Gap perception in bumblebees

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Abstract

A number of insects fly over long distances below the natural canopy where the physical environment is highly cluttered consisting of obstacles of varying shape, size and texture. While navigating within such environments animals need to perceive and disambiguate environmental features that might obstruct their flight. The most elemental aspect of aerial navigation through such environments is gap identification and passability evaluation. We used bumblebees to seek insights into the mechanisms used for gap identification when confronted with an obstacle in their flight path and behavioral compensations employed to assess gap properties. Initially, bumblebee foragers were trained to fly though an unobstructed flight tunnel that led to a foraging chamber. After the bees were familiar with this situation, we placed a wall containing a gap that unexpectedly obstructed the flight path on a return trip to the hive. The flight trajectories of the bees as they approached the obstacle wall and traversed the gap were analyzed in order to evaluate their behavior as a function of the distance between the gap and a background wall that was placed behind the gap. Bumblebees initially decelerate when confronted with an unexpected obstacle. Deceleration was first noticed when the obstacle subtended around 35° on the retina but also depended on the properties of the gap. Subsequently the bees gradually traded off their longitudinal velocity to lateral velocity and approached the gap increasing lateral displacements and lateral velocity. Bumblebees shaped their flight trajectory depending on the salience of the gap, in our case, indicated by the optic flow contrast between the region within the

35 gap and on the obstacle, which increases with decreasing distance between the gap and

36 the background wall. As the optic flow contrast decreased the bees spent increasing

37 time moving laterally across the obstacles. During these repeated lateral maneuvers the

38 bees are likely assessing gap geometry and passability.

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40

41 **Introduction**

42

43 Even with relatively tiny brains insects display a rich repertoire of behaviors, the

44 operation of many of which still remains unclear. Aerial locomotion below the natural

45 canopy is one such behavior that has received increased attention in the last decade

46 from both biologists and engineers alike (Shyy et al., 2016). Natural flight at the small

47 scale of insects, where the sensory and mechanical constraints are particularly

48 challenging, requires the concerted coordination of their computationally parsimonious

49 sensorimotor system (Dudley, 2002). The spatial environment close to the Earth's

50 surface consists of a myriad of natural and artificial objects that can vary widely in

51 shape, size and texture. This renders the physical environment to be unpredictable and

52 poses challenges to aerial locomotion. Steady level flight for sustained durations is

53 generally unfeasible in this domain with obstacles constantly coming in the way. Thus,

54 in order to achieve safe transit through such environments flying systems need to be

55 adept at perceiving the environment to identify obstacles and devise alternative flight

56 paths. From a biophysical standpoint, apart from performance limitations based on

57 allometric body size scaling other factors, such as collision avoidance and properties of

58 the physical environment, also influence flight trajectories and overall performance of

59 insects (Crall et al., 2015; Dudley, 2002). Terrestrially bound insects utilize a number of

60 strategies at the sensory and motor level in dealing with cluttered and uneven terrain

61 including active and passive body compliance, gait coordination, and preflexion. A

62 commensurate level of understanding is yet to be arrived at for flying animals.

63

64 Unlike during legged locomotion where tactile sensory inputs can augment vision in

65 gaining environmental information, flying insects rely only on the latter for safe passage

66 and path planning. For long distance navigation, flying insects might use, apart from

67 vision, other sensory modalities such as odor and geomagnetic fields (Knaden and

68 Graham, 2016) In order for a flying animal to arrive at its intended destination or ensure

69 safe locomotion, at a basic level, the animal needs to process the obstacles that lie in its

70 path and identify gaps. Obstacle and gap detection may thus be considered the most

71 basic element of flight through clutter. A few recent studies have analysed the response
72 of flying insects in minimally cluttered environments and revealed that when confronted
73 with obstacles with varying spacing, insects such as bumblebees and honeybees choose
74 the larger gap (Baird and Dacke, 2016; Ong et al., 2017). This might seem as an obvious
75 response, yet it highlights the active response of insects in avoiding collisions, which
76 otherwise can result in irreparable damage to body and wings. Baird and Dacke (2016)
77 suggested bumblebees may utilize a simple brightness based strategy in making a choice
78 among the different gaps, i.e. bigger gaps are likely to be brighter than smaller gaps.
79 Though a few experiments have observed insects behaving around individual obstacles
80 and minimally cluttered environments, the mechanisms mediating the elemental
81 process of obstacle and gap perception and the factors that influence the assessment of
82 passability are still unclear.
83
84 Especially fast flying animals, such as many insect species, rely on optic flow as the main
85 source of spatial information, i.e. on the continuous stream of retinal image changes
86 induced during self-motion and, thus, is particularly relevant for behavior in cluttered
87 environments (Egelhaaf 2006; Egelhaaf et al., 2012). Optic flow has also been shown to
88 aid in estimating flight distance, flight path centering, identifying foraging locations and
89 many other behaviorally relevant tasks, see (Baird et al., 2013; Kern et al., 2012; Serres
90 and Ruffier, 2017; Serres et al., 2008; Srinivasan, 2015; Srinivasan and Zhang, 1997).
91 Observations of the flight trajectory of insects such as flies and bees has shown that
92 insects actively shape the temporal structure of their visual input by employing
93 prototypical flight maneuvers, especially to separate translational from rotational optic
94 flow and, thus, to facilitate discerning spatial information about the surroundings
95 (Braun et al., 2010; Braun et al., 2012; Egelhaaf et al., 2012b). Rotations that are
96 inevitably required to change flight direction are squeezed into brief saccadic turns with
97 rotation velocities often exceeding 4000deg/s (Hateren and Schilstra, 1999). Between
98 saccadic turns the insect keeps its gaze basically straight for more than 80% of overall
99 flight time to induce purely translational optic flow (Boeddeker et al., 2010; Braun et al.,
100 2012; Dickinson, 2005; Hateren and Schilstra, 1999; Mertes et al., 2015; Schilstra and
101 Hateren, 1999). Since only the translational optic flow contains spatial information, this
102 active flight and gaze strategy is believed to facilitate spatial vision and thus may be
103 particularly relevant for navigation in cluttered terrain (Egelhaaf et al., 2014). However
104 this vision-based strategy relying on the closed action perception loop has not been
105 investigated systematically in cluttered environment and, thus, needs further
106 investigation. Specifically, how does an insect react to unexpected obstacles obstructing

107   its flight path? What flight maneuvers does it perform in order to detect gaps and assess

108   passability?

