The effect of changing topography on the coordinated marching of locust nymphs

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Collective motion has traditionally been studied in the lab in homogeneous, obstacle-free environments, with little work having been conducted with changing landscapes or topography. Here, the impact of spatial heterogeneity on the collective motion exhibited by marching desert locust nymphs was studied under controlled lab conditions. Our experimental circular arenas, incorporating a funnel-like narrowing followed by re-widening, did not constitute a major barrier to the locusts; but, rather, mimicked a changing topography in the natural environment. We examined its effects on macroscopic features of the locust collective behavior, as well as the any changes in their marching kinematics. A major finding was that of the limited extent to which the changing topography affected system-level features of the marching locust group, such as the order parameter and the fraction of walking individuals, despite increased crowding at the funnel. Overall, marching kinematics was also very little affected, suggesting that locust marching bands adjust to the environment, with little effect on the overall dynamics of the group. These findings are in contrast to recent theoretical results predicting that environmental heterogeneities qualitatively alter the dynamics of collectively moving particles; and highlight the crucial role of rapid individual plasticity and adaptability in the dynamics of flocks and swarms. Our study has revealed other important features of the marching behavior of the desert locust in addition to its robustness: the locusts demonstrated both, clear thigmotaxis and a tendency to spread-out and fill the available space.

1   The effect of changing topography on the coordinated marching of locust nymphs

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21 **Abstract**

22 Collective motion has traditionally been studied in the lab in homogeneous, obstacle-free

23 environments, with little work having been conducted with changing landscapes or topography.

24 Here, the impact of spatial heterogeneity on the collective motion exhibited by marching desert

25 locust nymphs was studied under controlled lab conditions. Our experimental circular arenas,

26 incorporating a funnel-like narrowing followed by re-widening, did not constitute a major barrier

27 to the locusts; but, rather, mimicked a changing topography in the natural environment. We

28 examined its effects on macroscopic features of the locust collective behavior, as well as the any

29 changes in their marching kinematics. A major finding was that of the limited extent to which the

30 changing topography affected system-level features of the marching locust group, such as the

31 order parameter and the fraction of walking individuals, despite increased crowding at the

32 funnel. Overall, marching kinematics was also very little affected, suggesting that locust

33 marching bands adjust to the environment, with little effect on the overall dynamics of the group.

34 These findings are in contrast to recent theoretical results predicting that environmental

35 heterogeneities qualitatively alter the dynamics of collectively moving particles; and highlight

36 the crucial role of rapid individual plasticity and adaptability in the dynamics of flocks and

37 swarms. Our study has revealed other important features of the marching behavior of the desert

38 locust in addition to its robustness: the locusts demonstrated both, clear thigmotaxis and a

39 tendency to spread-out and fill the available space.

40

41 **Keywords**

42 Collective motion, Swarming, Environmental effects, Topological changes, Spatial

43 heterogeneity, Locust marching bands, *Schistocerca gregaria*.

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47 **Introduction**

48 Locust swarming constitutes a unique model of animal collective motion (recent review in Ariel

49 and Ayali 2015). Collective motion, being a dominant feature of the behavior of these insects, is

50 also responsible for their notorious reputation as a major pest. Of particular importance is the

51 behavior of the swarms of locust nymphs, comprising millions of insects forming marching

52 bands that may cover vast areas of land, stretching across hills and valleys as far as the eye can

53 see (e.g. Ellis and Ashal 1957; Uvarov 1977; Hunter et al., 2008; our own personal observations

54 of the desert locust in Israel's Negev desert, spring 2013).

55 Different aspects of locust motion, the interactions between conspecifics and their impact on the

56 build-up and maintenance of coordinated movement, have been studied using controlled

57 laboratory experiments (e.g. Ellis 1951; Buhl et al. 2006; Bazazi et al. 2012; Ariel and Ayali

58 2015, and references therein). In recent years, advanced tracking algorithms have been utilized to

59 monitor up to several dozen animals at a time at high spatio-temporal resolution for later off-line

60 analysis (e.g, Buhl et al. 2006; Ariel et al. 2014). However, those studies were limited to

61 homogeneous, obstacle-free environments, in order to facilitate emergence of the locust

62 collective motion. Such an environment clearly differs from that encountered by the marching

63 locust swarm (or by any other animals demonstrating mass terrestrial movement) in natural

64 conditions, which may feature a complex terrain, vegetation etc., obscuring and obstructing the

65 path of the locusts.

66 The effects of an heterogeneous environment on the ability of large systems of moving animals

67 (or particles) to form collective dynamic patterns have been mostly studied in simulations.

68 Theoretical work, using simplified models of collective motion, has predicted that the effect of

69 spatial heterogeneities on the ability of swarms to organize and form synchronized motion is

70 highly non-trivial and to some extent non-intuitive. For example, obstacles may significantly

71 change the phase diagram of the system, either disrupting or promoting coherent motion,

72 depending on obstacle density, noise intensity, and other model parameters (Hatzikirou and

73 Deutsch 2008; Chepizhko et al. 2013; Chepizhko and Peruani 2015; Quint and Gopinathan

74 2015). Boundaries can promote the formation of vortices (Duparcmeur et al. 1995; Czirok et al.

75 1996; Szabo et al. 2006; Barbaro et al. 2009; Potiguar et al 2014), induce traffic-lane patterns

76 (Hernandez-Ortiz 2009; Ariel et al. 2013) and introduce heterogeneity in densities (Drocco et al.

77 2012; Hernandez-Ortiz 2005). Several theoretical studies have considered the effect of

78 heterogeneous environments on specific animal systems, such as birds (analyzing risks of

79 collision with wind turbines; Croft et al. 2015), fish (predicting the location of Capelin off the

80 Icelandic shores; Barbaro et al. 2009), and living cells (studying the collective cell dynamics of

81 tissue cells in micro-fabricated arenas; Szabo et al. 2006). The study of pedestrian flow through

82 bottlenecks has a rich history of over 100 years (e.g. Helbing 2001; Appert-Rolland et al. 2009).

83 Some of the basic phenomena reported to be associated with a locally reduced mobility or

84 increased density include a drop in flow capacity (depending on bottleneck width), division into

85 free-flowing and congested areas, appearance of shock-like waves, and more. Ample research

86 has also been conducted on the interactions of swarms of autonomous agents (robots) with

87 obstacles (e.g. Trianni et al. 2006) and of virtual particles, within the scope of swarm

88 optimization methods (e.g. Shklarsh et al. 2011).

89 In contrast to the theoretical studies discussed above, relatively few experimental reports are

90 available on the macroscopic dynamics of collectively moving organisms within an

91 heterogeneous environment. These include microbial swarms interacting within complex

92 substrates (Tuson and Weibel 2013), tissue cells in micro-fabricated arenas (motivated by the

93   highly heterogeneous media that form the extracellular matrix; e.g. Friedl and Broecker 2004;

94   Szabo et al 2006), and pedestrians at bottlenecks, demonstrating a continuous reduction in flow

95   capacity following a reduction in bottleneck width (Hoogendoorn and Daamen 2005; Appert-

96   Rolland et al. 2009). Experiments using different species of ants have shown that topology can

97   have varying effects on the collective movement of the different species. For example, it has

98   been shown that in *Atta cephalotes* (Burd 2002), increased density due to a reduction in trail

99   width reduces the mean traveling speed and the flux of ants across a barrier. In contrast, the flow

100   of black garden ants (*Lasius niger*) does not seem to depend on trail width (Dussutour 2004). To

101   the best of our knowledge, locusts, as well as other animal models of collective motion, have

102   been little studied in this respect. The movement of ants along trails fundamentally differs from

103   that of locusts, as ants seldom turn while walking, being typically either non laden when exiting

104   the nest, or laden when returning to it (Burd 2002, Dussutour 2004). In contrast, the frequency of

105   turning (when changing from a standing to a walking state) has been found to be central in the

106   ability of locusts to form and maintain collective movement (Ariel et al., 2014).

