egocentric target position could perhaps simply serve to determine the  
31 environmental reference providing  $\theta_0$ , but further work is needed on this subject.  
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39 However all this may be, the two experiments of the present contribution once again  
40 confirmed that in a structured environment locomotor interception is not guided by (i) a  
41 strategy based on nulling egocentric target direction (i.e.,  $\beta_{e1}$ -nulling), as suggested by  
42 Rushton et al. (1998), (ii) a strategy based on nulling changes in egocentric target direction  
43 (i.e.,  $d\beta_{e2}/dt$ -nulling), as suggested by Fajen and Warren (2004; also see Rushton & Allison,  
44 2013), or (iii) a strategy based on nulling optically-specified changes in target-heading angle  
45 (i.e.,  $d\beta_{os}/dt$ -nulling, as suggested by Zhao et al. (2019, 2021). The general results are,  
46 however, once again compatible with a strategy of nulling changes in the target's bearing  
47 angle (with the caveat that such change-nulling is based on  $d\theta^\alpha/dt^\alpha$  rather than on  
48 conventional  $d\theta/dt$ -nulling).  
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54 Change in bearing angle is specified by local flow *around* the target. This can be most simply  
55 illustrated in the situation of a structured background against which the target is seen: the  
56 target's bearing angle is constant if the target does not move relative to the background.  
57 Change in the target's bearing angle is thus specified by relative motion between the target  
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1 and its (surrounding) background<sup>5</sup>. But even when the background is not sufficiently  
2 structured, changes in the target's bearing angle can be recovered from local target motion  
3 with respect to a structured ground plane or local motion parallax of ground surface elements  
4 around the target (cf. Cutting et al., 1995). It is thus only in the situation of an absence of any  
5 useful environmental structure that the strategy of nulling changes in the target's bearing  
6 angle cannot be used. The agent, then, cannot but revert to a strategy based on (changes in)  
7 egocentric target direction, as this is the only information available. This was most likely the  
8 case in Rushton et al.'s (1998) study, where uncontrolled (and apparently low) target speed  
9 evoked pursuit-like interception behavior.  
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13 Finally, the present work leads us launch a plea in favor of a clear distinction and systematic  
14 labeling of potential information sources. Neither Fajen and Warren (2004) nor Chardenon et  
15 al. (2004) clearly distinguished target-heading angle  $\beta$  from the target's bearing angle  $\theta$ ,  
16 resulting in the erroneous default-based conclusion in favor of egocentric target direction. In  
17 fact, the literature on direction-constrained locomotor interception has almost systematically  
18 referred to the target's bearing angle when, in fact, the work focused on the target-heading  
19 angle (Bastin et al., 2006, 2008; Chardenon et al., 2002, 2004, 2005; Chohan, 2006, 2008;  
20 Francois et al., 2011; Lenoir et al., 1999a, 1999b, 2002; Morice et al., 2010; also see  
21 Louveton et al., 2010, 2012)<sup>6</sup>. The confusion between potential information sources, due to  
22 non-systematic distinction and labeling, is quite wide-spread throughout the animal literature  
23 as well; as an example, Kane et al. (2014) refer to target-heading angle as bearing angle and  
24 to bearing angle as absolute target direction. Our plea in favor of a clear distinction and  
25 systematic labelling of potential information sources not only applies to reporting of one's  
26 own work, but also to interpreting and reporting results of other studies.  
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51 <sup>5</sup> Lenoir et al.'s (1999b) results with respect to a background effect on interception behavior might in this light  
52 be re-interpreted as relating to the detection of changes in the target's bearing angle (facilitated in the presence of  
53 a textured background) than rather than as relating to perceived target speed, because perceived target speed is  
54 not a pertinent variable in the framework of the proposed locomotor interception control strategy.  
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56 <sup>6</sup> Present contribution author RB co-authored several of these studies, at the time simply having been unaware of  
57 the distinction. In direction-constrained locomotor interception paradigms used in those studies the two angles  
58 indeed typically covary and the research focused on the interception control strategy of striving to null the rate of  
59 angular change. Confounding target-heading angle with the target's bearing angle in a direction-constrained  
60 paradigm is then not necessarily harmful ... unless, of course, experimental manipulations involve displacement  
61 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,  $\beta_{e1}$ , Rushton et al., 1998), egocentric target direction defined relative to felt (proprioceptively perceived) locomotor direction ( $\beta_{e2}$ , Fajen & Warren, 2007), and target direction defined relative to optically-specified heading direction ( $\beta_{os}$ ). **(B)** Agent heading  $\phi$  and target bearing  $\theta$  are defined with respect to an exocentric reference direction (dashed blue line). Target-heading angle  $\beta$  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 ( $0^\circ$ ) or SIDE ( $23^\circ$ ) 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  $0^\circ$ ,  $+30^\circ$  and  $-30^\circ$ , 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  $0^\circ$ ,  $10^\circ$  outward and  $10^\circ$  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 ( $\theta$ , black lines) and the target-heading angle ( $\beta$ , 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  $\beta$  under the CENTER eccentricity condition. The subsequent change from an early lag (negative  $\beta$ , indicating steering behind the target) to a later lead (positive  $\beta$ , 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.

