A bee in the corridor: centering and wall-following — **Source link** ⇗

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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

56   honeybees (*Apis mellifera*) under four experimental conditions. The experimental set-up (Fig.

57   1a) consisted of a relatively wide (95cm) and long (300cm) rectangular corridor (25cm-

58   height). The two walls were wallpapered with a pattern of vertical grey-and-white stripes of

59   spatial wavelength λ = 10cm using a solvent free glue (Sader© Fortissimo, MS polymer-

60   based glue). The Michelson contrast was m = 0.41, as measured in the green spectral range

61   (specific for motion vision in the honeybee: Kaiser and Liske, 1974).

62   By using a pattern with a relatively large spatial wavelength (10cm), we made sure

63   that the bee would see it whatever its lateral positioning in the wide corridor, given the small

64   bee's interommatidial and acceptance angles, which are both in the order of 2.5 deg for

65   laterally oriented ommatidia (Seidl and Kaiser, 1981; Horridge, 2003).

66   In the last experiment, a 1.5m long central part of the left wall was removed (between

67   abscissae X = 75cm and X = 225cm). Through this wide opening, the nearest (15m) trunk of a

68   tree that the bee could see produced an OF of only 4°/s (see 4th column in Table 1).

69   The coarsely textured wooden floor was white, maximizing the contrast between the

70   insect and the floor in the video sequences. The corridor was roofed with see-through insect

71   netting allowing efficient corridor ventilation and closed with a white plank at each end. Bees

72   could enter the corridor only through one of three entrance holes in the insect netting (left

73   Entrance: E_L, central Entrance: E_C, right Entrance: E_R). This arrangement forced the bees to

74   enter the corridor with a quasi zero forward speed.

75

76   *Bee training*

77

78   Experiments were conducted outdoors on clear days with no wind. Bees were trained to enter

79   the corridor through one of the three entrances (E_L, E_C, E_R, see Fig. 1a), depending on the

80   experiment. Bees were first trained for three days to feed on a honey-flavoured sweet that was

81   placed each time deeper and deeper in the corridor, up to the final position shown in Fig. 1a.

82   At the end of the training session, the sweet was replaced by a sugar solution feeder (35%

83   w/w, i.e., 1.2M sucrose concentration) for an additional two days to exclude any unwanted

84   olfactory cues. The feeder was placed at one of the three positions (left F_L, central F_C or right

85   F_R), depending upon the experiment. After the training session, trajectories of single bees

86   flying to the feeder were video-filmed from above. Bees' return paths home across the

87   corridor were not recorded.

88

89   *Video-recording and flight path analysis*

90

91   The bees' flight trajectories to the feeder were filmed at a rate of 20 frames/s with a high-

92   resolution digital black-and-white CMOS camera (*Prosilica*[TM] EC1280: 1280x1024 pixels)

93   placed at 220cm above the corridor floor (Fig. 1a). We only consider bees entered one at a

94   time in the camera field of view during the recordings. The data were stored on a standard

95   notebook computer equipped with an image sequence acquisition software program. The

96   camera field of view was adjusted to 150cm in length and 95cm in width, centered on the

97   corridor. Despite the area covered by the video camera being 64-fold larger than in other

98   studies (Kirchner and Srinivasan, 1989; Srinivasan et al., 1991), the camera resolution still

99   made it possible to record an image of the bee's body in the form of an oriented ellipse

100   consisting of about 14 pixels in length by about 8 pixels in width. Image sequences were

101   stacked, calibrated and thresholded by ImageJ macros (http://rsb.info.nih.gov/ij/). We

102   processed all the 156 recorded flight trajectories using a *Matlab*[TM] script to determine for each

103   frame the bee's ordinate (y) as a function of the abscissa (x) along the corridor axis (Fig. 1c).

104

105   *Statistical analysis*

106

107   For each bee's trajectory, the current forward speed at each abscissa x was computed using a

108   four-point derivative smoothing filter. We associate each bee's trajectory with an average

109   forward speed V_x and an average ordinate y. Then, we indicate in the Table 1 (2nd column), the

110   mean value and standard deviation of the average speed calculated for each trajectory.

111   Statistical data analyses were performed with the 'R' software program (http://www.r-

112   project.org/). Student's *t*-tests were used to compare two mean ordinates: the significance

113   level was taken at $\alpha \leq 0.05$ to determine differences. When data-sets were used for more than

114   one statistical comparison, the significance level was corrected using Bonferroni's correction:

115    $\alpha_c = 0.05/N$ (with N the number of comparisons).