109

110   Here we sought to uncover the mechanisms implemented by flying insects in gap

111   identification and perception. Bumblebees are excellent model organisms because much

112   is known about their flight and navigational performance (Baird and Dacke, 2012; Crall

113   et al., 2014; Mirwan and Kevan, 2013; Osborne et al., 2008; Ravi et al., 2013; Riabinina et

114   al., 2014; Lobecke et al. 2018). We presented unsuspecting bumblebees with an altered

115   environment consisting of a wall obstructing their flight path but containing a gap that

116   prevented direct passage to their goal and observed their behavior as they approached

117   and traversed the gap. We analyzed the flight trajectory of the bees in different distances

118   from the gap and computed key visual metrics such as: angle subtended by the obstacle

119   and gap on the retina, mean optic flow and optic flow contrast, in order to identify

120   factors that influence gap identification and assessment of passability. Our data suggest

121   that bumblebees employ an active gazing flight strategy in enabling the identification of

122   gaps and critical environmental parameters that affects safe passage.

123

124

125   **Materials and Methods**

126

127   **Experiment Setup**

128

129   Experiments were conducted with individuals from a *Bombus terrestris* colony that was

130   maintained within the lab. A healthy hive sourced from a commercial breeder (Biobest

131   Group NV, Westerlo, Belgium) was placed within a 0.5x0.5.0.3m mesh enclosure that

132   was covered with dark cloth to simulate the natural underground habitat of the bees.

133   The hive enclosure was connected to a flight tunnel 0.25x0.25x1.5m that lead to a

134   1x1x0.75m foraging chamber where gravity feeders containing 30%/vol. sucrose

135   solution blended with 1% commercial honey were placed. Connections between the

136   hive enclosure, flight tunnel and foraging chamber were made using 30mm ID and

137   150mm long flexible silicon tubing. Finely ground pollen was placed directly within the

138   hive and bees were permitted to access sucrose in the foraging chamber ad libitum.

139   Consistent foraging flights by numerous (>20) worker bees were observed within one

140   day of immigration to the enclosure. The bees and hive were given one week for

141   habituation to the environment before experiments.

142

143   During experiments gates on either sides of the flight tunnel were used to regulate

144   traffic, and only one bee at a time was permitted to enter the flight tunnel. Only bees

145   returning to the hive were considered for analysis. The experiment procedure will be

146   described from the perspective of the bee returning to the hive as per Fig. 1a. An

147   obstacle was created within the flight tunnel by placing an artificial vertical wall that

148   contained a rectangular hole that was 50mm wide and started from the middle

149   extending to the top, see Fig. 1a. The sidewalls of the tunnel were lined with an

150   achromatic random checkerboard pattern while the floor was lined with a random cloud

151   with spatial frequencies varying by 1/f, similar to the one used by (Monteagudo et al.,

152   2017). A second vertical wall was placed behind the wall containing the gap. The same

153   checkerboard pattern was also placed on both obstructing verticals, Fig. 1. Five different

154   experiment conditions were tested where the distance between the gap and rear wall

155   was varied by 550, 300, 150, 50 or 0 mm. During the different scenarios the wall

156   containing the gap was always placed at 0.9m from the entrance of the tunnel, see Fig.

157   1a. Twenty flights were recorded for each condition while the conditions were varied

158   pseudo-randomly between each recording. Once the bees approached and passed the

159   gap the rear wall was removed to permit their onward flight back to the hive. For the

160   condition when the rear wall was adjacent to the gap (d = 0mm) passage was obviously

161   impossible, once 20 sec of recording was completed, the wall with the gap and rear wall

162   were both removed by opening the roof of the flight tunnel. We also observed the flight

163   of the bees when the wall behind the gap was lined with non-textured white paper and

164   placed immediately adjacent to the gap, i.e. similar to the d = 0mm, Fig. 1.

165

166   To ensure we captured the response of naïve bees dealing with a complex environment

167   and negotiating a gap, experiment bouts lasted no longer than 1 hour, and the gap and

168   rear wall were removed after each flight recording to inhibit the bees from becoming

169   familiar with the experiment paradigm. Bees were not individually marked in this study,

170   though this increased the possibility of taking unequal numbers of measurements

171   amongst the different individuals for each condition, the likelihood was greatly reduced

172   since consecutive flights were taken from different bees returning to the hive from the

173   foraging arena. Additionally, due to the large number of foragers and flight trajectories

174   recorded it is likely to be representative of the population. All experiments were

175   completed within five consecutive days.

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Fight Trajectory Analysis and Optic Flow Estimation

An Optronis CR6 high-speed camera was placed 1.7m above the midline of the flight tunnel looking directly downward. The flights of the bees were recorded at 200Hz, and a region covering 950mm leading to the gap was kept in the field of view. During post processing lens distortion was corrected by using standard MATLAB Image Processing Toolbox routines. An object of known dimension was placed within the field of view at mid-height of the tunnel and related to the pixels in the rectified image for 2D spatial calibration. Custom MATLAB code was written to process each frame and fit an ellipse to the body of the bees; subsequently the centroid location, body length and heading were all measured over the entire flight. The bees displayed a wide diversity in flight behaviors. In the flight tunnel flights ranged from appearing to explore the space to making directed flights along the tunnel. Only flights of individuals that appeared to be returning from foraging trips, considered as those bees that made a steady and direct flight towards the gap, were used for analysis. At least one such flight was observed every minute. Among all the flights recorded the body length of the individual bee varied by less than 5% indicative of the nominally constant altitude maintained during the entire flight. In order to attenuate digitizing error the flight trajectories were passed through a 30Hz 2nd order Butterworth filter. Flight speed along the longitudinal and lateral directions was estimated by differentiating the flight trajectory along the respective axis and applying a coordinate transformation matrix to obtain body centered values. Heading orientation was calculated with respect to the flight tunnel using the right-hand-rule. Since the flights were recorded only through a single perspective, pitch and roll could not be measured.

Geometric optic flow measured as the angular displacement of the vector between an arbitrary point in space and the retina due to relative motion, see EQU1 was calculated in MATLAB using the flight trajectory and flight tunnel geometry. Here, for each flight in all conditions the true optic flow of only the wall containing the gap and the rear wall was calculated using the respective flight trajectory, assuming constant head-body alignment, a spherical eye and the retina approximated as a point. A similar approach has been implemented in numerous previous studies (Bertrand et al., 2015; Floreano et al., 2010; Serres and Ruffier, 2017; van Breugel et al., 2014).