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

		SR (%)	TCD (s)	Mol (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 ( $M \pm SD$ ) for Experiment 2 of Success Rate (SR), Time until Closest Distance (TCD) and Moment of Initiation of first steering action (Mol) 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)			Mol (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 <b>32.5%</b>	25 <b>31.3%</b>	15 <b>18.8%</b>	30 <b>18.8%</b>	18 <b>22.5%</b>	12 <b>15.0%</b>

Figure 1

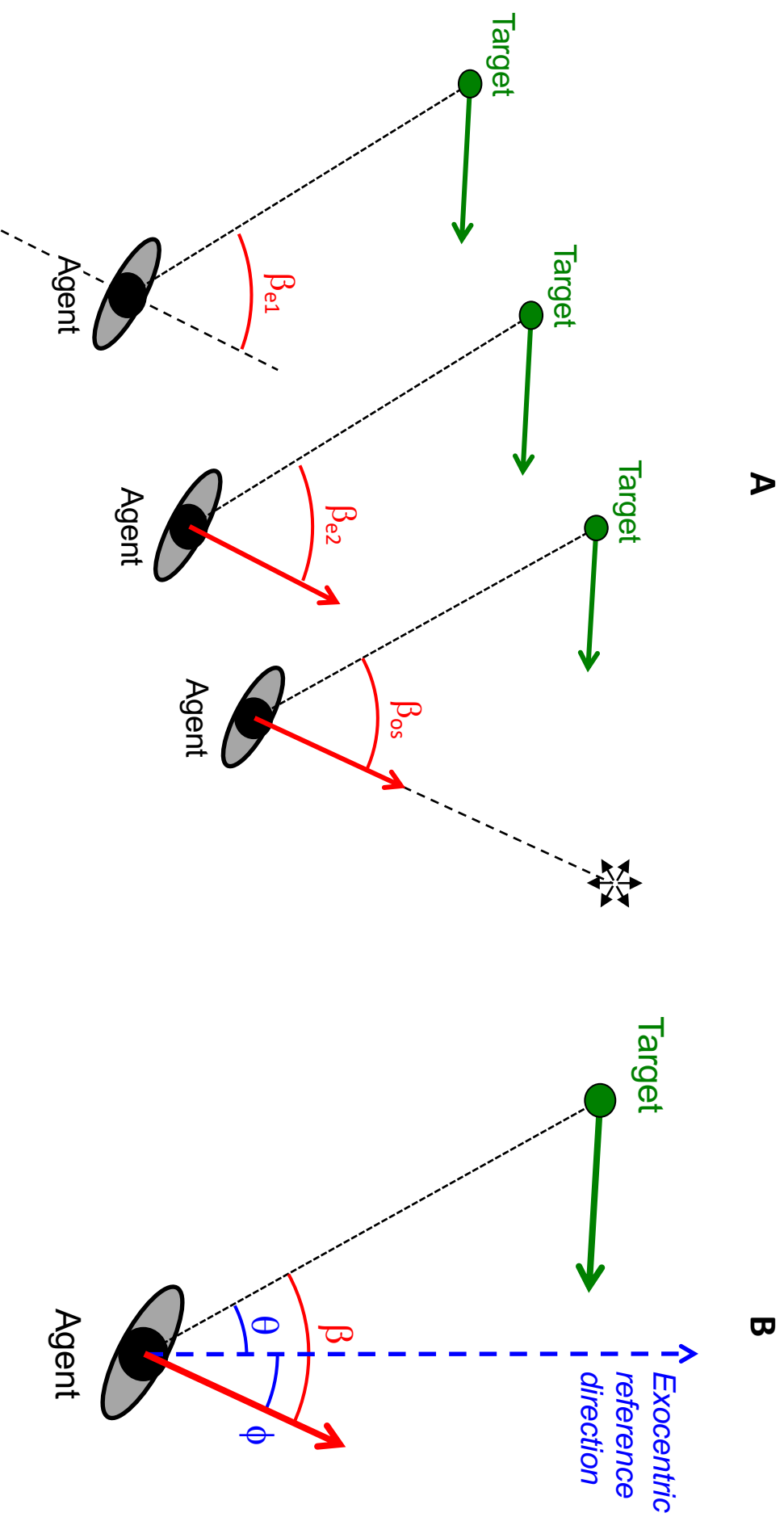


Figure 2

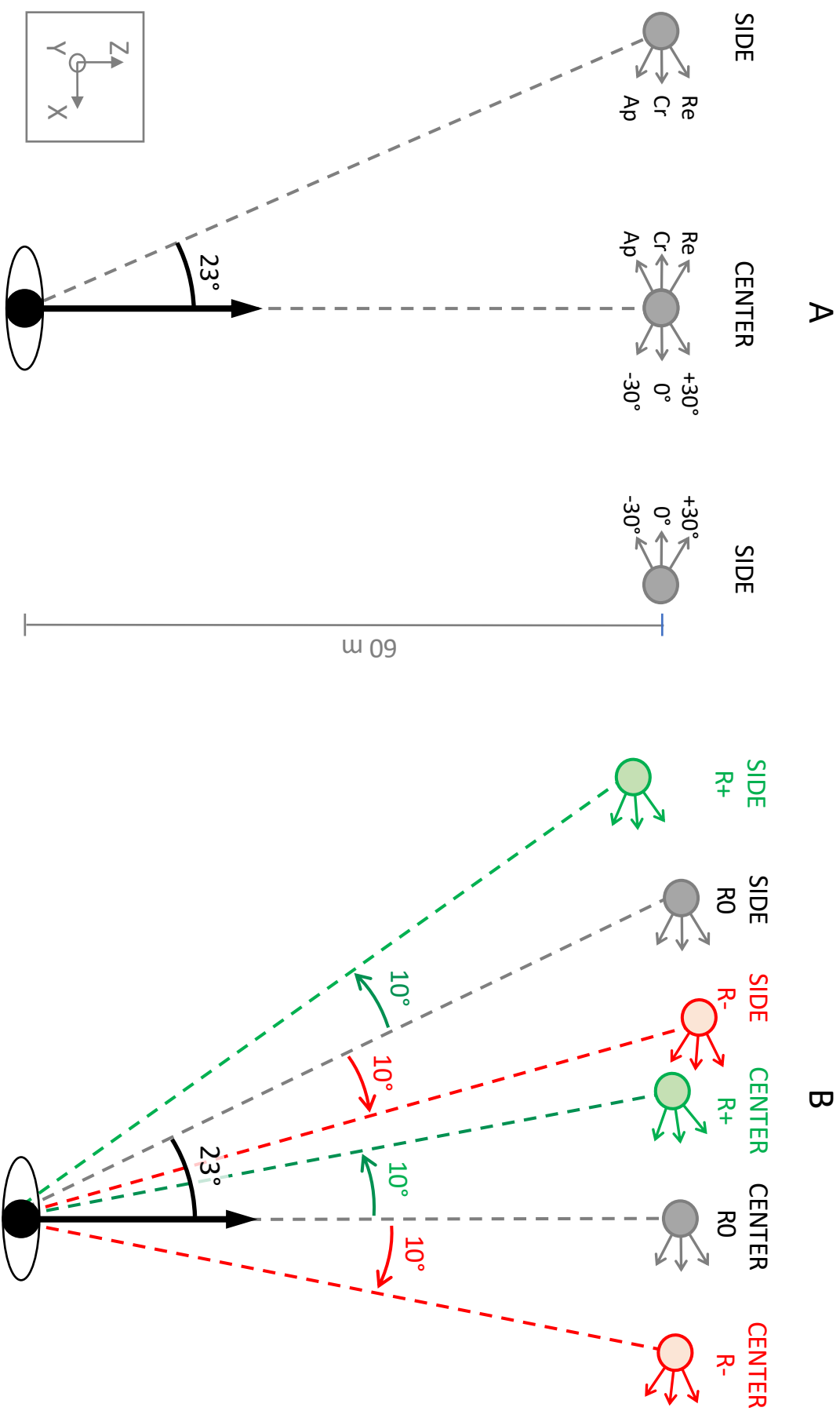


Figure 3

