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A bee in the corridor: centering and wall-following

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Abstract

In an attempt to better understand the mechanism underlying lateral collision avoidance in flying insects, we trained honeybees (*Apis mellifera*) to fly through a large (95cm-wide) flight tunnel. We found that depending on the entrance and feeder positions, honeybees would either center along the corridor midline or fly along one wall. Bees kept following one wall even when a major (150cm-long) part of the opposite wall was removed. These findings cannot be accounted for by the 'optic flow balance' hypothesis that has been put forward to explain the typical bees' 'centering response' observed in narrower corridors. Both centering and wall-following behaviours are well accounted for, however, by a mechanism called the lateral *optic flow regulator*, i.e., a feedback system that strives to maintain the unilateral optic flow constant. The power of this mechanism is that it would allow the bee to guide itself visually in a corridor *without having to measure its speed or distance from the walls.*

Key words: insect flight, honeybee, *Apis mellifera*, vision, optic flow, collision avoidance, image motion.

Introduction

Winged insects navigate swiftly in unfamiliar environments by processing visual cues. A major visual cue is the *optic flow* (OF), that is, the *angular velocity* at which any environmental feature sweeps past their eyes, in particular as a consequence of locomotion (Kennedy, 1939; Gibson, 1950; David, 1978; Lee, 1980, Buchner, 1984; Collett et al., 1993). Flies and bees possess smart OF sensors, in terms of neurons whose firing rates grow monotonically with speed (Collett and King, 1975; Ibbotson, 2001, Straw et al., 2008).

Evidence that bees rely on the lateral OF to control their flight was provided by ingenuous experiments on bees that were trained to enter deep into a corridor formed by two walls. Each wall carried a pattern consisting of a vertical black-and-white grating, and one of the two walls could be moved (Kirchner and Srinivasan, 1989). As long as the corridor walls remained stationary, bees tended to fly equidistant from the two walls, producing what has been called the '*centering behaviour*'. However, when one of the gratings was moved, the bee's trajectory shifted *off center*. To explain this shift, the authors hypothesised that the flying bee balances the angular velocities (i.e., the OFs) of the walls, as perceived laterally by the two eyes (Kirchner and Srinivasan, 1989).

This type of experiment on honeybees was always performed (i) with entrance and feeder centered along the corridor midline, and (ii) in relatively *narrow* corridors of either a constant width D (D=12cm in Kirchner and Srinivasan, 1989, and Srinivasan et al., 1991; D=15.5cm in Srinivasan et al., 1993; D=10cm to 20cm in Hrncir et al., 2004; D=22cm to 32cm in Baird et al., 2005), or a variable width (a corridor tapering from 38cm to 12cm and expanding again to 38cm, in Srinivasan et al., 1996).

Honeybees are able to adopt a terrain-following behaviour on the basis of a *ventral OF regulator* controlling the bee's vertical lift (Franceschini et al., 2007). In the present account we adress the question of whether honeybees are able to adopt a wall-following behaviour on the sole basis of the lateral OF.

Materials and Methods

Experimental corridor

The experiments were carried out in the south of France, near Marseille (43.40°N, 5.55°E, 336m) in September (day temperature: 20-31°C), and October 2005 (day temperature: 18-23°C). Experiments consisted in making video recordings of the free-flight trajectories of

honeybees (*Apis mellifera*) under four experimental conditions. The experimental set-up (Fig. 1a) consisted of a relatively wide (95cm) and long (300cm) rectangular corridor (25cm-height). The two walls were wallpapered with a pattern of vertical grey-and-white stripes of spatial wavelength λ = 10cm using a solvent free glue (Sader© Fortissimo, MS polymer-based glue). The Michelson contrast was m = 0.41, as measured in the green spectral range (specific for motion vision in the honeybee: Kaiser and Liske, 1974).

By using a pattern with a relatively large spatial wavelength (10cm), we made sure that the bee would see it whatever its lateral positioning in the wide corridor, given the small bee's interommatidial and acceptance angles, which are both in the order of 2.5 deg for laterally oriented ommatidia (Seidl and Kaiser, 1981; Horridge, 2003).