107   This current study sought to investigate locust marching behavior in a changing topography: in

108   our case, a circular arena incorporating a funnel-like narrowing followed by a re-widening. This

109   spatial heterogeneity did not constitute a major barrier to the locusts but, rather, introduced

110   certain simple features that are also found in natural environments, such as a path among large

111   rocks or simply a narrowing gorge. We were interested in examining the effects of such

112   topographical changes on macroscopic features of the locust collective behavior, such as the

113   order parameter, as well as any resultant changes in statistics of the marching behavior of

114   individuals (e.g. speed, walking-bout duration etc.), and in the dynamics of local interactions

115   between the insects, such as distance between neighboring marching locusts, and how these, in

116   turn, translate to swarm dynamics.

117   One of the key questions regarding the response of the individual to a changing environment is

118   that of the effect of topography on the coordinated movement of the crowd. Specifically, it is not

119   clear whether such a response is universal, i.e., common to all swarms, from single cells to

120   locusts and humans; or, alternatively, it significantly differs across species. The main goal of the

121   current study was to revisit previous experimental and theoretical work and to provide novel

122   insights into the effect of a specific type of heterogeneous environment on the collective

123   dynamics of marching locusts. In particular, we sought to unravel the mechanisms by which

124   individual locusts alter their kinematic parameters in order to adjust to the changing environment

125   and diminish its effect on the swarm.

126   **Materials and Methods**

127   ***Animals***

128   Desert locusts, *Schistocerca gregaria* (Forskål), were obtained from our colony at the

129   Department of Zoology, Tel Aviv University, Israel. The locusts, approaching the gregarious

130   phase, were reared over many generations in 60-liter metal cages at a density of 100-160 animals

131   per cage, under a controlled temperature of $30^{\circ}C$ and 35-60% humidity, and a 12D:12L cycle.

132   Additional radiant heat was provided by 25W incandescent electric bulbs during daytime to

133   reach a final day temperature of $35\text{-}37^{\circ}C$. The locusts were fed daily with wheat seedlings and

134   dry oats. All experiments were performed on nymphs of the final (Vth) nymphal-instar (3-4 cm

135   in length and ~0.5 cm in width).

136   ***Behavioral setup***

137   We conducted a series of experiments in each of which a group of nymphs was allowed to move

138   freely in a circular arena. The basic experimental arena was composed of a flat blue Perspex

139   sheet circumscribed by an outer flexible blue plastic wall (60 cm diameter × 55 cm high). An

140   inner circular wall made of similar plastic (diameter 30 cm) was inserted to create a ring shaped

141   sphere (Fig. 1A). The different experimental conditions were achieved by either leaving the inner

142   circle in the middle (no displacement), or moving it by 5 or 10 cm sideways towards the outer

143   wall (creating a funnel 10 or 5 cm wide, respectively; see Fig. 1B). The lower 10 cm of the

144   arena walls were thinly coated with Fluon (Whitford Plastics Ltd, Runcorn, UK) to prevent the

145   nymphs from climbing. The arena was placed in our temperature-controlled room (30ºC) and lit

146   from above by a 100W ring bulb. The propensity of locusts to swarm in an experimental arena is

147   highly sensitive to the number of animals introduced into it (Buhl et al. 2006). Hence, fifty

148   nymphs were introduced into the arena in each experiment, which is a sufficiently high density to

149   facilitate the formation of synchronized movement (Ellis 1951; Buhl et al. 2006; 2011; Ariel et

150   al. 2014), and also approximates the range of densities observed in the field (Ayali et al.

151   unpublished). The locusts were continuously monitored and their movement recorded, using a

152   Sony HDR-XR550E digital camera with a 30 fps rate, for later off-line analysis. Using a custom-

153   designed continuous multiple-target tracking method (Ariel et al. 2014, Fig. 1C), we

154   simultaneously tracked the movement of all individuals at high spatio-temporal resolution (full

155   HD allowed a detailed analysis of the behavior of each individual). We conducted overall 15

156   experiments, 5 under each experimental condition (inner circle displacement of 0, 5, or 10 cm).

157   Each experiment lasted approximately 4 hr, from which the last 200,000 frames were selected

158   (ca. 2 hr), for consistency between experiments and to ensure that we had captured robust locust

159   marching. These were then divided into one hour blocks, providing ample data for statistics. A

160   10 minute period (which is several times longer than the typical resting or walking duration) at

161   the end of each block was discarded to ensure that the blocks were independent of one another.

162   Division into a smaller number of blocks did not qualitatively change the results. Hence, we

163   were left with two sections from each of the five experiments, under each of three experimental

164   condition, totaling 30 experimental sections for further comparative analysis (n=10 for each

165   experimental condition).

166

167   *Analysis of behavior*

168   All data analysis was performed in the MATLAB environment (MathWorks, Natick,

169   Massachusetts, USA). To minimize bias wherever possible, blinded methods were used to

170   analyze data. Following smoothing of trajectories as detailed in Ariel et al. (2014), specific

171   attributes of the system and the individual locusts were defined and analyzed as follows.

172   **Identification of walking bouts:** An animal was classified as **walking** if it was moving at a

173   speed greater than 2 mm/sec for at least 11 frames. We denote by $w_k(t) = 0$, 1 or -1 if at time t

174   animal k is standing, walking in the counter clockwise (CCW) direction, or walking in the

175   clockwise (CW) direction, respectively. We denote by $f(t)$ the **fraction of moving animals** at

176   time t,

$$f(t) = \frac{1}{N} \sum_k |w_k(t)|,$$

178   where N is the number of animals in the arena. Thus, $0 \le f(t) \le 1$, where $f(t) = 0$ implies that

179   all animals are standing, while $f(t) = 1$ implies that they are all walking.

180   For a given animal, the time series $w_k(t)$ can be divided into periods of walking and resting, i.e.

181   continuous segments in which either $w_k(t) = 1$ or -1. Accordingly, we consider the distribution

182   of **walking and resting durations**, denoted t_{walk} and t_{rest}, respectively.

183   **Walking speed:** The speed of animal k at time t is denoted $v_k(t)$.

184   **The order parameter:** To quantify order and synchronization in the system, we defined the

185   instantaneous order parameter as the average direction (CW or CCW) of walking animals at time

186   t. More precisely,

187
$$\phi(t) = \frac{1}{Nf(t)} \sum_k w_k(t).$$
(1)

188   When no animals are moving, the system does not have a preferred direction and $\phi(t) = 0$. Thus,

189    $|\phi|$ is a measure of the level of coordination within the swarm; a value of $|\phi|$ close to zero

190   indicates that the swarm is disorganized, with animals moving in random directions; while a

191   value close to one indicates a highly synchronized state with all directions aligned. The sign of

192   the order parameter indicates the direction of the swarm: positive ϕ refers to CCW motion,

193   while negative ϕ indicates CW motion. Note that ϕ here differs from the order parameter used

194   by many authors, since it depends only on walking animals.

195   **Number of neighbors:** For each frame, we collected all the locations of all locusts and

196   calculated the number of conspecifics up to a distance of 6 cm from each focal animal

197   (corresponding to circa two locust-body-lengths). The number of neighbors of animal k at time

198   t is denoted $n_k(t)$.

199 **Number of close moving neighbors:** Similar to the number of neighbors, ignoring standing

200 animals. In other words, the number of moving neighbors, $n_{\text{move},k}(t)$, defined only if animal k is

201 moving at time t, is the number of conspecifics walking within a distance of 6 cm from animal

202 k. Both the number of neighbors and the number of moving neighbors describe the visual

203 stimulus of an animal and have been previously shown to affect the propensity of animals to start

204 moving (Ariel et al. 2014).

205 **Significance tests:** In the comparison of the different arena types the p-Values (in parenthesis)

206 report the probability that the means of all three arenas are the same (an ANOVA analysis

207 calculated using Matlab's One-way analysis of variance function). In the comparison of the arena

208 halves the p-Values (in parenthesis) report the probability that the means obtained from the two

209 halves are the same.

210 **Correlation coefficients:** The correlation coefficient, ρ, where noted (between any pair of the

211 measurements described above), is the Pearson coefficient using all data points. Correlations

212 were considered as significant for $|\rho| > 0.3$, which, for $n = 30$ corresponds to a (one-sided) P-

213 value of 0.05 or lower.