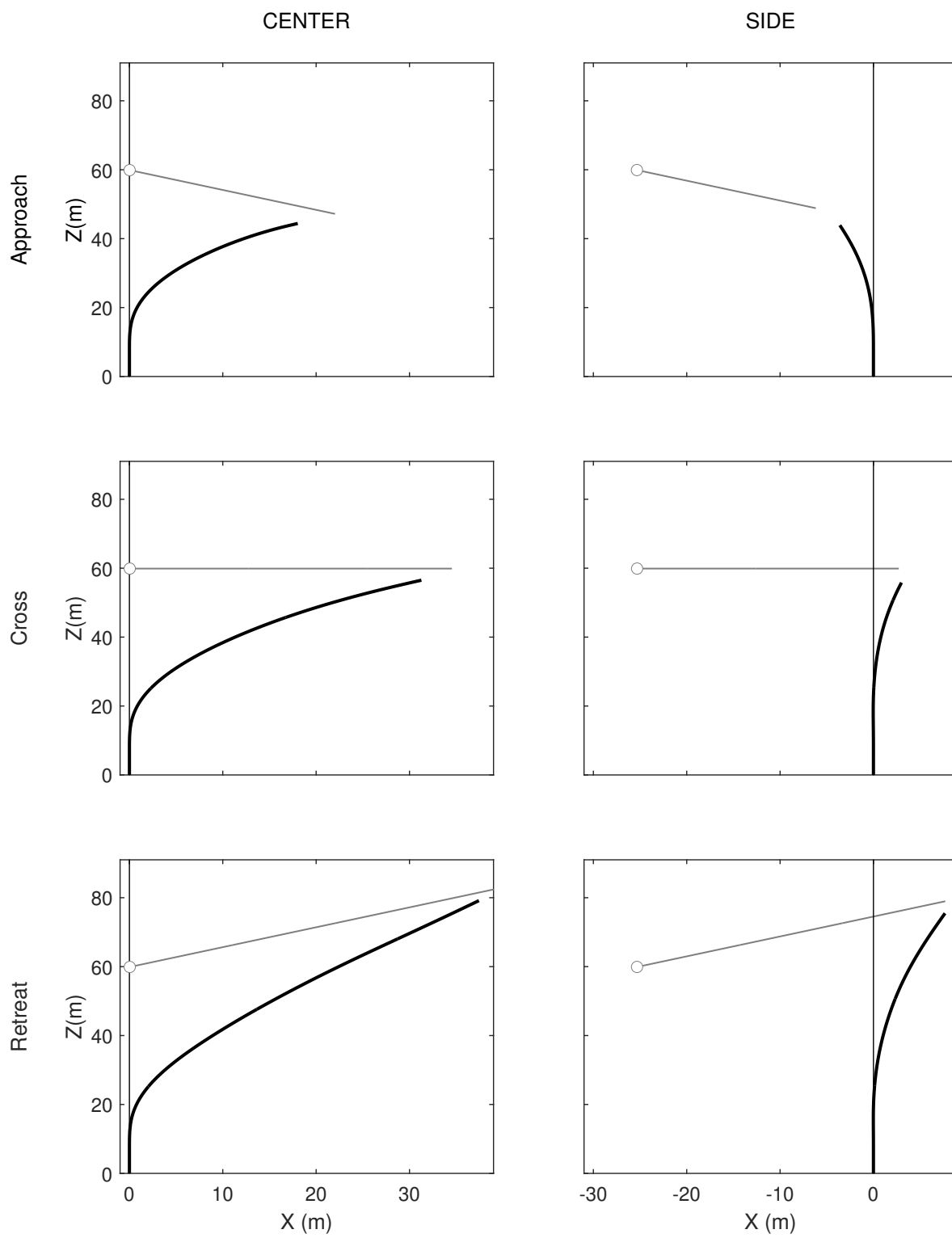


Figure 4

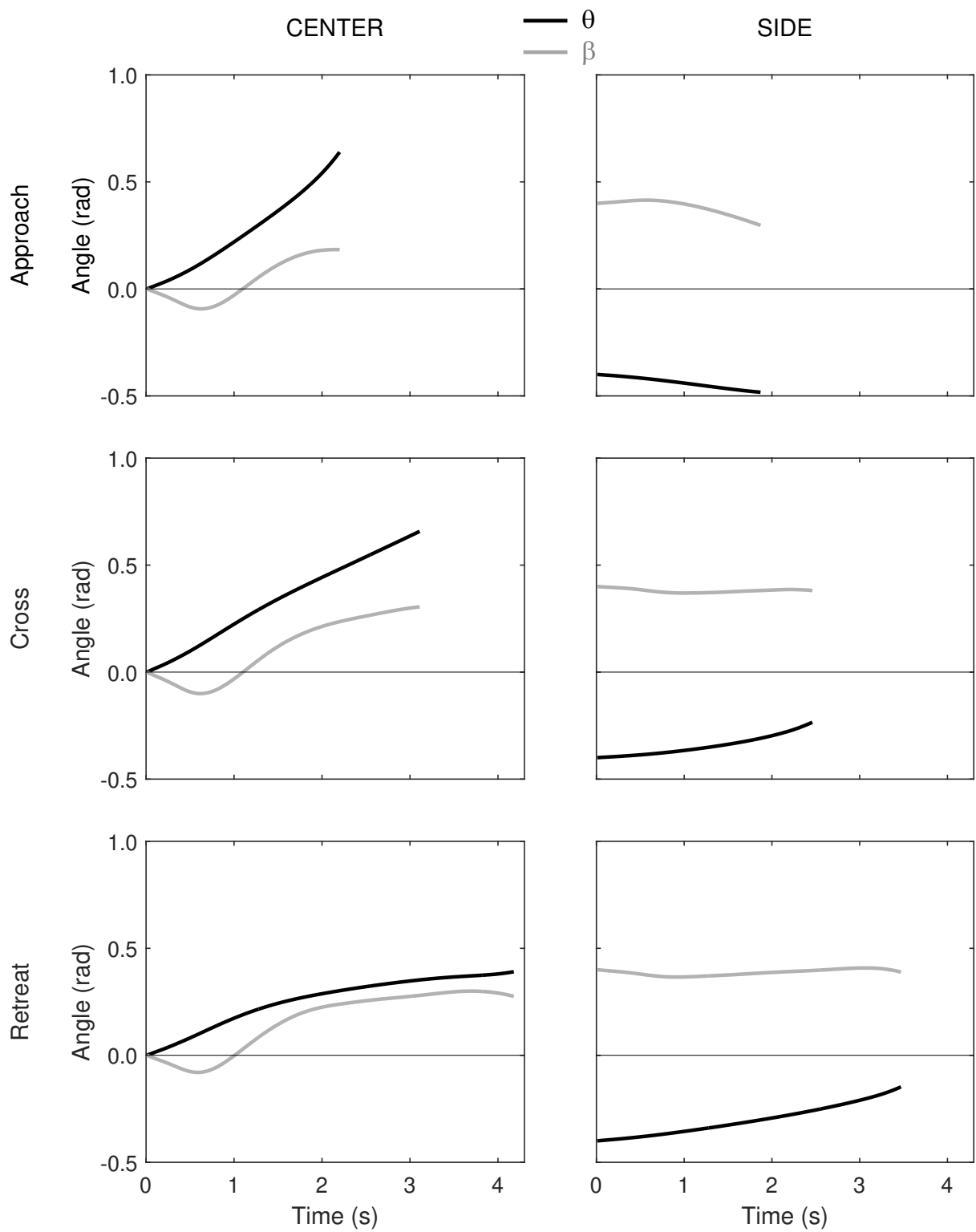




Figure 5

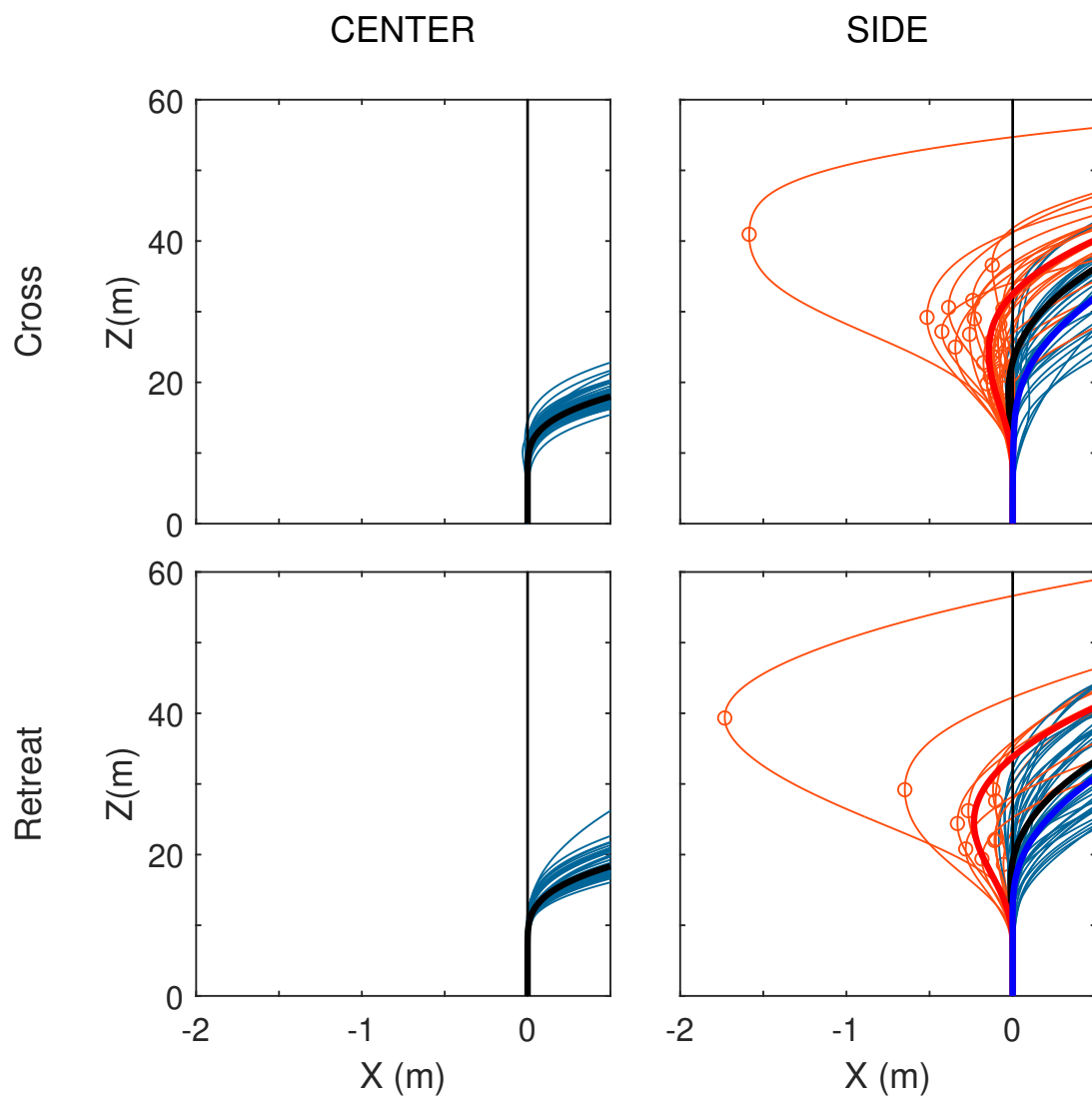


Figure 6