116

117 **Results**

118

119 *Centering and not centering*

120

121 Figures 2a-c show trajectories of freely flying honeybees in the straight corridor lined with

122 vertical stripes (cf. Fig. 1). The arrows show the bees' entrance position (E_L, E_C, or E_R) and

123 the circles give the feeder position (F_L, F_C, or F_R). Each solid line corresponds to one bee's

124 trajectory obtained by processing the successive video frames.

125   Figure 2a shows the bees' trajectories observed when both the entrance and the feeder

126 were centered in the corridor (E_C and F_C). The bees can be seen to have flown along the

127 midline of the corridor, consistent with the "centering response" described by Kirchner and

128 Srinivasan (1989). The mean value of the mean ordinates of the 30 trajectories was 48±11cm

129 (± S.D.), which is very close to the corridor midline ordinate: 47.5cm (*t*-test, $t=-0.162$, $df=29$

130 $p=0.872$).

131   By contrast, bees trained to enter and collect the food near one wall were seen to fly

132 close to that same wall (Figs. 2b,c). In Fig. 2b, for example, where both entrance and feeder

133 were placed on the left-hand side (E_L and F_L), the mean value of the mean ordinates of the 27

134 trajectories is 30±8cm, a value that departs considerably (*t*-test, $t=-7.01$, $df=51.9$, $p<0.001$)

135 from the result obtained in Fig. 2a where bees flew centered on average. This major deviation

136 from the midline is confirmed by the converse experiment (Fig. 2c), where both entrance and

137 feeder were on the right-hand side of the corridor (E_R and F_R): bees can be seen to have

138 hugged the right wall. In this case, the mean value of the mean ordinates of the 42 trajectories

139 is 71±8cm, a value that again is at odds with the centering behaviour observed in Fig. 2a (*t*-

140 test, $t=9.57$, $df=50.1$, $p<0.001$).

141

142 *Removing part of the wall on one side*

143

144 We then tested the bees trained as in Fig. 2c (i.e., E_R and F_R) in a situation where we removed

145 a major, 150cm long portion (between abscissae $X=75$cm and $X=225$cm) of the left wall

146 during the trials, so as to considerably degrade the OF on that side (see Materials and

147 Methods).

148   As shown in Figure 2d, the bees flew near the right wall in much the same way as they

149 did in Fig. 2c, without seemingly being affected by the absence of the left wall. Indeed, the

150   mean value of the mean ordinates of the 57 trajectories is 71±10cm, that is, a value strikingly

151   similar to that (71±8cm) obtained in the presence of the left wall (Fig. 2c) (*t*-test, *t*=0.026,

152   *df*=94.6, *p*=0.979).

153   When under this same condition (absence of the left wall), entrance and feeder were

154   placed on the *left-hand* side (E_L and F_L) bees seemed to be highly confused during the trial.

155   Some bees flew out of the opening and returned to the corridor. Some of these flew backward

156   towards the starting-point, or attempted to cross the corridor toward the opposite (right) wall

157   (no trajectory shown here).

158   Taken together, these results show that bees flying along a straight corridor do not

159   systematically center along the midline. They may instead adopt a flight path that keeps them

160   close to one wall. Upon hugging the wall, they seem to rely on a close visuomotor interaction

161   with it and are not flummoxed by the absence of the opposite wall.

162

163   *Comparing the left and right optic flows*

164

165   Table 1 gives for each experiment (Fig. 2) the mean and standard deviation values of the right

166   (ω_R) and left (ω_L) OFs, calculated as the speed divided by the distance from the respective

167   wall. Right and left OFs did not differ significantly when the bees centered in the corridor (*t*-

168   test, *t*=-0.187, *df*=57.1, *p*=0.852), but differed markedly in the three cases of wall-following

169   behaviour (Fig.2b-d: *t*-test for all right/left pairs of lateral OFs, *p*<0.001). Most striking is the

170   fact that the *unilateral* OF value is nearly the same for the three cases of wall-following

171   behaviour (Table 1), (*t*-test, α_c=0.025, *p*>α_c for each comparison).