214 **Heat map representations**: An image of the arena was divided into 248*248 pixels. For each

215 pixel, we summed all the times that the center of a locust appeared in it (within one experiment).

216 In order to account for differences between the experiments in terms of overall density, we

217 summed the values from all the pixels together and divided the value of each pixel by that sum.

218 In other words, each pixel now had a value representing the fraction of the animals in that

219 experiment. We visualized this by representing each pixel, according to its value, with a specific

220 color.

221   Because trajectories are smoothed, they are not as accurate as the raw resolution allows (the error

222   is 3-5 pixels, corresponding to about 1mm). Hence, the reduced resolution used for heat-maps

223   (and only for heat maps) allows convenient representation without any significant loss of

224   accuracy.

225   **Heat map of movement:** Similar to the heat map, with only moving animals taken into account.

226

227

228   **Results**

229   ***Changing topography does not affect the global parameters of the locust collective motion***

230   The order parameter, $\phi(t)$, is an accepted measure of synchronization in a system (Buhl 2006;

231   Ariel and Ayali 2015). Figure 2A presents two examples of the evolution of the order parameter

232   and the overall fraction of walking locusts, $f(t)$, during a 50 min time section in our

233   experiments. In accordance with these examples, when plotting the average of $|\phi|$ against f in all

234   experiments, they were consistently found to be highly correlated, confirming previous findings

235   regarding the increased tendency of animals to join their conspecifics as the number of walkers

236   increases (Ariel et al. 2014). Neither this correlation nor the actual magnitude of ϕ and f were

237   affected by the topography of the arena, i.e. they were independent of the displacement of the

238   inner circle, d (Figs. 2C1 and 2C2, p-Values 0.57 and 0.53, respectively).

239   Other attributes of the overall kinematics of the marching locusts were also not affected by the

240   arena topography (Fig. 3). These include the average speed of all locusts in the arena (Fig. 3A1,

241   p-Value 0.99), and the duration of a locust's walking or pausing bout (Figs. 3B1 and 2B2, p-

242   Values 0.4 and 0.41). This is not surprising, as many of the marching kinematics showed a

243   significant correlation with ϕ and with f, again irrespective of the arena topography (see for

244   example a plot of speed vs. f, Fig. 3A2). No differences in density-related parameters, such as the

245   number of locusts or of marching locusts only, within a short range from a focal locust were

246   found (Figs. 3C1 and 3C2, p-Values 0.55 and 0.19).

247   ***Effect of changes in topography as reflected by comparing different parts of the arenas***

248   In contrast to the above findings, a comparative investigation of the local environments within

249   the different experimental arenas (the wide vs. narrow half or, alternatively, the narrowing vs. re-

250   widening section; Fig. 1B) revealed clear effects of the changing topography. Each arena was

251   divided into two equal-area halves. In the case of the symmetrical condition this resulted in two

252   similar-interchangeable halves. In the asymmetrical-heterogeneous conditions, one section

253   contained the funnel and the other section constituted the wider area (Fig. 1B; left and right

254   halves respectively). The duration of a pausing bout showed a clear dependency on the type of

255   experimental arena when comparing the arena sections containing the funnel, i.e. the pause

256   duration was shorter as the funnel became narrower (Fig. 4A, p-Value 0.02). However, although

257   less pronounced, the correlation was opposite in direction when comparing the opposite halves

258   among the different arenas (i.e. longer pause durations in the wider parts of the asymmetric

259   arenas; Fig 4B). In contrast to the clear dependence of rest durations on the arena topography,

260   analysis of the effect on walking durations gave inconclusive results (p-Values 0.18 and 0.21 for

261   the left and right halves). This is in accordance with our previous finding that locusts modulate

262   their rest durations rather than their walking durations (reported previously for a homogeneous

263   environment; Ariel et al. 2014).

264   Focusing on the heterogeneous-asymmetric arenas only, we further compared the kinematics of

265   the locust marching, measured in the arena-half containing the funnel, to those in the arena-half

266   characterized by the wider path (see Fig 5A1). The Most pronounced differences were those

267   found in the arena resulting from the largest displacement (narrowest funnel; the right-hand

268   topography illustrated in Fig. 1B) in respect to the locusts' average walking speed (Fig. 5A2, p-

269   Value$<10^{-8}$), and the distribution of the durations of the walking and pausing bouts (Figs. 5A3,

270   5A4; p-Values$<10^{-7}$). As can be seen, around the funnel the locusts' speed tended to be lower,

271   with rest or stop durations shorter, but walking durations longer. Interestingly, only a few

272   differences in kinematic parameters were found when comparing the section of the arena

273   containing the narrowing part of the funnel with that containing the widening section (Fig. 5B1).

274   Only the mean speed of the locusts was found to differ (i.e. somewhat increased speed when

275   emerging from the funnel, Fig. 5B2), while the durations of a walking or pausing bout tended to

276   be more similar (Figs. 5B3 and 5B4; p-Values>0.05).

277   The parameter most affected by the arena topography was found to be the local density of the

278   locusts, as reflected in the number of locusts within a short range from a focal locust. For

279   example, the distribution of close-neighbors count or that of close-moving-neighbors count

280   (comprising only walking insects) was very different in the two halves of the arena formed by a

281   10 cm displacement (Fig. 6A, p-Value$<10^{-8}$). This suggests that the marching locusts do not

282   maintain constant distances from one another, but, rather, tend to temporarily crowd together in

283   response to a narrowing environment. Furthermore, the increase in neighbors-count was found to

284   be positively correlated with the displacement in the arena half containing the funnel, i.e.,

285   negatively with the width of the funnel (Figs. 6B1 and 6B2, p-Values$<10^{-4}$). In contrast, in the

286   opposite, wide half of the arena, the neighbors-count decreased with the displacement (Figs. 6C1

287   and 6C2, p-Value$<10^{-4}$), suggesting a tendency of the locusts to spread out and fill the available

288   space (see also Fig. 7, showing an example of locust trajectories in the re-widening section of the

289   arena).

290   ***Effect of changes in the topography as reflected in density heat-maps***

291   Figure 8A shows three examples (one for each of the three experimental conditions) of a heat

292   map generated by attributing to each pixel in the arena a color related to the cumulative number

293   of times it was occupied by a locust during the experiment - from black (unoccupied) to white

294   (most frequently visited). Next, we converted the color code to a value between 0 (unoccupied)

295   to 1 (most frequently visited), and generated a plot of a slice of the mid-wide half of the arena

296   (Fig. 8B). The resultant mean plots from the different experimental conditions were then overlaid

297   to reveal similarities and topography-dependent differences (Fig. 8C). Three clear features of the

298   locust motion in the different topographies could be observed:

299   1. Under all the experimental conditions most of the marching took place close to the

300   perimeter of the arena (shaded dark in Fig. 8C). This is probably due to a combination of

301   its circular nature and the reported tendency of locusts to minimize changes in their

302   trajectory while actively marching (Ariel et al. 2014). The three plots (different

303   experimental condition) are very similar in this respect.

304   2. Nonetheless, it is also clear that the locusts were using the entire space available to them

305   (compare plots in the light shaded areas in Fig. 8C, and see also Fig. 7). This is mostly

306   seen in the plot of the moving locusts (Fig. 8C2).

307   3. Irrespective of the arena topography, or of the space available to the locusts, the level of

308   marching near the inner wall of the arena was the same (compare the peaks within the

309   light shaded areas in Fig. 8C).

310

Discussion

312   The principal findings of the current study were somewhat unexpected and even surprising. We

313   refer to the limited extent to which the changing topography affected both, the macroscopic or

314   system-level features of the marching locust group (order parameter and fraction of walking

315   individuals), and the marching kinematics (average speed, duration of walking or standing bouts)

316   and more (Figs. 2 and 3). Our experimental manipulation involved narrowing the path available

317   to the locusts by a factor of 3 (from 15 cm in the symmetrical arena to only 5 cm in the case of

318   the 10 cm displacement). However, despite a clear increase in local densities, this funnel-like

319   obstacle was insufficient to disrupt the order and collective movement, at least within the tested

320   experimental parameters. These findings serve as a strong indication of the stability and

321   robustness of locust collective behavior and its tendency to adapt in order to maintain the

322   marching activity.