In the last experiment, a 1.5m long central part of the left wall was removed (between abscissae X = 75cm and X = 225cm). Through this wide opening, the nearest (15m) trunk of a tree that the bee could see produced an OF of only 4°/s (see 4th column in Table 1).

The coarsely textured wooden floor was white, maximizing the contrast between the insect and the floor in the video sequences. The corridor was roofed with see-through insect netting allowing efficient corridor ventilation and closed with a white plank at each end. Bees could enter the corridor only through one of three entrance holes in the insect netting (left Entrance: E_L, central Entrance: E_C, right Entrance: E_R). This arrangement forced the bees to enter the corridor with a quasi zero forward speed.

Bee training

Experiments were conducted outdoors on clear days with no wind. Bees were trained to enter the corridor through one of the three entrances (E_L, E_C, E_R, see Fig. 1a), depending on the experiment. Bees were first trained for three days to feed on a honey-flavoured sweet that was placed each time deeper and deeper in the corridor, up to the final position shown in Fig. 1a. At the end of the training session, the sweet was replaced by a sugar solution feeder (35% w/w, i.e., 1.2M sucrose concentration) for an additional two days to exclude any unwanted olfactory cues. The feeder was placed at one of the three positions (left F_L, central F_C or right F_R), depending upon the experiment. After the training session, trajectories of single bees flying to the feeder were video-filmed from above. Bees' return paths home across the corridor were not recorded.

Video-recording and flight path analysis

The bees' flight trajectories to the feeder were filmed at a rate of 20 frames/s with a high-resolution digital black-and-white CMOS camera (*Prosilica*^{TM} EC1280: 1280x1024 pixels) placed at 220cm above the corridor floor (Fig. 1a). We only consider bees entered one at a time in the camera field of view during the recordings. The data were stored on a standard notebook computer equipped with an image sequence acquisition software program. The camera field of view was adjusted to 150cm in length and 95cm in width, centered on the corridor. Despite the area covered by the video camera being 64-fold larger than in other studies (Kirchner and Srinivasan, 1989; Srinivasan et al., 1991), the camera resolution still made it possible to record an image of the bee's body in the form of an oriented ellipse consisting of about 14 pixels in length by about 8 pixels in width. Image sequences were stacked, calibrated and thresholded by ImageJ macros (http://rsb.info.nih.gov/ij/). We processed all the 156 recorded flight trajectories using a *Matlab*^{TM} script to determine for each frame the bee's ordinate (*y)* as a function of the abscissa (*x*) along the corridor axis (Fig. 1c).

Statistical analysis

For each bee's trajectory, the current forward speed at each abscissa *x* was computed using a four-point derivative smoothing filter. We associate each bee's trajectory with an average forward speed V_x and an average ordinate *y*. Then, we indicate in the Table 1 (2nd column), the mean value and standard deviation of the average speed calculated for each trajectory. Statistical data analyses were performed with the 'R' software program (http://www.r-project.org/). Student's *t*-tests were used to compare two mean ordinates: the significance level was taken at $\alpha \leq 0.05$ to determine differences. When data-sets were used for more than one statistical comparison, the significance level was corrected using Bonferroni's correction: $\alpha_c = 0.05/N$ (with N the number of comparisons).

Results

Centering and not centering

Figures 2a-c show trajectories of freely flying honeybees in the straight corridor lined with vertical stripes (cf. Fig. 1). The arrows show the bees' entrance position (E_L, E_C, or E_R) and the circles give the feeder position (F_L, F_C, or F_R). Each solid line corresponds to one bee's trajectory obtained by processing the successive video frames.

Figure 2a shows the bees' trajectories observed when both the entrance and the feeder were centered in the corridor (E_C and F_C). The bees can be seen to have flown along the midline of the corridor, consistent with the "centering response" described by Kirchner and Srinivasan (1989). The mean value of the mean ordinates of the 30 trajectories was 48±11cm (± S.D.), which is very close to the corridor midline ordinate: 47.5cm (*t*-test, t=-0.162, df=29 p=0.872).