172   Another striking observation is that bees flew faster when entering and feeding on the

173   left side than on the right side of the corridor (compare the V_x values in Table 1). One reason

174   for this may be that the temperature on the day we performed the left wall experiment was

175   higher (23°C) than on the day we performed the *right* wall experiment (18°C). Given that

176   bees' activity depends notably on temperature, this 5°C increase in temperature might account

177   for the higher forward speed observed. If speed differs significantly between the two

178   situations (*t*-test, *t*=3.58, *df*=39.9, *p*<0.001), so does the distance from the nearer wall (*t*-test,

179   *t*=2.98, *df*=57.4, *p*=0.004). Distance and speed appear to be tuned to each other, as if flying

180   closer to a wall would imply flying at a reduced speed and vice versa (see Table 1). Important

181   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

Discussion

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

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

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

In the three cases of wall-following behaviour observed (Fig. 2b-d), bees were sometimes heading at a small angle Ψ (Fig. 1c) from the corridor axis towards the wall they followed (see Table 1). Since the bee's frontal binocular field in the horizontal plane is not negligible (about +/- 15 deg: Seild and Kaiser, 1981), the eye contralateral to the wall followed may have contributed in part to the observed behaviour. Yet the heading remained, 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 (ω < 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

References

Straw AD, Rainsford T, O'Caroll DC (2008). Contrast sensitivity of insect motion detectors to natural images. J. of Vision 8:1-9.

Baird E, Srinivasan MV, Zhang SW, Cowling A (2005). Visual control of flight speed in honeybees. J. of Exp. Biol. 208:3895-3905.

Buchner E (1984). Behavioral analysis of spatial vision in insects. In Photoreception and vision in invertebrates (ed. M.A. Ali, New York : Plenum), 561-621.

Collett T, King AJ (1975). Vision during flight. In The compound eye and vision of insects (Ed. G.A. Horridge, Clarendon Press, Oxford), 437-466

Collett TS, Nalbach H-O, Wagner H (1993). Visual stabilization in the arthropods. In Visual motion and its role in the stabilization of gaze (Eds. F.A. Miles and J. Wallman), chap 11, 239-263.

David CT (1978). The relationship between body angle and flight speed in free flying *Drosophila*. Physio. Entomol. 3:191-195.

Franceschini N, Ruffier F, Serres J (2007). A bio-inspired flying robot sheds light on insect piloting abilities. Current Biology 17:329-335.

Gibson JJ (1950). In The perception of the visual world, Boston: Houghton Mifflin Co.

Heusser D, Wehner R (2002). The visual centring response in desert ants, *Cataglyphis fortis*. J. of Exp. Biol. 205:585-590.

Horridge GA (2003). Visual resolution of gratings by the compound eye of the bee *Apis mellifera*. J. of Exp. Biol. 206:2105-2110.

Hrncir M, Jarau S, Zucchi R, Barth FG (2004). Thorax vibrations of the stingless bee (*Melipona seminigra*). I. No influence of visual flow. J. Comp. Physiol. A 190:539-548.

Ibbotson MR (2001). Evidence for velocity-tuned motion sensitive descending neurons in the honeybee. Proc. R. Soc. B 268:2195-2201.

Kaiser W, Liske E (1974). Die optomotorischen Reaktionen von fixiert fliegenden Bienen bei Reizung mit Spektrallichtern. J. Comp. Physiol. 89:391-408.

Kennedy JS (1939). Visual responses of flying mosquitoes. Proc. Zool. Soc. Lond. 109:221-242.

Kirchner WH, Srinivasan MV (1989). Freely flying honeybees use image motion to estimate object distance. Naturwissenchaften 76:281-282.

Lee DN (1980). The optic flow field : the foundation of vision. Phil. Trans. Roy. Soc. Lond. B 290:169-179.

Ruffier F, Franceschini N (2005). Optic flow regulation: the key to aircraft automatic guidance. Robotics and Autonomous Systems 50(4):177-194.

Seidl R, Kaiser W (1981). Visual field size, binocular domain and the ommatidial array of the compound eyes in worker honey bees. J. of Comp. Physiol. A 143:17-26.

Serres J, Dray D, Ruffier F, Franceschini N (2008). A vision-based autopilot for a miniature air vehicle : joint speed control and lateral obstacle avoidance. Autonomous Robots 25:103-144.

Shoemaker PA, O'Caroll DC, Straw AD (2005). Velocity constancy and models for wide-field visual motion detection in insects. Biol. Cybern. 93:275-287.