323   It was only when comparing between local sub-environments (the two halves of the experimental

324   arena) that the effects of the funnel-like topography, or the opposite wider space, became evident

325   (Figs. 4-6). A swarm of marching locusts encountering a funnel like structure in their

326   environment could respond in several possible manners. These include changes in the behavior

327   of the individual locusts as well as in the swarm dynamics. The individual locust may slow down

328   or, alternatively, speed up when encountering an obstacle (a wall or a standing conspecific in our

329   case) in order to bypass it. The locusts may increase their density, i.e. reduce the average

330   distance between conspecifics (Fig. 9A), or change the relative position towards one another

331   (aligning or forming queues), and more. Similarly, at the level of the swarm, various responses

332   could be envisioned for a marching swarm exiting a funnel or experiencing a widening of its

333   path. In this case the two major alternative behaviors would be to spread out and fill the available

334   space (Fig. 9B), or to show a kind of memory of their path history as reflected in the shape of the

335   swarm, i.e. to refrain from spreading out when exiting the funnel (Fig. 9C).

336   Our study provided two important insights. The first: that the locusts tended to spread out and fill

337   the space available to them (as in Fig. 9B rather than in Fig. 9C). Hence, there should be a

338 theoretical and practical scenario in which this behavior will be opposed or limited by the strong

339 and instrumental tendency of gregarious locusts to aggregate (this limit was not reached in the

340 current work, but may appear at higher animal densities). As we have shown, the funnel-like

341 topography and the narrowing of the path resulted in alteration of the marching kinematics, such

342 that both speed and pausing durations were reduced. Our previous findings, suggesting that it is

343 the locusts' rest durations rather than walking durations that are typically modulated in order to

344 adjust the swarm dynamics (Ariel et al. 2014), are thus confirmed, supporting the instrumental

345 role of the intermittent motion (pausing) in the marching dynamics.

346 The second prominent feature demonstrated by the locusts in our experimental arenas was that of

347 their attraction to the inner wall. What might appear to be attraction to the outer wall could be, at

348 least partly, a result of a tendency to maintain the walking trajectory (Ariel et al. 2014). Many

349 animals, insects included, exhibit an attraction to walls while moving in a defined space (see for

350 example cockroaches: Jeanson et al., 2005, or flies: Soibam et al., 2012). The tendency to orient

351 in space by means of mechanical contact is termed "thigmotaxis" (Fraenkel and Gunn 1961).

352 Thigmotactic animals have a higher probability of walking adjacent to walls, although different

353 curvatures of walls may have different effects: concave wall has a higher "attraction level" than a

354 convex one (Creed and Miller, 1990). A tendency to follow walls (or, alternatively, a crest or

355 ridge in the landscape) could potentially be advantageous for swarm maintenance, by way of

356 increasing the likelihood of encountering a conspecific, and could thus be important in the

357 collective behavior (Jeanson et al. 2003).

358 It is important to note that there are probably species-specific differences related to the above

359 features, i.e. the density within the swarm and, mostly, the shape of the swarm (e.g. Uvarov

360 1977; Hunter et al. 2008; Buhl et al. 2011; Ariel and Ayali 2015). Species may also differ in the

361   landscape- or topography-dependent effects on the behavior of individuals and on the consequent

362   changes in the spatial attributes of the swarm. In accordance with our present findings, *S.*

363   *gregaria* marching bands under natural conditions have indeed been reported to spread out

364   widely along very large distances, in contrast to the long ribbon-like structures reported for other

365   species (Kennedy 1939, 1951; Uvarov 1977).

366   One should of course also be cautious when extrapolating from the results of laboratory

367   experiments to the natural behavior of locusts in the field. The current study constitutes a first

368   step in exploring the important yet very broad question of the effect of topology on the collective

369   dynamics of marching locusts. Hence, we chose here to concentrate on a relatively

370   straightforward regime of experimental conditions, i.e. a specific number of animals and an arena

371   area that had been found to be favorable for promoting locust marching. In other words, the

372   experimental conditions were chosen so that the only disrupting factor for the marching animals

373   would be the narrowing funnel. The effects of other sources of disruption to the coherent

374   marching (for example, over- or under-crowding, large or small distances from the walls,

375   different nutrition etc.), may be non-additive and could significantly change some of the

376   conclusions of the current study. Nonetheless, our results show that even under "optimal"

377   marching conditions, a simple topological heterogeneity has an interesting and somewhat

378   unexpected impact on the locust dynamics.

379   Finally, we emphasize our findings regarding the capacity of locusts to adapt their response to

380   their surroundings (the swarm dynamics) in order to compensate for barriers and bottlenecks in

381   their path. Such behavioral strategies can explain the non-intuitive independence of the order

382   parameter from the funnel width. This experimental finding contradicts several previous

383   theoretical predictions, which suggested that environmental heterogeneities can qualitatively

384   alter the dynamics of collectively moving particles in a complex way – decreasing the flux

385   through the bottleneck, promoting particular swarming patterns, and even changing the phase-

386   behavior of the system (see Introduction for details). Our results show that, at least under the

387   density regimes tested, persistent and stable dynamics can be promoted by means of individual

388   adaptability. For example, whereas Shklarsh et al. (2011) demonstrated that individual

389   adaptability can enhance search efficiency in swarm optimization methods, our results suggest

390   that adaptability can lead to an opposite effect and increase robustness and resilience. Future

391   experimental and theoretical studies should thus investigate organisms and models with

392   performance-adaptable interactions.

393

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478

479 **Figure legends**

480 Figure 1

481 **A**. A top view of the experimental circular arena. **B**. The different experimental settings:

482 displacement of the inner circle results in different-width funnel-like structures. The width of the

483 different sections of the arena are noted. **C**. A snap-shot from a video monitoring of the locusts'

484 collective motion. All nymphs are assigned numbers and their velocities are noted.

485 Figure 2

486 Global parameters of the locust collective motion. **A**. The correlated changes in the order

487 parameter, ϕ (blue), and the overall fraction of walking locusts, f (red), during a 50 min section

488 of two experiments. **B**. The correlation between the size of the order parameter, $|\phi|$, and the

489 overall fraction of walking locusts, f, in all the experiments with the different arenas, as depicted

490 in Fig 1B: symmetrical (red), 5 cm (blue) and 10 cm displacement (black). N=10 each. Linear

491 regression is shown in solid lines and the significance of the regression is noted. C. The overall

492 fraction of walking locusts, f (C1) and the calculated average order parameter, $|\phi|$ (C2) in the

493 different arenas. No arena-type-related differences were found and the non-significant

494 correlation is noted.

495 Figure 3

496 **A**. No arena-type-related differences were found in average walking speed (A1) However,

497 significant correlations (P-value<0.05) were found between the locust average walking speed and

498 the overall fraction of walking locusts (A2) in all three arena types (marked with different

499 colors). **B**. No arena-type-related differences were found in the average duration of resting (B1)

500   or walking (B2) bouts. **C**. No arena-type-related differences were found in the average number of

501   overall neighbors (C1) or walking neighbors (C2) within a short range around a focal locust. The

502   correlation coefficients are noted above each graph.

503   Figure 4

504   **A.** A clear arena-type-related difference in the average duration of resting (pausing) bouts was

505   found when comparing the arena halves containing the funnel (in the symmetric, 0 displacement

506   arena, one half was selected randomly). **B.** A similar comparison of the opposite half of the arena

507   yielded a non-significant correlation. The correlation coefficients are noted above each graph.

508   Figure 5

509   A comparison of the distribution of different marching kinematic parameters between the two

510   halves of the arena with a 10 cm displacement: **A**. the narrow vs. the wide half, and **B**. the

511   converging vs. the widening half. In both **A** and **B**, panel **1** shows a schematic sketch (direction

512   of marching is noted in **B1**); **2**. The average walking speed; **3**. Durations of resting bouts; and **4**.