By contrast, bees trained to enter and collect the food near one wall were seen to fly close to that same wall (Figs. 2b,c). In Fig. 2b, for example, where both entrance and feeder were placed on the left-hand side (E_L and F_L), the mean value of the mean ordinates of the 27 trajectories is 30±8cm, a value that departs considerably (*t*-test, t=-7.01, df=51.9, p<0.001) from the result obtained in Fig. 2a where bees flew centered on average. This major deviation from the midline is confirmed by the converse experiment (Fig. 2c), where both entrance and feeder were on the right-hand side of the corridor (E_R and F_R): bees can be seen to have hugged the right wall. In this case, the mean value of the mean ordinates of the 42 trajectories is 71±8cm, a value that again is at odds with the centering behaviour observed in Fig. 2a (*t*-test, t=9.57, df=50.1, p<0.001).

Removing part of the wall on one side

We then tested the bees trained as in Fig. 2c (i.e., E_R and F_R) in a situation where we removed a major, 150cm long portion (between abscissae X=75cm and X=225cm) of the left wall during the trials, so as to considerably degrade the OF on that side (see Materials and Methods).

As shown in Figure 2d, the bees flew near the right wall in much the same way as they did in Fig. 2c, without seemingly being affected by the absence of the left wall. Indeed, the

mean value of the mean ordinates of the 57 trajectories is 71±10cm, that is, a value strikingly similar to that (71±8cm) obtained in the presence of the left wall (Fig. 2c) (*t*-test, t=0.026, df=94.6, p=0.979).

When under this same condition (absence of the left wall), entrance and feeder were placed on the *left-hand* side (E_L and F_L) bees seemed to be highly confused during the trial. Some bees flew out of the opening and returned to the corridor. Some of these flew backward towards the starting-point, or attempted to cross the corridor toward the opposite (right) wall (no trajectory shown here).

Taken together, these results show that bees flying along a straight corridor do not systematically center along the midline. They may instead adopt a flight path that keeps them close to one wall. Upon hugging the wall, they seem to rely on a close visuomotor interaction with it and are not flummoxed by the absence of the opposite wall.

Comparing the left and right optic flows

Table 1 gives for each experiment (Fig. 2) the mean and standard deviation values of the right (ω_R) and left (ω_L) OFs, calculated as the speed divided by the distance from the respective wall. Right and left OFs did not differ significantly when the bees centered in the corridor (*t*-test, t=-0.187, df=57.1, p=0.852), but differed markedly in the three cases of wall-following behaviour (Fig.2b-d: *t*-test for all right/left pairs of lateral OFs, p<0.001). Most striking is the fact that the *unilateral* OF value is nearly the same for the three cases of wall-following behaviour (Table 1), (*t*-test, α_c=0.025, $p>\alpha_c$ for each comparison).

Another striking observation is that bees flew faster when entering and feeding on the left side than on the right side of the corridor (compare the V_x values in Table 1). One reason for this may be that the temperature on the day we performed the left wall experiment was higher (23°C) than on the day we performed the *right* wall experiment (18°C). Given that bees' activity depends notably on temperature, this 5°C increase in temperature might account for the higher forward speed observed. If speed differs significantly between the two situations (*t*-test, t=3.58, df=39.9, p<0.001), so does the distance from the nearer wall (*t*-test, t=2.98, df=57.4, p=0.004). Distance and speed appear to be tuned to each other, as if flying closer to a wall would imply flying at a reduced speed and vice versa (see Table 1). Important is the fact that in both situations the *unilateral optic flow* remained virtually the same (*t*-test,

182 t=0.483, df=49.2, p=0.632), as attested by Table 1 (grey shades for ω_L and ω_R corresponding
183 to Fig. 2b and 2c, respectively).
184
185

186 **Discussion**

187

188 The present experiments on honeybees trained to fly in a *wide* corridor toward an 'artificial
189 nectar source' show that they do not systematically fly along the corridor midline (Fig. 2b,c).
190 Clearly, bees can also hug one wall, keeping a tight visual contact with it and controlling their
191 lateral positioning without caring much about the opposite wall (Fig. 2b,c). This view is
192 strengthened by the observation that bees keep hugging one wall even when a large part of the
193 opposite wall is removed (Fig. 2d). Corridor 'wall-following' is thus another visual ability of
194 the bee that adds to the 'centering behaviour' observed repeatedly over the last 20 years
195 (Kirchner and Srinivasan, 1989, Srinivasan et al., 1991; review: Srinivasan and Zhang, 2004).