A total of 100 flights (20/condition x 5 conditions) were recorded, and statistical significance of the variation in quantities between experiment conditions was tested

215   using a on way ANOVA and a Tukey Post-Hoc test confirmed significant conditions

216   within the group. For comparison of quantities within each experiment condition a

217   paired t-test was used to assess statistical significance. No statistical analysis was

218   conducted for the condition where a glossy white background was placed immediately

219   in the rear of the gap, only five flights was permitted and the analysis was qualitative.

220

221   **Results**

222

223   Upon entering the flight tunnel all bees took off and flew smoothly as they approached

224   the unfamiliar wall blocking their flight path. For all experiment conditions enroute to

225   the gap the flight trajectories of the bees were not straight, but contained some smooth

226   lateral movements, see Fig. 1b-f. The bees performed increased lateral maneuvers closer

227   to the gap as the distance between the gap and rear wall was reduced, see Fig. 1d-f. For

228   conditions when the distance between the gap and rear was <60mm the bees engaged in

229   forward facing crescent-shaped maneuvers close to the gap (<100mm), see Fig. 1e, prior

230   to passing through. When the gap was not present i.e. the rear wall was directly adjacent

231   to the gap, the bees continued to preform crescent flight while facing forwards close to

232   the center of the tunnel with increasing arc size. None of the bees attempted to pass

233   through in this condition, see Fig. 1f. This also included the condition when a non-

234   textured white wall was placed immediately adjacent to the gap, similar to the d = 0mm

235   condition (data not shown). An apparent increase in the sideward component in the

236   flight path is evident with decreasing distance between the gap and rear wall. These

237   crescent shaped flight paths bear nominal similarity to learning flights of bumblebees

238   after they leave their nest hole and are assumed to gather information about its

239   surroundings (e.g. Lobecke et al., 2018; Philippides et al., 2013).

240

241   In order to quantify the flight trajectories, the tunnel was binned into six segments and

242   the longitudinal flight speed of the bees within each bin was calculated, see Fig. 2a.

243   Irrespective of the distance between the gap and rear wall, the flight speed among the

244   different individuals remained statistically similar when they were >375mm to the gap,

245   Fig. 2a ($F_{(4,95)}$ = 0.79, p = 0.55). The flight speed of the bees within this region was

246   nominally similar to those reported by (Baird et al., 2010) where a similar sized tunnel

247   was used. However there exists considerable variation in flight speed (up to 1.5x

248   variation in magnitude) among the different flights across all conditions. At distances

249   <375mm the bees approached the gap while steadily decelerating wherein the rate of

250   deceleration was dependent on the distance between the gap and background, Fig. 2a.

251 The mean longitudinal velocity of the bees was significantly lower when the distance

252 between the gap and rear wall was <150mm (d = 150mm p = 0.043, d = 60mm p = 0.029

253 & d = 0mm p = 0.0068). When d > 150mm the longitudinal velocity was lower but not

254 statistically significant, d = 300mm p =0.068 & d = 550mm p = 0.075. For the d = 550,

255 300 and 150mm the flight speed of the bees was significant reduced when they were

256 <225mm to the gap compared to when they were <375mm (d = 550mm p = 0.022, d =

257 300mm p = 0.046 and d = 150mm p = 0.013), Fig. 2a. When the bees where <150mm to

258 the gap there was a monotonic reduction in their mean speed with decreasing distances

259 between the gap and rear wall (F(4,95) = 3.18, p = 0.02).

260

261 For all experiment conditions, the mean absolute lateral speed of the bees was small but

262 existent at large distances to the gap (>225mm) and monotonically increased as they

263 approached the gap, see Fig. 2b. Unlike the longitudinal speed, the mean absolute lateral

264 flight speed did not become significantly different across the different conditions until

265 the bees were <225mm; in this condition the bees' lateral velocity was maximum when

266 the rear wall was adjacent to the gap (d = 0 p = 0.00935), Fig. 2b. Similar to the forward

267 speed, the rate of increases in the mean lateral speed of the bees was also dependent on

268 the distance between the gap and rear wall. By comparing the ratio of mean lateral

269 speed to the total speed of the bees it is evident that the bees summarily increase their

270 mean lateral movement over longitudinal movement, Fig. 2c. For the non-passable

271 condition where d = 0 over the duration of the recording the bees mostly moved

272 laterally at distances <75mm to the gap (Fig. 2b&c). The lateral distance traveled by the

273 bees within each segment also increased, as they got closer to the gap. This can also be

274 qualitatively observed in the representative flight trajectories, Fig. 1b-f.

275

276 To further understand the mechanics of the lateral movements and the flight maneuvers

277 performed close to the gap for conditions where the distance between gap and rear wall

278 was small, the total acceleration of the bees in the body coordinate system at three

279 different segments along the tunnel was represented as a rose histogram, Fig. 3. The

280 length of each angular column in the rose histogram indicates probability of the total

281 acceleration of the bee to be within the range of the respective bin. This was done for the

282 d = 0mm condition where lateral movements were most significant. The angle between

283 the total acceleration and the long axis of the body was binned into twenty segments of

284 18° width for all recorded flights. When the bees were >375mm from the gap, the total

285 acceleration was oriented laterally with respect to their body and minimally in

286 longitudinal direction. Between 375 – 150mm to the gap the bees began decelerating

287   (Fig. 3b), and this is evident in the acceleration histogram where the total acceleration
288   was distributed mostly laterally with a rearward skew (2nd & 3rd quadrant). In the
289   proximal regions of the gap (<150mm) the total acceleration was predominantly
290   orientated orthogonal to the long body axis, Fig. 3c. The magnitude of acceleration, as
291   indicated by the hue in Fig. 3, was also lowest when the bees were far from the gap. It
292   progressively increased near the gap where the flight was characterized by the largest
293   accelerations oriented nominally orthogonal to the longitudinal axis, Fig. 3a-c.