513   Durations of walking bouts. Colors are matched to the different arena halves as shown in **A1** and

514   **B1**. While all tested parameters differ between the two halves in **A**, the only noticeable

515   differences in **B** are in speed.

516   Figure 6

517   A comparison of locust densities in the narrow and wide halves of the arena. As expected, the

518   number of neighbors (both total as well as walking only) within 6 cm of a moving focal animal is

519   highly dependent on the displacement (type of arena). **A**. Distribution of the number of neighbors

520   (left) or moving neighbors (right) in the arena with a 10 cm displacement (narrowest funnel;

521   curve colors match the halves of the arena in the enclosed schematic drawing). **B.** Average

522   number of neighbors in each experiment (narrow half). **C.** Average number of neighbors in each

523   experiment (wide half). The correlation coefficients are noted above each graph.

524

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526

527   Figure 7

528   Example trajectories of locusts leaving the funnel (overall 10 nymphs passing within a few

529   seconds through the section marked white in the inset). A tendency of locusts to spread out and

530   fill the available space can be observed.

531   Figure 8

532   Density heat maps and their analysis. **A**. Example heat maps for all three arena types. White

533   regions denote frequently visited areas. **B.** Schematic sketch showing a cut through heat map,

534   translated into a graph. Density along the cut is rescaled to values between 0 (no locusts) and 1

535   (maximal observed density). The abscissa denote the location along the section, with the

536   perimeter of the arena on the right and its center on the left. **C.** Density through similar cuts as in

537   B, averaged over all experiments in each arena type. 1. Density of animals. 2. Density of moving

538   animals only. Shaded areas are explained in the text.

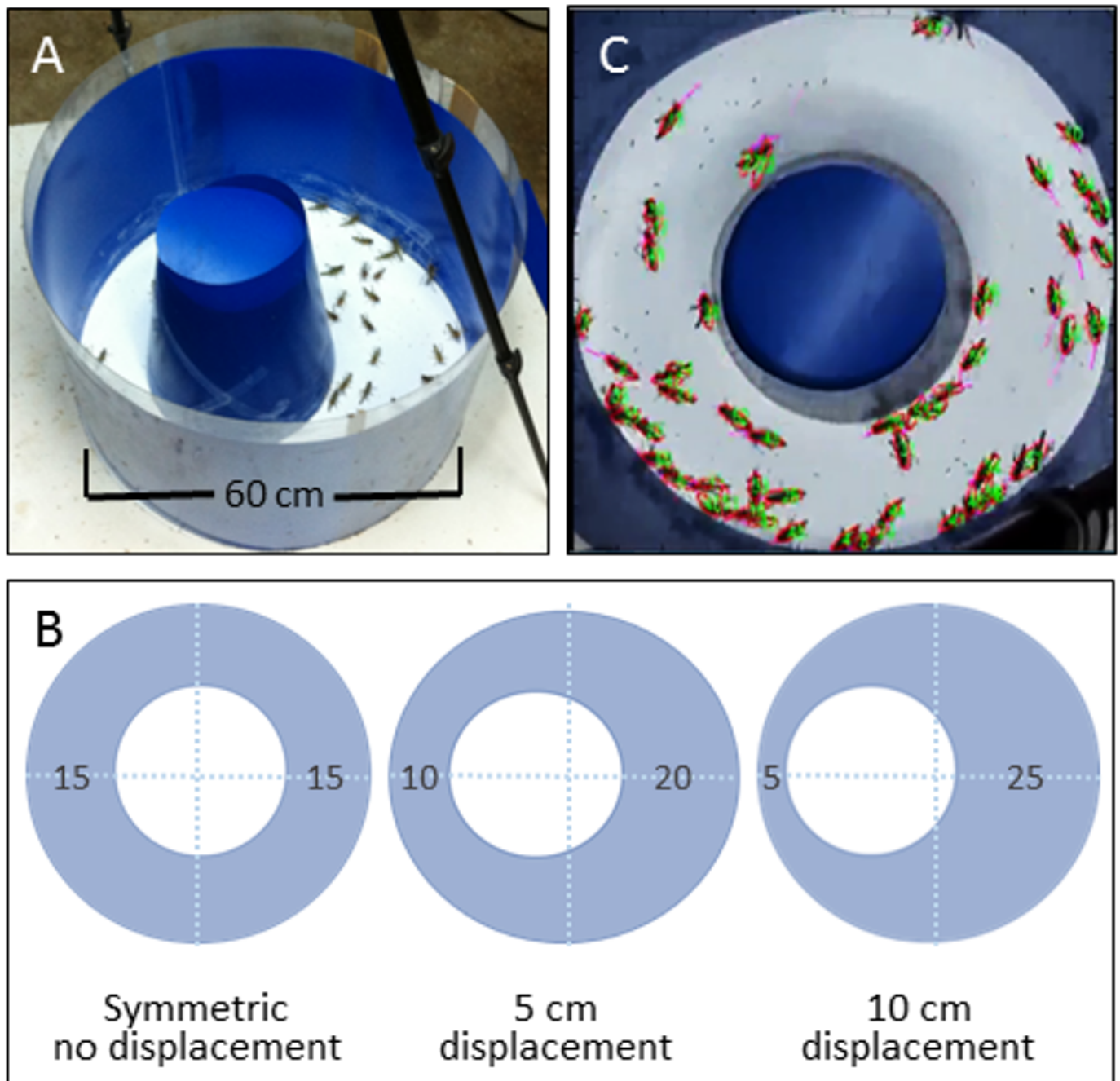
539   Figure 9

540   Cartoon showing possible swarm behavior in nature. **A**. Converging into a funnel results in

541   increased density. **B**. Spreading out of a funnel. **C** Exiting a funnel while preserving the swarm's

542   shape. See further details in the text (Discussion).