196 In our large corridor, bees adopted a wall-following behaviour whenever both entrance
197 and feeder were located near the same wall (Fig. 2b,c). In former experiments, bees had been
198 trained to enter a narrow (12cm-wide) corridor, one wall of which was movable (Srinivasan et
199 al., 1991). The authors had observed that bees would normally fly along the corridor midline
200 but shifted off center when the wall was moved. This striking reaction shows that bees gauge
201 neither the actual distance to the walls (which is not altered by the movement of the wall
202 whatsoever) nor the angular subtense of the walls (which is not altered by the movement of
203 the wall either) (Srinivasan et al., 1991). They also observed that the bee's *centering response*
204 is largely independent of the spatial structure of the walls in terms of both spatial frequency
205 and contrast. All these observations (Srinivasan et al., 1991) showed compellingly that the
206 visuomotor control mechanism at work in *flying* bees relies on the OF, which is a dynamical
207 visual cue. The mechanism therefore differs strikingly from that inferred for *walking* ants
208 (Heusser and Wehner, 2002), which were shown to rely on the angular subtense of the walls –
209 a stationary visual cue.

210 That bees can rely on their self-induced OF is consistent with the finding that several
211 *flying* insect species, including bees, have neurons that respond to the angular speed of an
212 image (i.e., the OF) to a large extent independently of the spatial frequency and contrast
213 (Ibbotson, 2001; Shoemaker et al., 2005;Straw et al., 2008).

214 In the three cases of wall-following behaviour observed (Fig. 2b-d), bees were
215 sometimes heading at a small angle Ψ (Fig. 1c) from the corridor axis towards the wall they
216 followed (see Table 1). Since the bee's frontal binocular field in the horizontal plane is not
217 negligible (about +/- 15 deg: Seild and Kaiser, 1981), the eye contralateral to the wall
218 followed may have contributed in part to the observed behaviour. Yet the heading remained,
219 on average, close to the tunnel axis ($|\Psi|<15$ deg), so that the OF perceived, e.g., by the *left* eye

220 on the *right* wall ($\omega < 50°/s$) was much smaller than the OF ω_R perceived by the *right* eye on
221 that same wall (see Table 1).
222
223 How can a bee fly so deftly along one side of a corridor at all, caring so little about the
224 absence of the opposite wall? If, in the experiment shown in Fig. 2d, bees had balanced the
225 lateral OFs perceived on both sides - as suggested by the "optic flow balance" hypothesis
226 (Kirchner and Srinivasan, 1989) - they would have rushed out of the large opening in the left
227 wall, in search of a left OF of comparable size to that perceived on the right-hand side.
228 Kirchner and Srinivasan (1989) recorded the bees' trajectories when one wall was replaced by
229 a homogeneously grey sheet (contrast $m<0.05$) that generated a poor lateral OF on one side.
230 The authors reported that the bees' trajectories shifted toward the homogeneous side, albeit
231 without bumping into it (Kirchner and Srinivasan, 1989; Srinivasan et al., 1991). In other
232 experiments, the authors further investigated this 'lateral response' by testing bees in a narrow
233 corridor (15.5cm-wide), one wall of which had a circular window (diameter 21cm) that
234 displayed no pattern. The bees were observed to shift toward this aperture too (Srinivasan et
235 al., 1993).

236 To explain these behavioural patterns, our working hypothesis is that a bee will follow
237 the right or left wall by *regulating* (i.e., maintaining constant) whichever *lateral* OF (right or
238 left) is *greater*. In another context, we have proposed a simple feedback mechanism, termed
239 the *OF regulator*, that explains *how* a miniature air-vehicle can maintain its lateral OF
240 constant throughout its travel through a corridor (Serres et al., 2008). Simulation experiments
241 showed that the agent can control its side slip on the sole basis of a *unilateral OF regulator*
242 (based on OF sensors mounted on either sides). At all times, the OF regulator strives to
243 maintain the greater of the lateral OFs perceived from the walls constant. Since by definition
244 the lateral OF is equal to the speed/distance ratio, this amounts to maintaining the distance to
245 the wall proportional to the current forward speed. The striking correlation noted above
246 between forward speed and distance from the wall is fully consistent with this 'unilateral optic
247 flow regulation' hypothesis. Indeed, the value of the optic flow experienced by the bee was
248 virtually the same (compare ω_L and ω_R for Fig. 2b and c: grey shades in Table 1), even though
249 both speed and distance were significantly different in the two situations.