Srinivasan MV, Lehrer M, Kirchner WH, Zhang SW (1991). Range perception through apparent image speed in freely flying honeybees. Vis. Neurosci. 6:519-535.

Srinivasan MV, Zhang SW, Chandrashekara K (1993). Evidence for two distinct movement-detecting mechanisms in insect vision. Naturwissenschaften 80:38-41.

Srinivasan MV, Zhang SW, Lehrer M, Collett TS (1996). Honeybee navigation en route to the goal: visual flight control and odometry. J. Exp. Biol. 199:237-244.

Srinivasan MV, Zhang SW (2004). Visual motor computations in insects. Annual Review of Neuroscience 27:679-696.

351
352 **Fig. 1** Experimental apparatus. **a** During the training session, bees entered the straight corridor (300x95x25 cm)
353 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
354 Feeder positions (F_L, F_C, or F_R). During the trials, a high-resolution digital camera placed 220cm above the
355 corridor filmed the trajectory of single flying bees (at 20 frames/s) over the central (150cm-long) part of the
356 corridor. An insect netting stretched flat over the flight tunnel prevented the bees from escaping upwards, while
357 enabling the camera to see through. Both walls were lined with a similar periodic pattern consisting of vertical
358 white-and-grey stripes (spatial period 10cm, contrast $m = 0.41$). **b** In one experiment, a major part (150cm-long)
359 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
360 angle with respect to the tunnel axis, x the body abscissa, y the body ordinate, V_x and V_y the forward and sway
361 components of speed, and D the corridor width.