Figure 1

Fig 1

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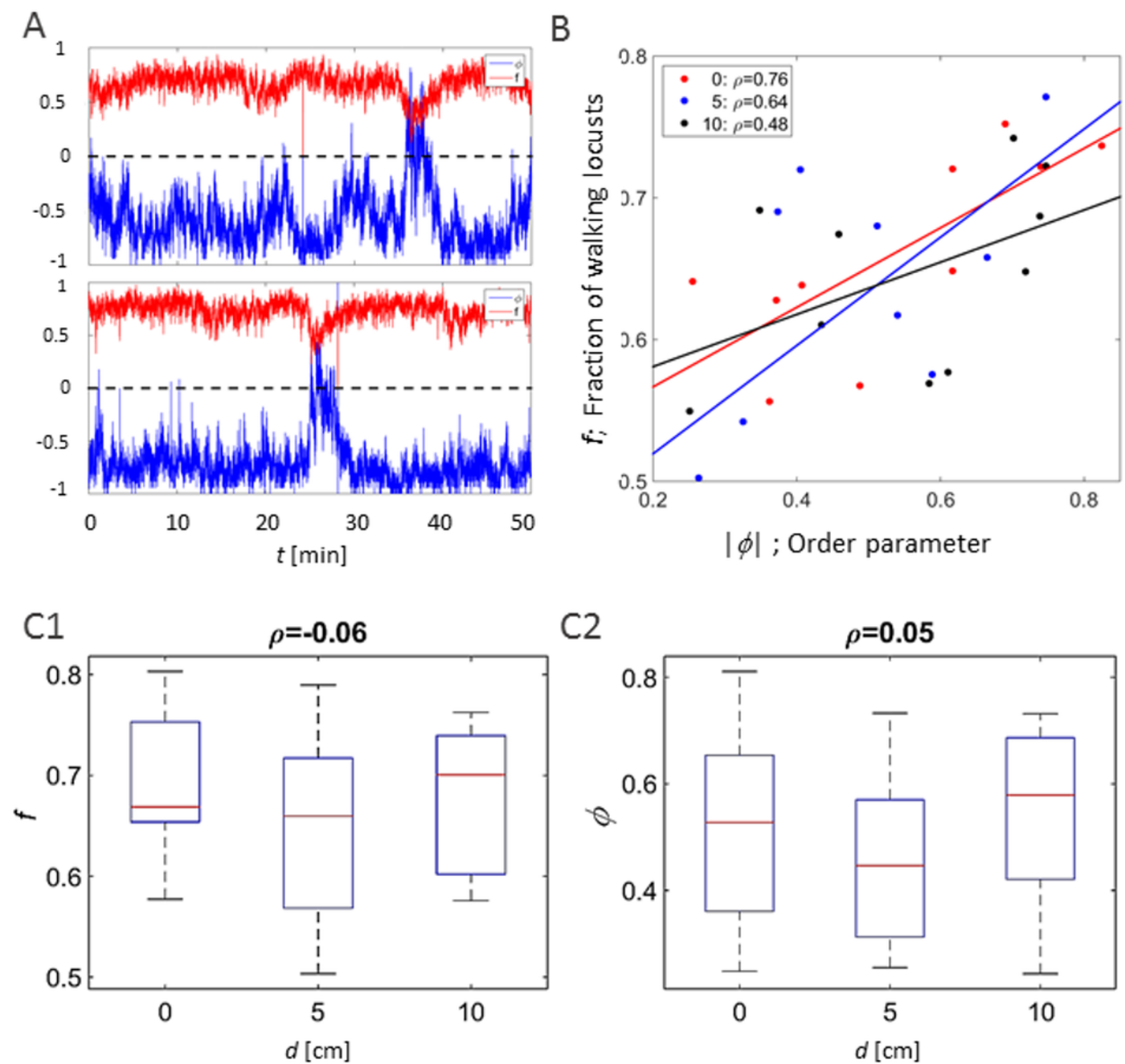
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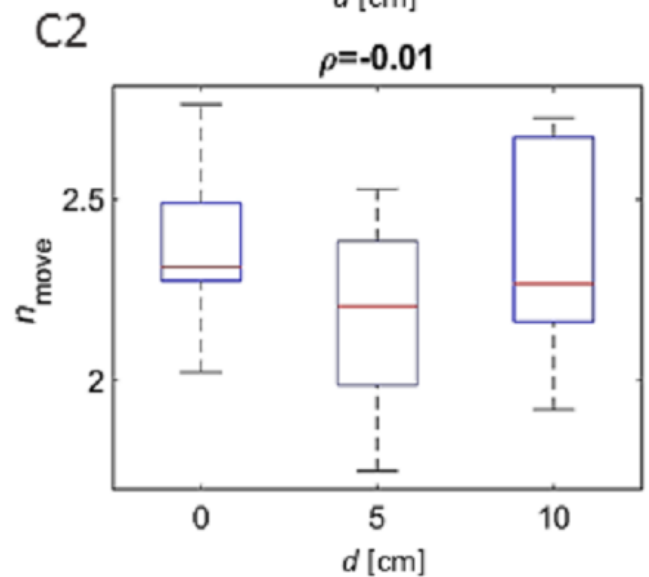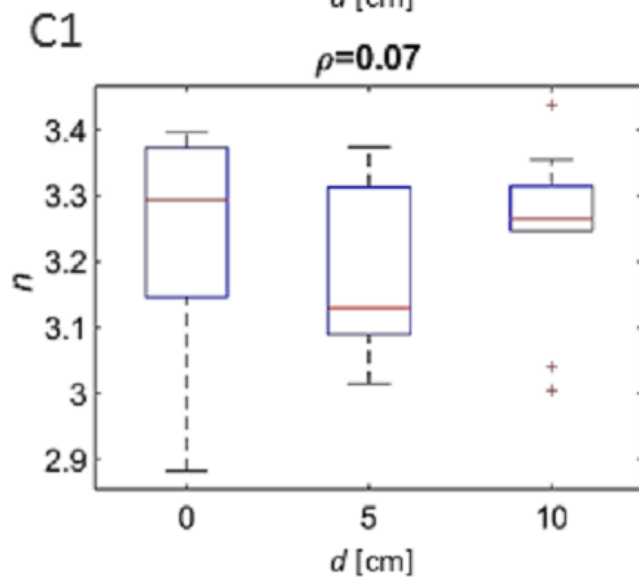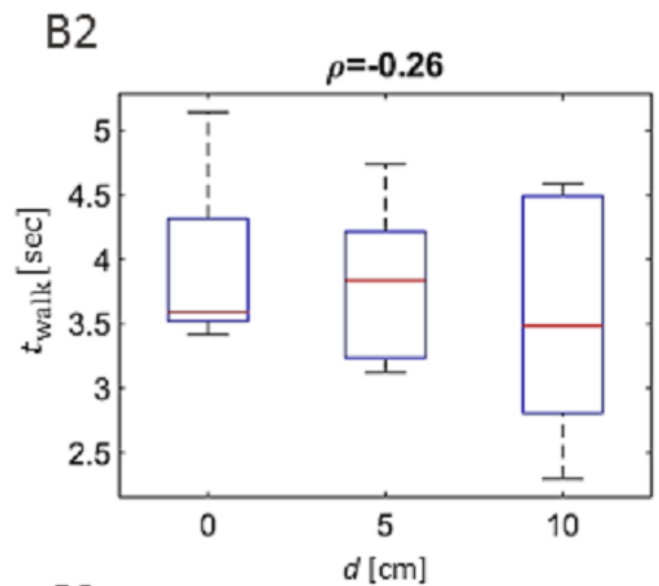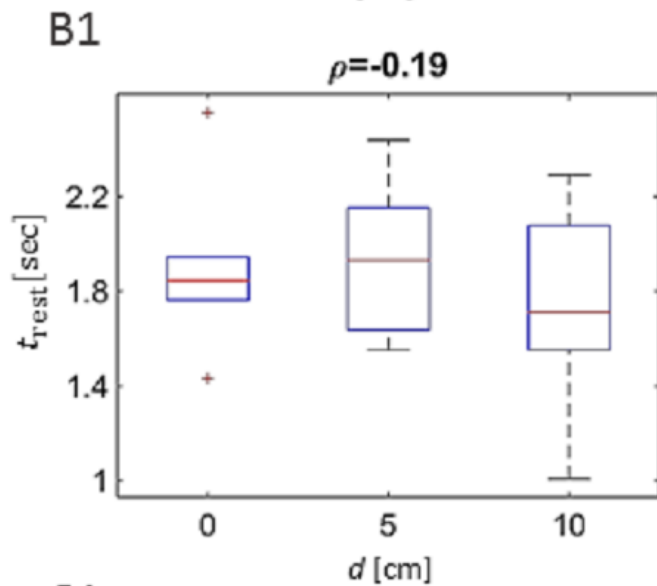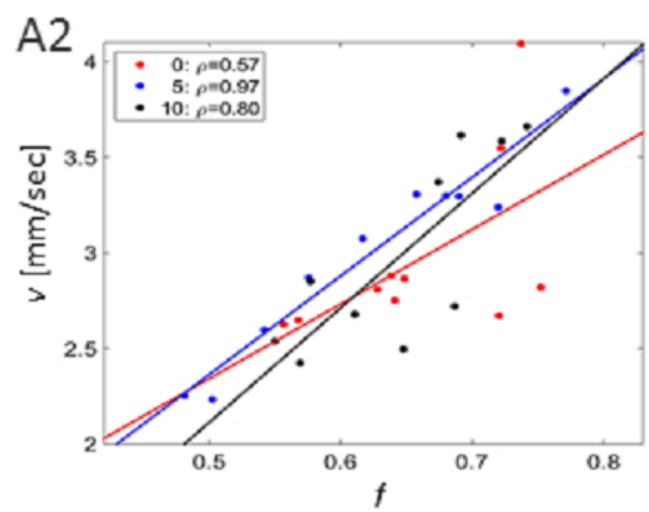