294

295

296   **Optic Flow Analysis**

297

298   The above results clearly revealed that flight behavior of bumblebees is strongly
299   affected by the distance between the gap and the rear wall. The most likely cue
300   providing information about the spatial layout under the different conditions is the optic
301   flow within the gap and in the adjacent parts of the visual field. Therefore, we
302   determined the optic flow difference between inside and outside the gap. The mean of
303   the absolute difference in total geometric optic flow across the inside and outside edge
304   of the gap (±12 mm along gap edge) is presented Fig. 4a. As expected, the difference in
305   optic flow across the edge of the gap was low when the bees were far from the gap and it
306   progressively increased as the bees neared the gap. Until the bees were <225mm from
307   the gap the difference in mean optic flow across the edge decreased significantly with
308   decreasing distance between the gap and the rear wall. However, in the near vicinity of
309   the gap (<150mm) the mean optic flow difference across the edge of the gap was
310   relatively lower and not statistical significant across the d = 550 – 60mm conditions
311   ($F(4,95) = 0.28$, $p = 0.74$), Fig. 4a. The optic flow difference for the d = 0 is nonzero (Fig.
312   4a) because of the offset in the wall position due to their thickness (1.5mm). The mean
313   optic flow on the wall containing the gap and the rear wall when the bees were <150mm
314   to the gap for all conditions is presented in Fig. 4b-f. A sharp discontinuity in the mean
315   optic flow at the edge of the gap is present when the rear wall is further away from the
316   gap, consequently, the distinctness of the gap clearly decreases with decreasing distance
317   between the gap and the rear wall in the different experiment conditions.

318

319   The difference in optic flow across the edge of the wall was normalized with respect to
320   the optic flow 12 mm outside the gap edge, on the wall containing the gap, to reveal the
321   mean motion contrast for the different conditions, see Fig. 5a. For all flights only the
322   flight trajectories of the bees when they were <75mm to the gap were considered for the

323   contrast estimation. A high motion contrast was present only when the distance

324   between the gap and rear wall was large and it monotonically decreased with

325   decreasing distance. Concomitant with the decreasing motion contrast an opposite trend

326   was noted with the time spent by the bees in the near vicinity of the gap (<75mm)

327   before passage, Fig. 5b. Bees spent a longer time <75mm to the gap as the distance

328   between the between the gap and rear wall decreased from 550 to 0 mm, Fig. 5b. For the

329   extreme condition when gap passage was impossible (d = 0) the time spent was not

330   calculated since the bees continued to traverse laterally and no attempts to pass were

331   made. We can conclude that the bees spend more time exploring the situation close to

332   the gap when the optic flow contrast across the gap and, thus, the distance between the

333   gap and the rear wall gets smaller. At the same time, they increase the lateral velocity as

334   a means to increase velocity contrast.

335

336

337   **Discussion**

338

339   Despite their tiny brains, bumblebees and other eusocial insects display a remarkable

340   capacity for navigation through inherently complex environments. The most elemental

341   aspect for locomotion through a cluttered terrain is the identification of a gap between

342   obstacles and subsequently assessing passability. In our experiments we sought insights

343   into the salient mechanisms utilized by bumblebees to identify a gap when presented

344   with an unexpectedly altered environmental situation relative to the conditions of an

345   unobstructed tunnel the bees were familiar with. The bumblebees could thus not learn

346   the gap properties. By considering only bees that were used to returning to the hive

347   through a familiarized unobstructed flight tunnel we exploited the high motivational

348   state of the organism in identifying a route through the altered environment that

349   required passage through the gap. In an alternative setup when the gap was presented

350   to bees that were en route from the hive to the foraging chamber, the bees were much

351   less amenable to the experimental paradigm and chose to return to the safety of the

352   hive.

353

354   Bees and other insects might also rely on other cues in facilitating gap detection and

355   passage decision making when flying through cluttered environments such as

356   brightness as shown by (Baird and Dacke, 2016). The few conditions in our

357   experimental analysis where a white background was placed immediately rear of the

358   gap created a scenario where high optic flow difference across the gap was present but

359   nearly zero optic flow within the gap. In this condition none of the bees attempted to

360   pass suggesting that apart from the difference in optic flow across the edges of the gap, a

361   non-zero optic flow within the gap maybe one of the conditions necessary for passage,

362   because only with optic flow inside the gap information about the spatial situation

363   behind the gap may be available. Additionally, the homogenous lighting used in our

364   setup might have not created the necessary brightness difference across the edges of the

365   gap to elicit a brightness-based response. Further investigations are necessary to

366   identify the presence of such virtuosic strategies.

367

368   **Approach**

369

370   When the bees were far from the gap their flight trajectory seemed to be driven by the

371   well-established mechanism of equalizing bilateral optic flow. Since the spatial

372   information on the side walls of the tunnel were similar, nominally consisting of

373   amplitudes varying by 1/frequency (Monteagudo et al., 2017) and a nominally

374   homogeneous illumination, the bees flew close to the centerline of the flight tunnel. This

375   is a familiar feature observed in a number of previous studies that have utilized flight

376   tunnels to study insect and bird flight (Bhagavatula et al., 2011; Schiffner et al., 2014;

377   Srinivasan, 2010). Apart from balancing bilateral optic flow, the flight speed has also

378   been shown to be dependent on the overall width of the flight tunnel as well as its

379   texture. Under the conditions of our experiments, the bees flew at around 0.7m/s in the

380   far field of the gap which was similar to those measured by (Baird et al., 2010) where a

381   similar experiment paradigm was used. Smooth sideward motion interlaced the

382   longitudinal velocity in the bees Fig. 2b-f, this lateral "casting" motion is also a common

383   feature noted in previous experiments on bumblebee flight (Chang et al., 2016; Dyhr and

384   Higgins, 2010; Linander et al., 2015; Ravi et al., 2013).

385

386   At around 375mm from the gap, evidence of changes in behavior is first noted as a

387   reduction in flight speed, Fig. 3a. Insects and birds have been shown to respond to

388   unpredictable or unfamiliar situations with reducing speed (Williams and Biewener,

389   2015). In this region of the flight tunnel the angle subtended by the obstructing wall

390   containing the gap and the gap itself is 36° - 42° and 9° - 14° respectively. (Baird et al.,

391   2010) reported that bumblebees modulate their flight speed using the frontal optic flow

392   and showed that bees responded to abrupt changes in flight tunnel width when it

393   subtended between 23° - 30° on the retina, which is consistent with our data. The bees

394   could either be responding to the obstructing wall, the properties of the gap or the

395   combination of the two. In eliciting a change in flight speed of the bees there appears to

396   be a combined influence of the obstructing wall and the distance between the gap and

397   rear wall when the bees were between 375 – 225mm from the gap. In this region the

398   first consistent reduction in flight speed of the bees across all conditions compared to

399   when they were > 375mm was noted however it was statistically significant only when d

400   < 60mm, see Fig. 2a. Within this region, the mean optic flow difference across the edge

401   of the gap was 60 – 120°/sec when d = 550mm, while the optic flow on the wall along

402   the gap edge was only 3 - 12 °/sec for the extreme non-passable condition (d = 0). The

403   deceleration of the bees for the non-passable condition may be considered as that

404   elicited purely by the obstructing wall. This suggests that in our experimental paradigm

405   the prominence of the gap modulated the approach flight speed of the bees.