250 There is an infinite number of combinations of flight speed and distance that will generate a
251 desired level of OF. If the bee has no information on its flight speed, then the OF of 235

252 deg/sec can be produced by flying at a speed of 117cm/sec at a distance of 30cm from the
253 wall, or at 58.5cm/sec at a distance of 15cm, etc. Inspired by the observation that the bee's
254 flight speed in a tunnel depends on the *sum of the right and left* OFs (Srinivasan et al. 1996),
255 we showed that this chicken-and-egg problem can be solved by adding a second *OF regulator*
256 that would be in charge of controlling the flight speed. In a recent paper dealing with realistic
257 simulation experiments (Serres et al., 2008), we have shown that the flight of an air vehicle in
258 a tunnel can be fully determined, as regards both speed and distance from the walls, on the
259 basis of two interdependent OF regulators. The power of the hypothesis is that sensible
260 behaviour is achieved without *measuring* speed, distance and tunnel width at all. Our
261 simulation experiments also showed (Serres et al., 2008) that by adding the second lateral OF-
262 based feedback loop controlling the forward speed, the robot's behaviour (in terms of both
263 *speed* and *distance* from the walls) would mimick the one observed on flying honeybees
264 travelling through a straight or tapered corridor (Kirchner and Srinivasan, 1989; Srinivasan et
265 al., 1996).

266 The *unilateral OF regulator* principle is similar in many respects to the *ventral OF*
267 *regulator* principle that was put forward to explain the behaviour of insects taking off,
268 following terrain and landing (Ruffier and Franceschini, 2005; Franceschini et al., 2007). But
269 whereas the *ventral OF regulator* served to control the bee's vertical lift (hence the height of
270 flight), the *unilateral OF regulator* put forward here serves to control the bee's sideways
271 thrust (hence the distance from a wall). Just as the *ventral OF regulator* maintained automatic
272 clearance from the ground below (thus preventing ground collisions), the *unilateral OF*
273 *regulator* maintains automatic clearance from the walls (thus preventing lateral collisions).
274 This simple system requires exclusively OF sensors which, as we now know, may be
275 provided by specific motion detecting neurons such as the bee's velocity tuned neurons (VT:
276 Ibbotson, 2001). On this view, the bee would approach or recess from a wall by simply
277 attempting to maintain the spike firing rate of some VT neurons constant and equal to a *set-*
278 *point*. This control scheme would present two advantages:

279 • A single parameter, the OF *set-point*, would allow the insect to keep a safe distance
280 from a wall without having to *measure* this distance. Nor would speed need to be *measured*.

281 • The *OF regulator* can be said to tune the animal's behaviour at all times such that the
282 OF will deviate little from the OF *set-point*. As noticed elsewhere (Franceschini et al., 2007),
283 this requirement to measure a mere OF *deviation* puts little constraint on the dynamic range of
284 the motion detecting neurons.

285 The control scheme suggested here is consistent not only with the bees' "wall-
286 following" behaviour we have described, but also with the existence in bees of visual neurons
287 that are able to evaluate the lateral OF. The scheme would confer upon the bee a safe
288 clearance from the walls - a clearance commensurate with its forward speed - whatever the
289 speed. Though simple, this control scheme is powerful as it would enable honeybees to
290 prevent lateral collisions *without any needs to measure distance and speed*. This is consistent
291 with the diminutive size of the insect's brain that is obviously not equipped with cumbersome
292 range finders, Doppler radars or GPS receivers.
293

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Fig. 1 Experimental apparatus. **a** During the training session, bees entered the straight corridor (300x95x25 cm) one by one, through one of the three Entrances (left: E_L, central: E_C, or right: E_R) and were fed at one of the three Feeder positions (F_L, F_C, or F_R). During the trials, a high-resolution digital camera placed 220cm above the corridor filmed the trajectory of single flying bees (at 20 frames/s) over the central (150cm-long) part of the corridor. An insect netting stretched flat over the flight tunnel prevented the bees from escaping upwards, while enabling the camera to see through. Both walls were lined with a similar periodic pattern consisting of vertical white-and-grey stripes (spatial period 10cm, contrast $m = 0.41$). **b** In one experiment, a major part (150cm-long) of the left wall was removed. **c** Top view of a bee flying at speed V along the corridor. Ψ is the bees's body yaw angle with respect to the tunnel axis, x the body abscissa, y the body ordinate, V_x and V_y the forward and sway components of speed, and D the corridor width.