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368 **Fig. 2** Trajectories of individual bees tested in the corridor under four experimental conditions. **a** Both the bee's
369 entrance (E_C) and the feeder (F_C) were placed on the corridor midline. **b** and **c** Entrance and feeder were placed
370 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-
371 hand side as in (c) (E_R and F_R), but part of the left wall was removed during the trial (see Materials and
372 Methods). The histograms on top give the distribution of the mean ordinate of each trajectory. The value given
373 for the mean ordinate is followed by the standard deviation of the distribution. n is the number of trajectories
374 recorded in each experimental condition.
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379 **Table 1**. Comparisons between the bees' ordinate y, the forward speed V_x, and the bee's body yaw angle Ψ for
380 each experimental condition (Fig. 2a-d). The last two columns indicate the values and standard deviations of the
381 right and left lateral optic flows (ω_L and ω_R) perceived by the bees in each case. These values were calculated as
382 the speed /distance ratio (in rad/s) and converted into °/s. Notice that the lateral optic flow perceived by the bees
383 with respect to the wall they choose to follow is of the same order of magnitude for the last three experimental
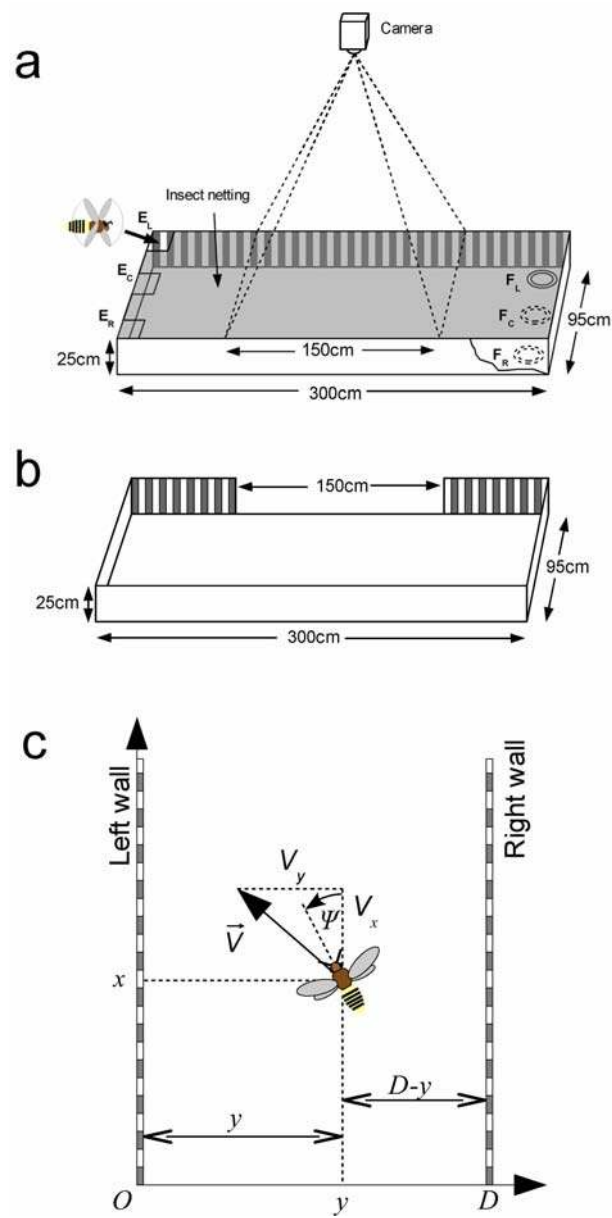384 conditions (grey shade).
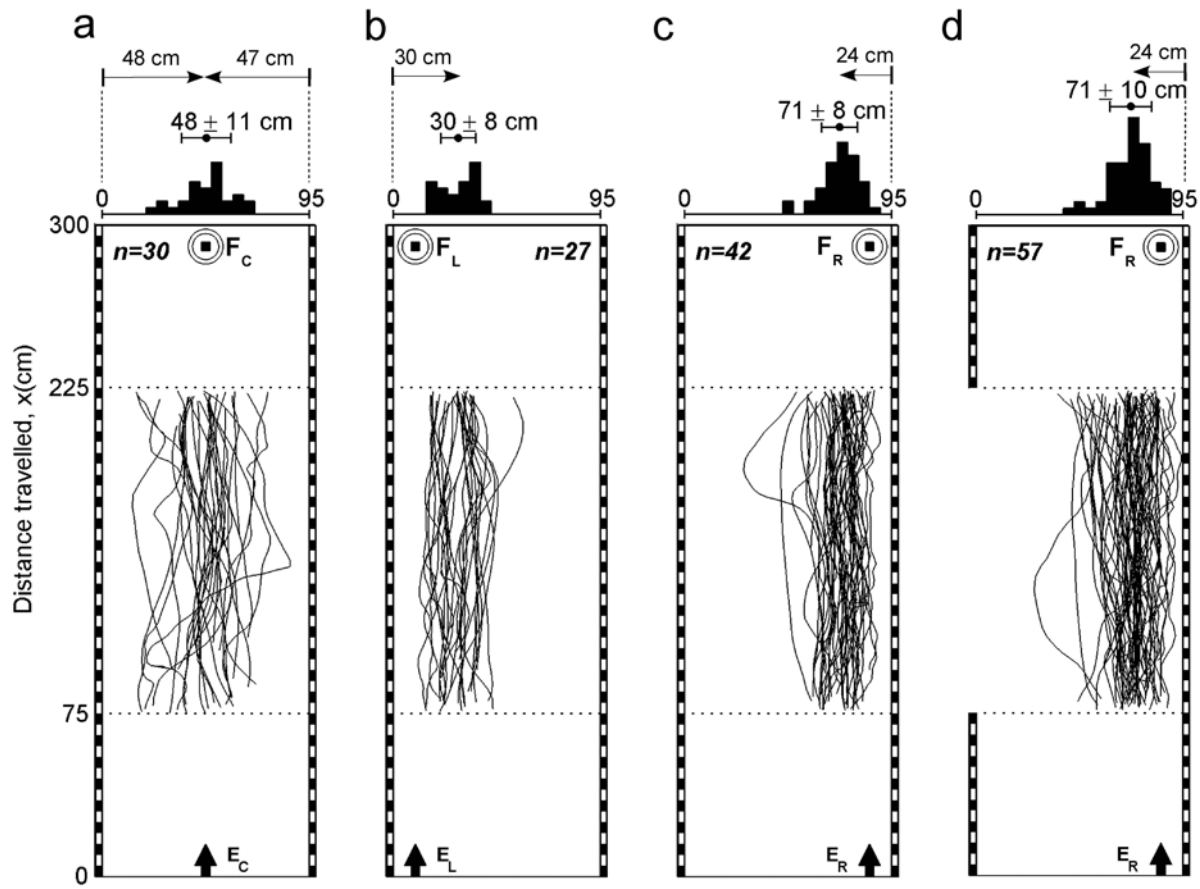385

386 **Table 1.**

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

389

390 **Figure 1.**

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393 **Figure 2.**

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