406   Comparatively, when they were <225mm from the gap further reduction in flight speed

407   appeared to be mainly influenced by the distance between the gap and rear wall (see,

408   Fig. 3a).

409

410

411   **Gap Perception**

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413   For all conditions concomitant with decelerating longitudinal flight speed the bees

414   increased their lateral speed as they neared the gap (Fig. 2). The bees also increased

415   both lateral displacement and speed significantly as the distance between the gap and

416   rear wall was decreased (Figs. 2 & 3). The total accelerations during these lateral

417   maneuvers are higher closer to the gap and mainly oriented normal to the body long

418   axis (Fig. 3). In such cases, the bees are "side slipping" performed by rolling their body to

419   redirect their aerodynamic force vector in the direction of movement, similar to a

420   helicopter (Ravi et al., 2016; Taylor, 2001). Such body roll mediated lateral maneuvers

421   are usually coupled with synchronous counter-rotations of the head to maintain a stable

422   visual field (Boeddeker and Hemmi, 2010; Doussot et al. in prep.). Performing lateral

423   maneuvers where body yaw is limited significantly increases the lateral translational

424   optic flow.

425

426   Flies, wasps and a number of other volant insects actively shape the optic flow on the

427   retina by modulating their head and body trajectory to increase the translatory

428   component while minimizing rotations (Egelhaaf et al., 2014). Optic flow derived from

429   translation contains information on the relative distance between environmental

430   features such as obstacles while optic flow from rotations lacks this vital information

431   wherefore volant insects tend to restrict rotations to rapid saccades (Egelhaaf et al.,
432   2012a). Bumblebees flew in our tunnel with minimal yaw rotations (Fig. 1b-f) thus
433   increasing translational optic flow. Optic flow derived through pure longitudinal motion
434   is not much sensitive to distance differences in the frontal visual field, since the flow
435   vectors are small close to focus of expansion. Increased optic flow sensitivity to distance
436   differences between environmental features in the frontal visual field can be achieved,
437   however, through lateral translation (motion parallax) (Collett, 2002). Even when the
438   bees were seemingly uninfluenced by the obstacles (>375mm, Fig. 2), their flight path
439   consisted of smooth lateral movements – casting. The significance of these voluntary
440   lateral movements performed by the bees (Ravi et al., 2016) are unclear. However, they
441   are likely to be used to increase lateral translational optic flow and, thus, to aid depth
442   perception.
443
444   A consequence of the increased lateral translations performed by the bees in the
445   proximity of the gap is the large difference in optic flow across the edges of the gap,
446   thereby increasing their salience (Fig. 4b-f). An example of active shaping of optic flow
447   through flight maneuverers can be seen by comparing the generated optic flow when
448   the rear wall was 150mm and 60mm, respectively, behind the gap (Fig. 4a). For these
449   two conditions, when the bees were far (>225mm) the difference in optic flow across
450   the gap edge was significantly higher than when the d > 150mm. However, in near field
451   of the gap (<75mm), due to the increased lateral maneuvers of the bees, the optic flow
452   difference across the gap edge was with 200 – 400 °/sec similar to the d = 550mm
453   condition (Fig. 4a). Active maneuvering in order to discern depth and increase salience
454   of the edges appears to be a compensatory strategy of the bees to the changing distance
455   of the rear wall. Wasps, honeybees and other insects have been observed to perform
456   nominally similar flight maneuvers, which consist of large lateral components, for
457   instance, during their learning flights after leaving an attractive goal location, such as a
458   food source or a nest hole (Zeil, 1996; Dittmar et al. 2010; Lobecke et al. 2018). Here we
459   show that bees actively modulate such behavior in a gap perception context and it
460   appears to depend on the salience of the gap.
461
462   In this case bees are likely utilizing a combination of information about the velocity of
463   self-motion, which is related to the input motor signals, and the relative optic flow in
464   discerning the gap salience. The monotonic increase in lateral velocity with decreasing
465   distance between the gap and rear wall does not increase at the same rate until the
466   extreme condition when the gap and rear wall are adjacent (Fig. 2c). Our results suggest

467   that it is likely that there exists a threshold dependent on salience of the gap. We believe

468   this threshold might reflect "passability" based upon identifying gap properties

469   including depth through lateral maneuvering. If the bees cannot assess safe passage,

470   they might resort to searching for alternative gaps in the environment or may fly back.

471   The nominally crescent-shaped flight pattern of the bees close to the gap for the cases

472   where the rear wall was <60mm bears similarity to searching flights and orientation or

473   learning flights performed by bumblebees upon their first departure from their nest

474   hole where they are assumed to probe the layout of the behaviorally relevant nest hole

475   environment (Lobecke et al., 2018; Philippides et al., 2013; Riabinina et al., 2014).

476

477   When confronted with a wall unexpectedly blocking their flight path, the bees search for

478   a gap and, therefore, need to probe the spatial layout of the environment. In such

479   conditions bees might utilize a number of cues, including brightness differences, to

480   ascertain the presence of gaps (Baird and Dacke, 2016), but, in particular as shown in

481   the present study, optic flow information. A number of factors are also likely to

482   influence the flight pattern of the bees in this condition including the geometry of the

483   flight tunnel and the obstacles. However, the similarity between the flights when

484   negotiating the gap in our flight tunnel to learning and searching flights of bees observed

485   in the context of local homing behavior merits further investigation. We suggest that in

486   both situation these characteristic meandering lateral flight manoeuvres serve the same

487   basic purpose, i.e. probing the spatial layout of the environment.