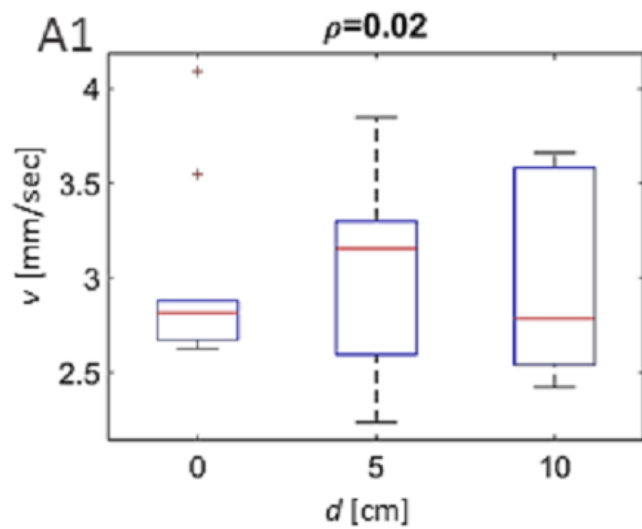
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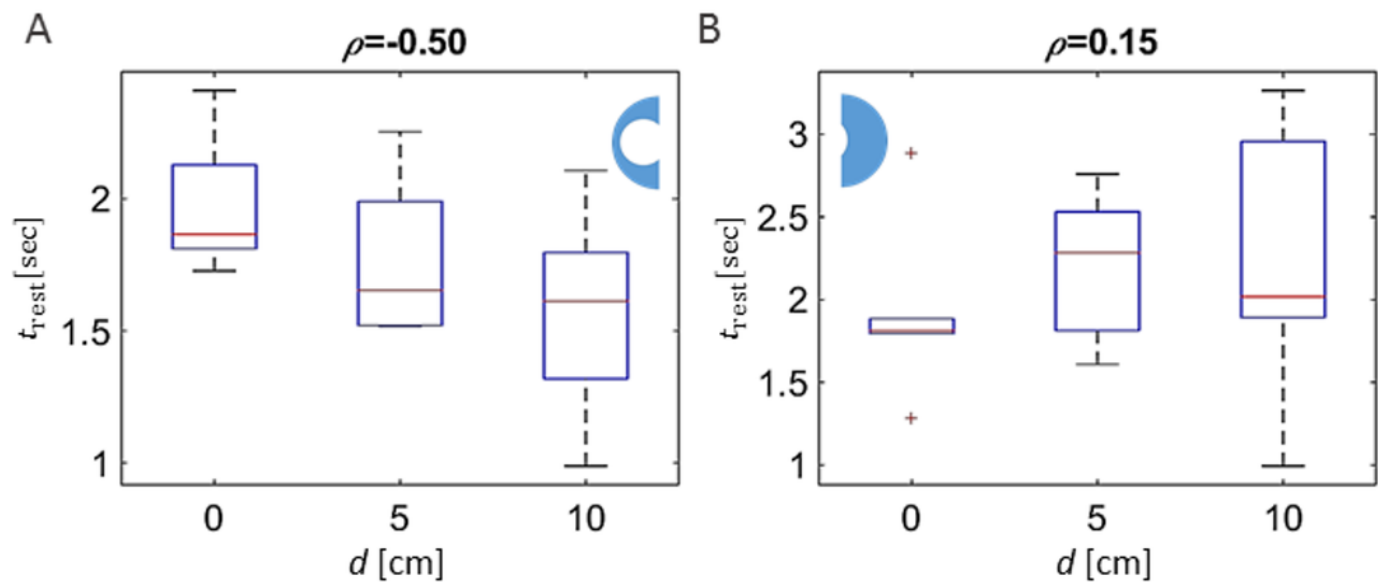
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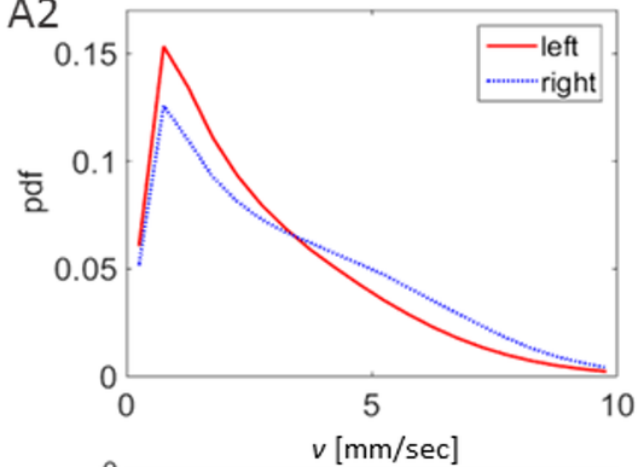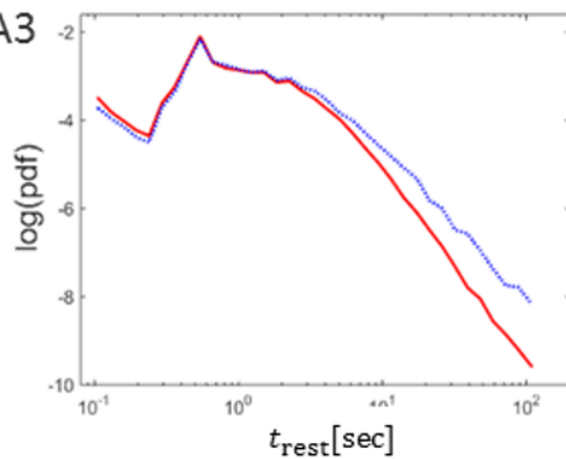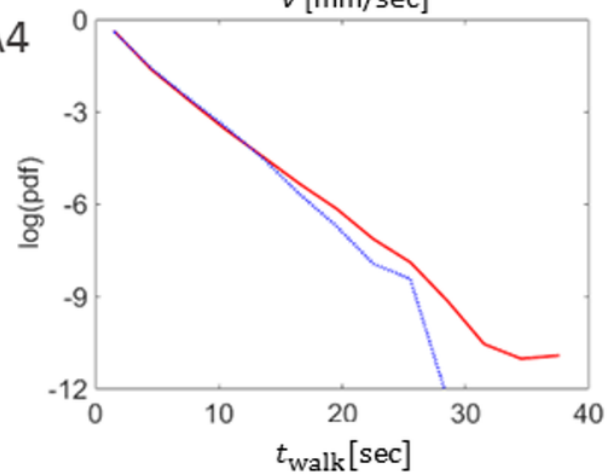