Fig. 2 Trajectories of individual bees tested in the corridor under four experimental conditions. **a** Both the bee's entrance (E_C) and the feeder (F_C) were placed on the corridor midline. **b** and **c** Entrance and feeder were placed on one side of the corridor (E_L and F_L, or E_R and F_R). **d** The bee entered the corridor and was fed on the right-hand side as in (c) (E_R and F_R), but part of the left wall was removed during the trial (see Materials and Methods). The histograms on top give the distribution of the mean ordinate of each trajectory. The value given for the mean ordinate is followed by the standard deviation of the distribution. n is the number of trajectories recorded in each experimental condition.

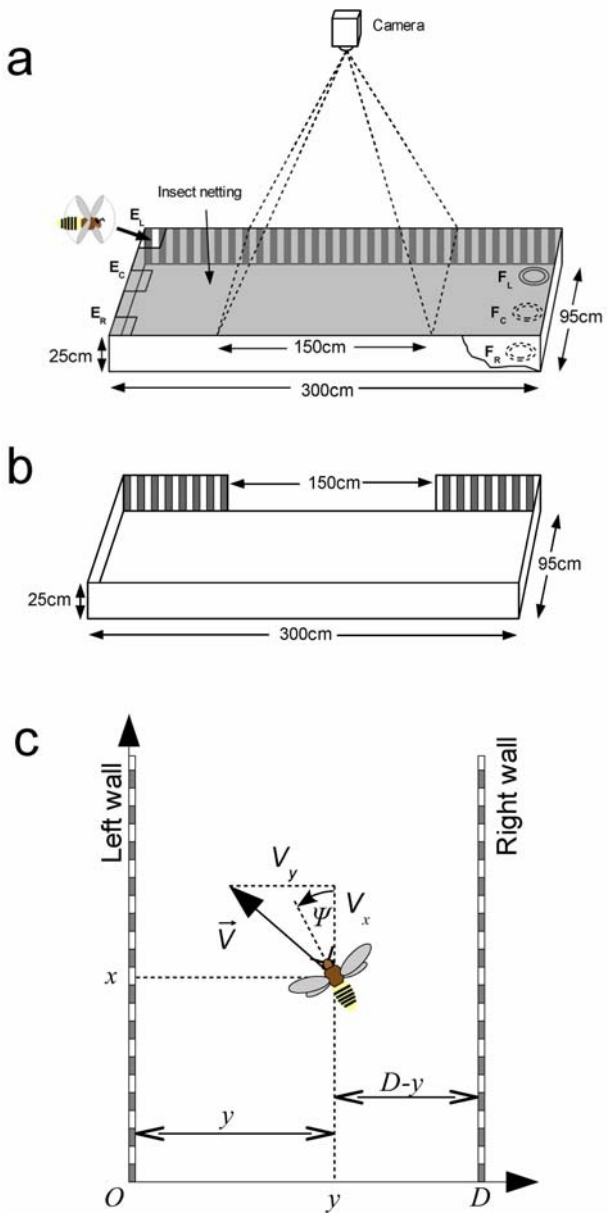
Table 1. Comparisons between the bees' ordinate y, the forward speed V_x, and the bee's body yaw angle Ψ for each experimental condition (Fig. 2a-d). The last two columns indicate the values and standard deviations of the right and left lateral optic flows (ω_L and ω_R) perceived by the bees in each case. These values were calculated as the speed /distance ratio (in rad/s) and converted into °/s. Notice that the lateral optic flow perceived by the bees with respect to the wall they choose to follow is of the same order of magnitude for the last three experimental conditions (grey shade).