488

489

490   **Time to Decision**

491

492   When flying within a complex cluttered environment an animal constantly needs to

493   evaluate the environmental features confronting it and to make decisions that influence

494   the flight course. Bees spend significant time in the near vicinity of the gap while

495   performing the rapid lateral maneuvers (Fig. 5b). The consistent repeated flights of the

496   bees, especially when the rear wall was <60mm to the gap, suggests that through these

497   flights the bees not only discern the gap geometry but also evaluate passability. Once the

498   potential for safe passage is established traversal through the gap occurs. Measuring the

499   time spent by the bees within the region where most of the lateral maneuvers occur

500   might provide an indication of the time taken by the bees in arriving at a decision.

501   Among all flights recorded none of the bees performed abrupt corrective maneuvers

502 once gap traversal had commenced indicating that decision-making occurs ahead of the

503 gap.

504

505 The optic flow contrast appears to be a critical parameter due to a strong and direct

506 inverse relationship with respect to the time spent by the bees evaluating the gap (Fig.

507 5). Through the repeated lateral movements, the bees appear to establish saliency of and

508 confidence about the geometry by actively generating visual information about

509 passability. The smaller the salience of the gap, the larger are the sideways velocities in

510 order to increase optic flow contrast and the longer do the bees probe the environment

511 to increase their confidence about the situation. As a consequence, decision-making is

512 delayed. Other factors such as familiarity and experience, though unlikely to play a

513 significant role in these experiments, are also likely to influence the bees' decision time

514 in assessing gap properties and passability in their natural environment, and further

515 experiments are necessary to quantify the influence of these factors on the neural and

516 biophysical mechanics of locomotion through spatially complex environments.

517

518 **Acknowledgements**

523

524 **References**

525

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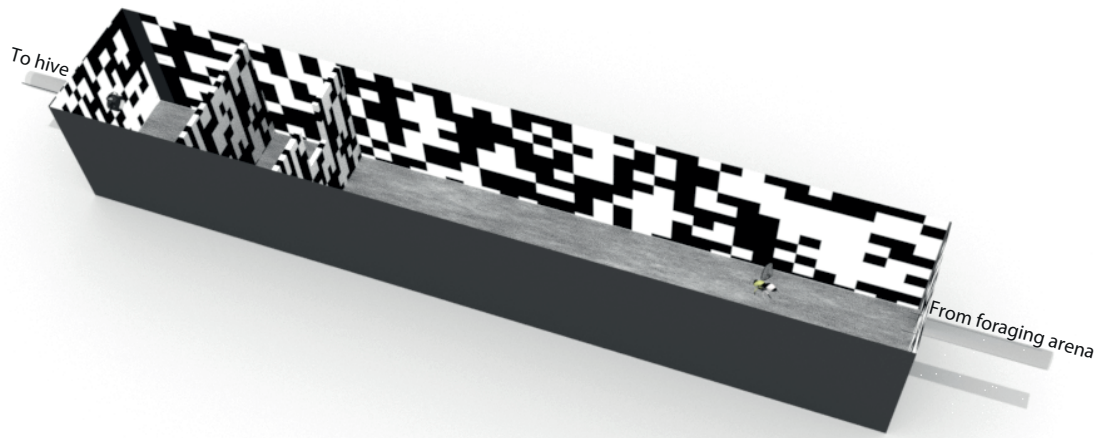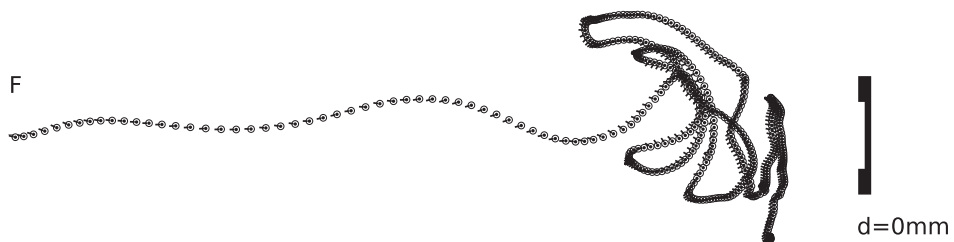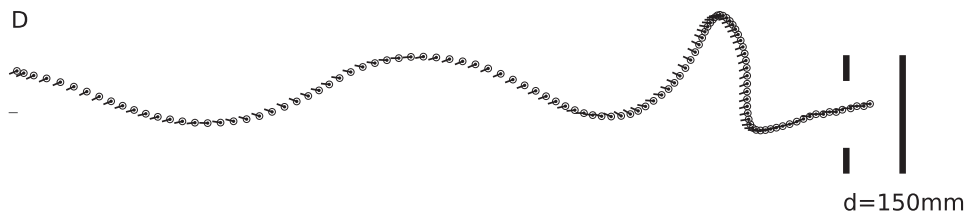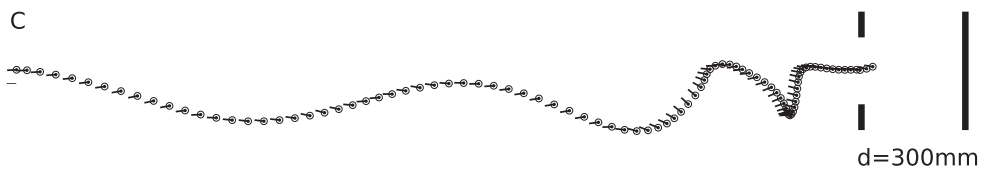
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B

d=550mm

C

d=300mm

D

d=150mm

E

d=60mm

F

d=0mm

683

-400   -300   -200   -100

684   Fig.1 a) Schematic of the experiment setup, d represents the distance between the wall

685   containing the gap to the rear wall. Only the flight of bees returning to the hive from the

686   foraging arena was considered for analysis. Sample flight trajectory of a bee when the

687   distance between the gap and rear wall was 550mm (b), 300mm (c), 150mm (d), 60mm

688   (e) and 0mm (f). The gap and rear wall on the right are for illustrative purposes only

689   and not to scale.