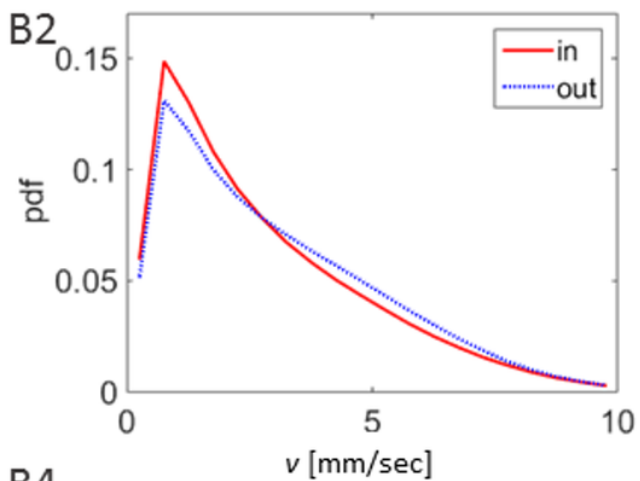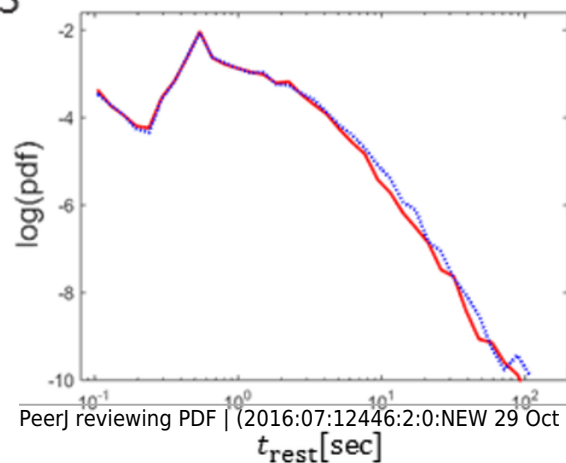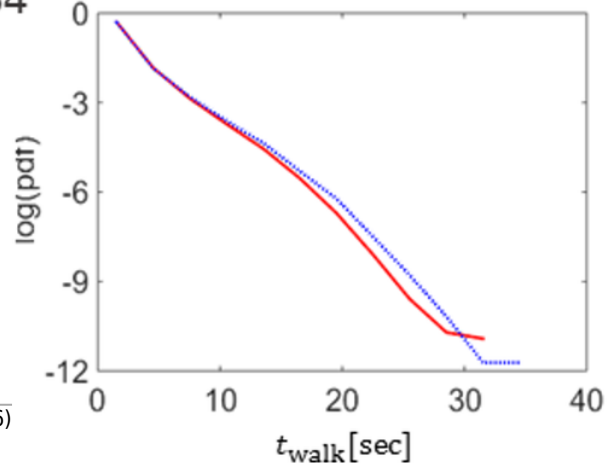
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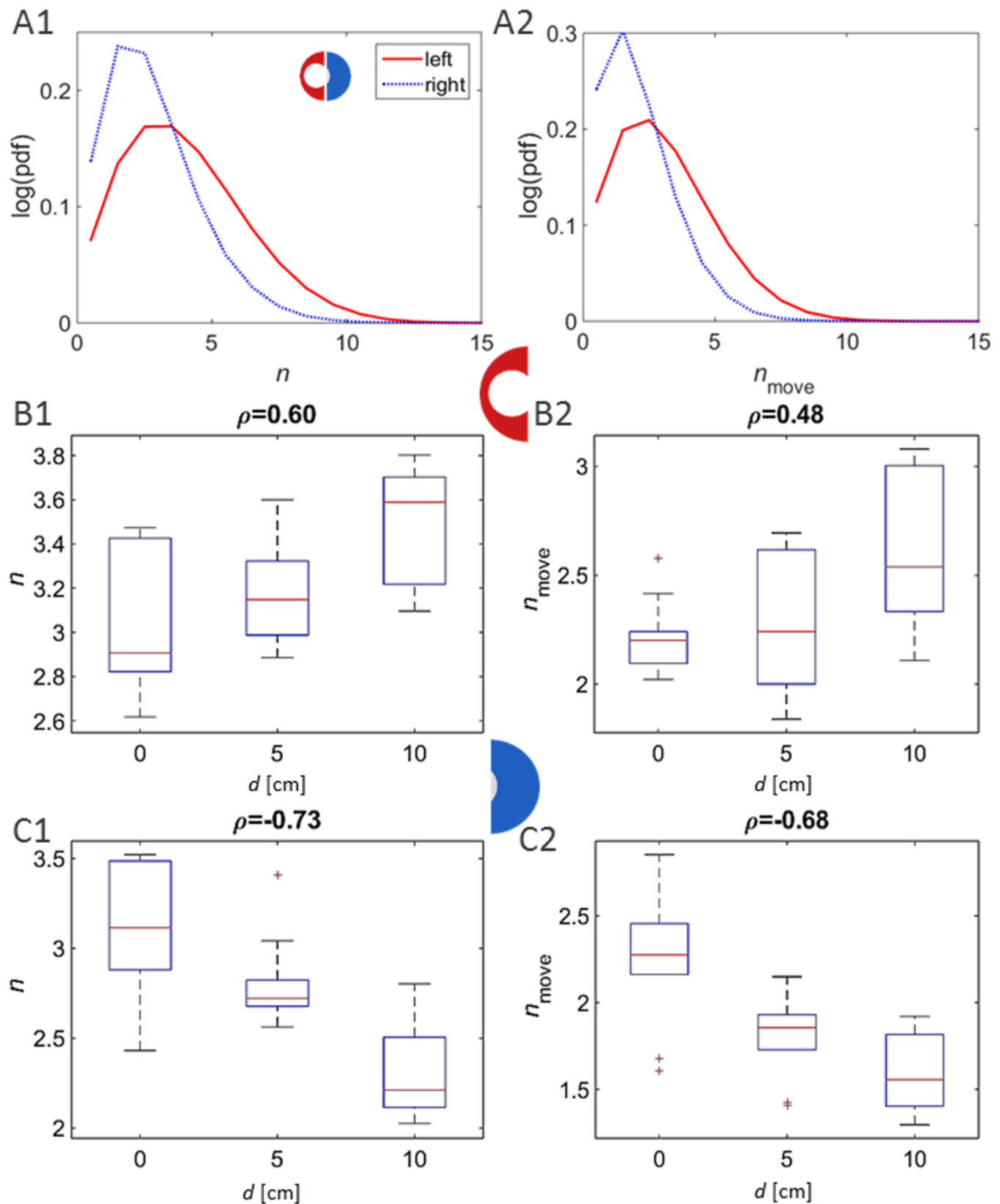
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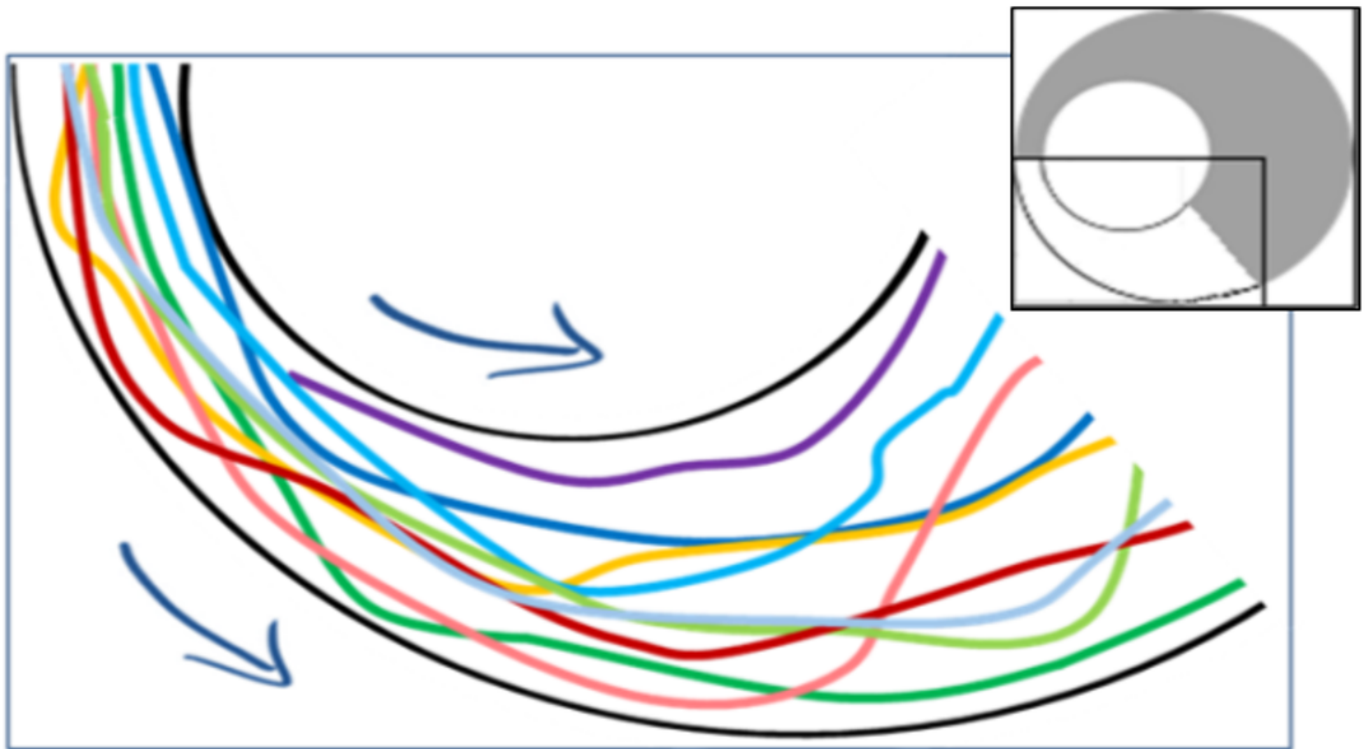
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