386 **Table 1.**
387
388

Experiments and n = number of trajectories	y (cm)	V_x (cm/s)	Ψ (°)	$\omega_L = V_x/y$ (°/s)	$\omega_R = V_x/(D\text{-}y)$ (°/s)
Fig. 2a, $E_C \rightarrow F_C$ (2 walls), n=30	47 ± 11	117 ± 36	0 ± 9	148 ± 54	151 ± 61
Fig. 2b, $E_L \rightarrow F_L$ (2 walls), n=27	30 ± 8	117 ± 38	5 ± 8	235 ± 80	106 ± 39
Fig. 2c, $E_R \rightarrow F_R$ (2 walls), n=42	71 ± 8	88 ± 24	-13 ± 9	73 ± 25	226 ± 68
Fig. 2d, $E_R \rightarrow F_R$ (1 wall), n=57	71 ± 10	98 ± 31	-9 ± 10	4 ± 1	265 ± 116

389

390 **Figure 1.**



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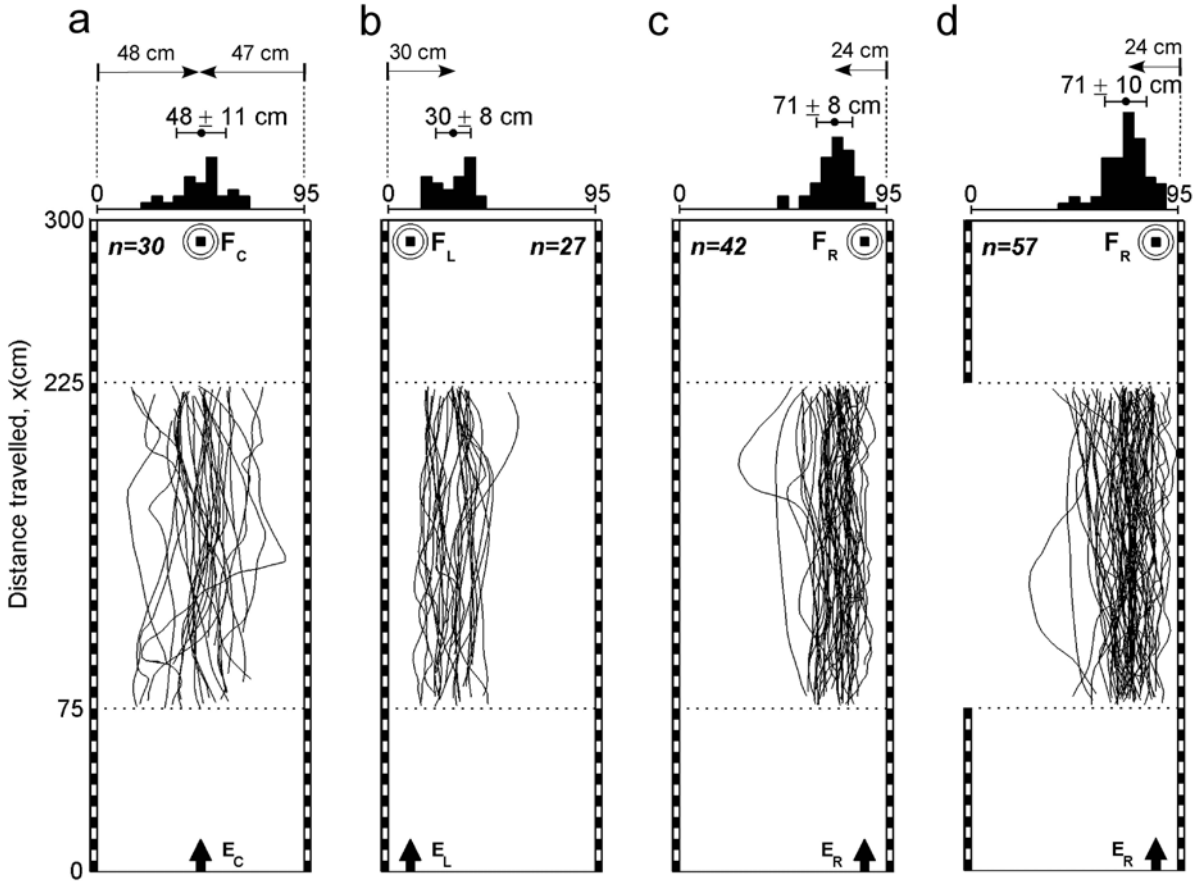
392

393 **Figure 2.**

394



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