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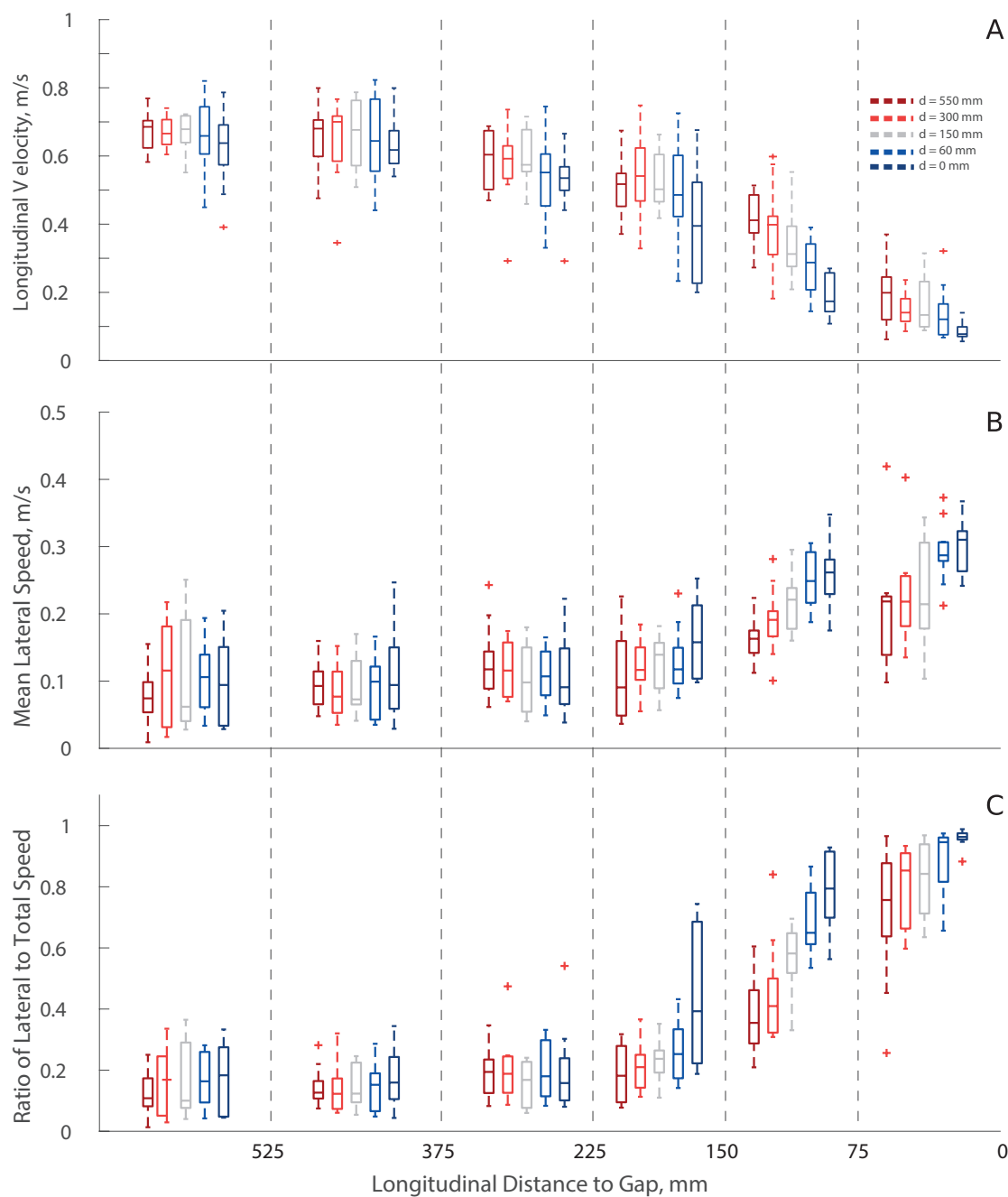
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693   Figure 2. The flight tunnel was binned into six sections leading to the gap. a) The

694   absolute mean longitudinal velocity of the bees at different longitudinal distances from

695 the gap. b) The absolute mean lateral velocity of the bees at different sections of the

696 flight tunnel. c) Ratio of the mean absolute lateral velocity and the total velocity.

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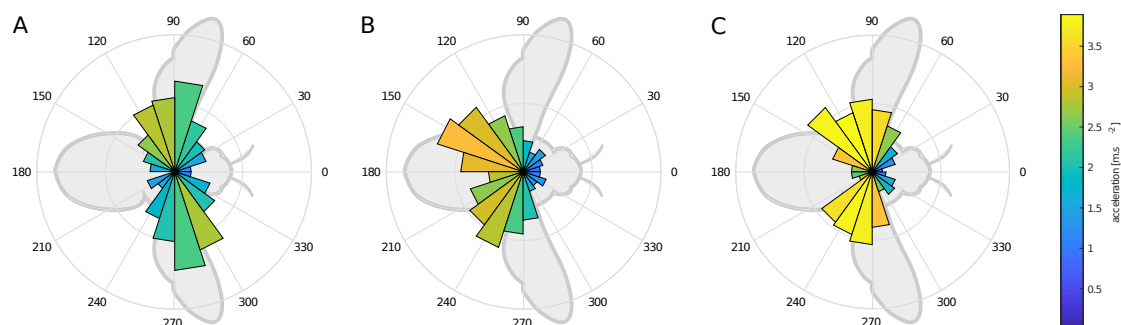
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700 Figure 3. Rose histogram of the total acceleration with respect to long body axis among

701 all flights at different section of the flight tunnel a) 300mm - 200mm, b) 200mm –

702 100mm & c) 100mm – 0mm. The length of each angular column in the rose histogram

703 indicates the probability of the total acceleration of the bee to be within the range of the

704 respective bin. The hue represents the magnitude of mean acceleration within the

705 respective angular bins.

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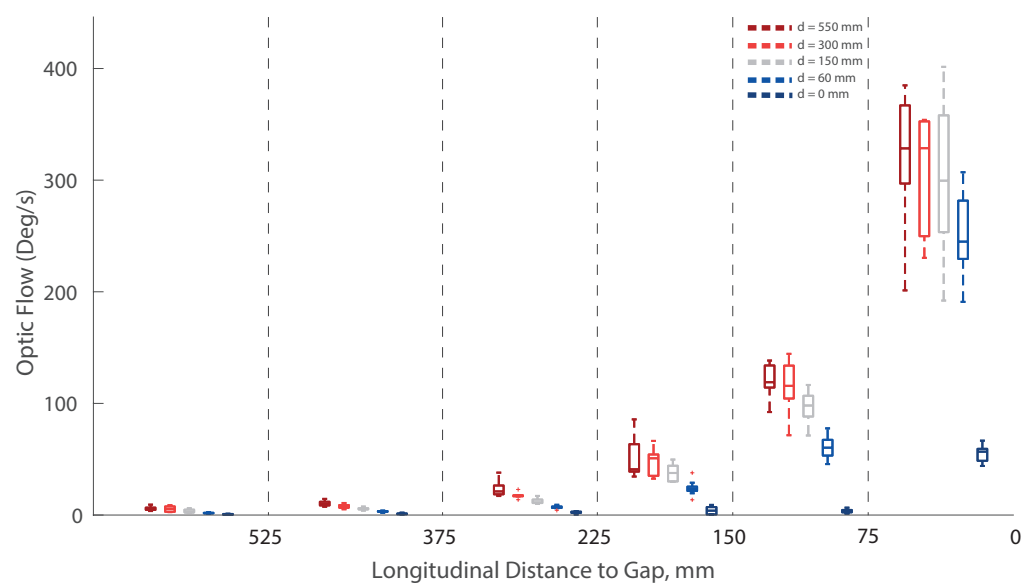
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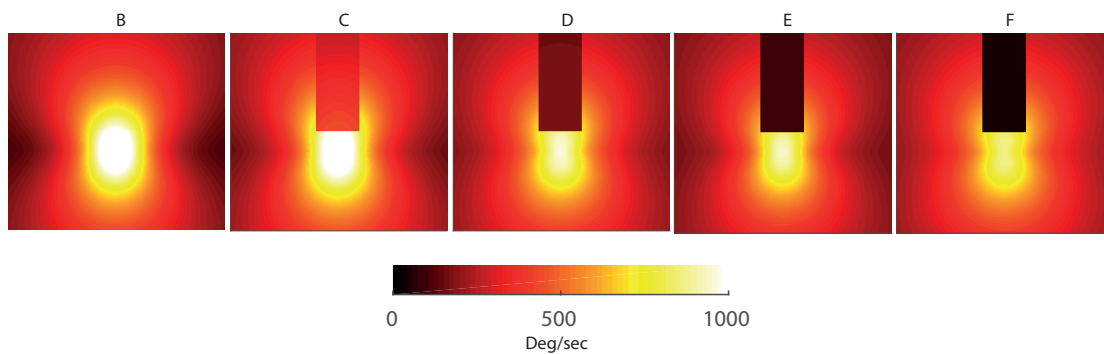
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710 Figure 4. a) The mean of the absolute difference in total optic flow across the inside and

711 outside edge of the gap (±12 mm along gap edge) at different sections of the flight

712 tunnel. b-f) Heat map showing the mean geometric optic flow over the wall containing

713 the gap across all flight trajectories when the bees were <75mm to the gap. The

714 geometric optic flow was calculated taking into account both the longitudinal and lateral

715 translation as well as yaw rotations of the bees as they approached the gap.

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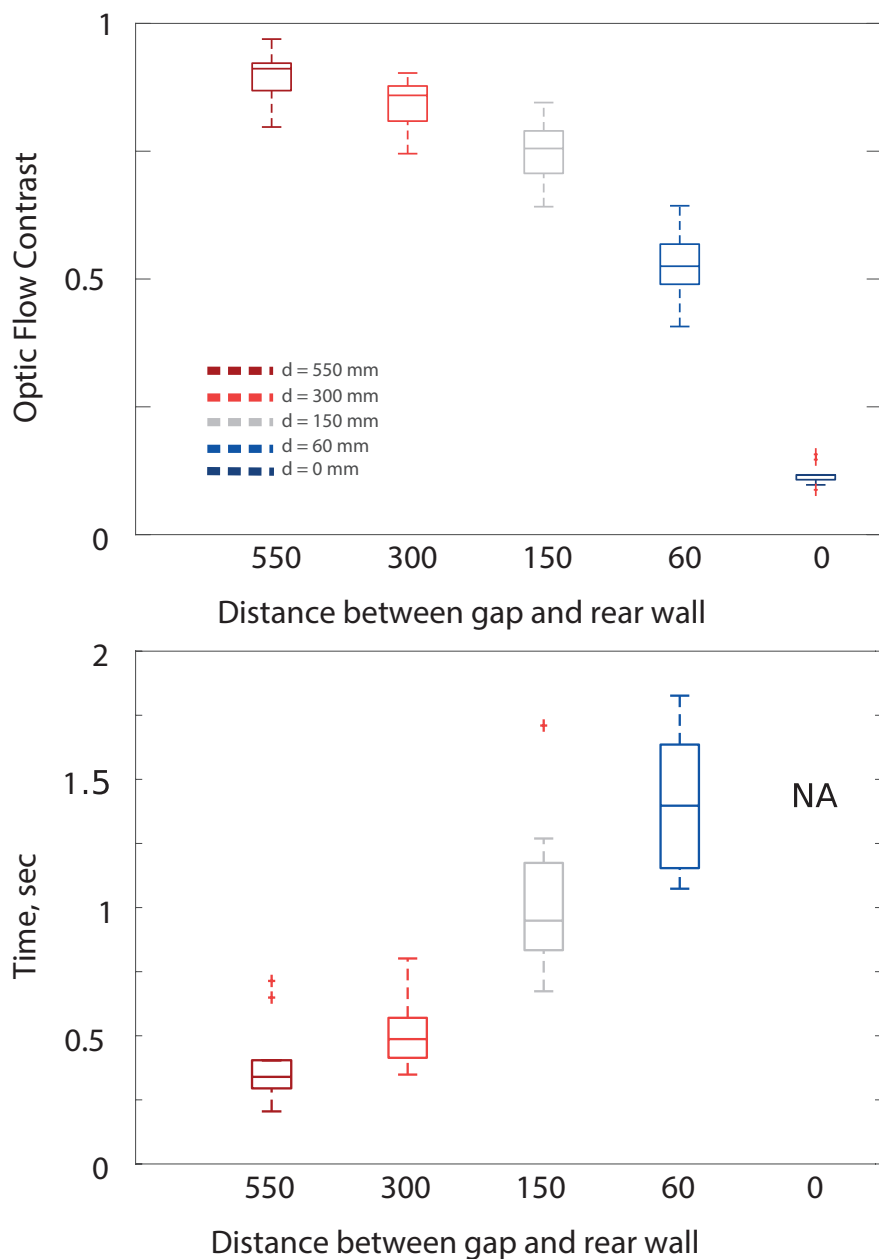
Figure 5. Optic flow contrast measured as the ratio between mean difference in optic flow across the edge of the gap and the optic flow along the outer edge of the gap. (b) Time spent by the bees in the vicinity of the gap (< 100mm) for the different experiment conditions.