1   Octopus arm movements under constrained conditions. Adaptation, modification and

2   plasticity of motor primitives

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16 ABSTRACT

17

18   The motor control of the eight highly flexible arms of the common octopus

19 (*Octopus vulgaris*) has been the focus of several recent studies. Our study is the first

20 to manage to introduce a physical constraint to an octopus arm and investigate the

21 adaptability of stereotypical bend propagation in reaching movements and the pseudo-

22 limb articulation during fetching. Subjects (n=6) were placed inside a transparent

23 Perspex box with a hole at the center that allowed the insertion a single arm. Animals

24 had to reach out through the hole toward a target, to retrieve a food reward and fetch

25 it. All subjects successfully adjusted their movements to the constraint without an

26 adaptation phase. During reaching tasks the animals showed two movement

27 strategies: stereotypical bend propagation reachings, which were established at the

28 hole of the Perspex box and variant waving-like movements that showed no bend

29 propagations. During fetching movements, no complete pseudo-joint fetching was

30 observed outside the box and subjects pulled their arms through the hole in a pull-in

31 like movement. Our findings show that there is some flexibility in the octopus motor

32 system to adapt to a novel situation. However, at the present it seems that these

33 changes are more an effect of random choices between different alternative motor

34 programs, without showing clear learning effects in the choosing between the

35 alternatives. Interestingly animals showed the ability to either adapt the fetching

36 movements to the physical constraint, or as alternative explanation, to switch the

37 motor primitive fetching to a different motor primitive "arm pulling".

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39 INTRODUCTION

40

41   Octopuses represent an interesting model for the research of motor control in a

42 soft-bodied animal due to their eight highly flexible arms and centralized nervous

43 system. Recently octopuses have been a model for developing bio-inspired robots

44 with highly flexible continuum appendages (Zheng et al., 2013; Pfeifer et al., 2014).

45   The lack of any skeletal structure (Feinstein et al., 2011) enables the animals

46 to move their arms in any direction, they can bend, twist, elongate and shorten and

47 use virtually infinite degrees of freedom (DOF) (Kier and Smith, 1985). To reduce the

48 complexity of arm control, the octopus uses motor primitives to perform stereotypical

49 motor patterns. Motor primitives are loosely defined as the building blocks of a

50 complex motion (Flash and Hochner, 2005), like an alphabet of elementary actions

51 (Del Vecchio et al., 2003). Although the motor primitives themselves are considered

52 invariant, they can be recombined dynamically to form complex movements (Moro et

53 al., 2012).

54   Two discrete, stereotypical movements have been described in the octopus:

55 *bend propagation reaching* and *pseudo-joint fetching*. During reaching toward a

56 target, a bend propagates in a wave-like manner from the base of the arm toward the

57 tip (Gutfreund et al., 1996). During these arm extension movements, motor neurons of

58 the nerve cord activate the muscles in a wave-like manner and propagate the bend

59 (Gutfreund et al., 1996; Gutfreund et al., 1998). This stereotypical movement can also

60 be elicited by stimulation of the nerve cord in an *in vitro* preparation, which

61 demonstrates that the respective motor program is embedded in the arm of the octopus

62 (Sumbre et al., 2001).

63   To fetch an object to their mouth, animals form quasi-articulated limbs based

64 on three dynamic joints (Sumbre et al., 2005). Here, two waves of muscle activation

65 travel toward each other and set a pseudo-joint location at their point of collision

66 (Sumbre et al., 2006). This emulates the situation in vertebrate arms with stiffened

67 joints and enables the octopus to use precise point-to-point movements. Both reaching

68 and fetching, are highly stereotypical and greatly reduce the number of DOFs and

69 therefore the complexity of movement control.

70   One of the most important questions is about the limitations of the octopuses

71 motor control system. To generate goal directed movements, both robustness and

72 adaptivity are equally important. Strict feed-forward motor programs are a trade-off

73 between reduction of complexity and flexibility. This trade-off could be compensated

74 by higher-order motor centers, but little is known about such adaptations in the

75 control system of the octopus.

76   The basal lobes, which are the higher motor centers in the octopus (Young,

77 1971; Wells, 1978), consist of about 2.5 million cells, but seem to lack somatotopical

78 organization at this level (Zullo et al., 2009), which suggests reduced interconnections

79   of sensory and motor neurons. The large number of neurons in axial nerve cords of

80   the arms on the other hand, may point toward an alternative control center for high

81   level information processing: The peripheral nervous system contains about 350

82   million cells, comprising about two thirds of all neurons in the octopus. Most of the

83   cells are located in axial nerve cords projecting from the brain to the arms

84   (Budelmann et al., 1995). While a special division of labor between the central

85   nervous system and the peripheral nervous system of the arms has been demonstrated

86   before (Altman, 1971; Wells, 1978; Sumbre et al., 2001; Sumbre et al., 2005), lesion-

87   studies suggest that at least in goal directed movements higher brain areas are

88   necessary to control planning and execution of the motion, for example during

89   fetching motions (Sumbre et al., 2006).

90   It is unknown to what extend reaching and fetching movements can be

91   controlled to overcome a physical constraint. To investigate the flexibility and

92   adaptability of the motor control system, we introduced a physical constraint to the

93   arm and studied how it affects the previously described behaviors *bend propagation*

94   *reaching* and *pseudo-joint fetching*. The limitation to the onset of the motor primitives

95   forced the animals to adapt to the new situation. Animals were able to adapt to the

96   constraint by dynamically generating feed-forward bend propagation reachings and

97   stereotypical pull-in fetchings. These results show that octopuses have a flexible and

98   dynamic motor control system, which adapts instantly to new situations.

99

100   RESULTS

101

102   Six octopuses were put into a Perspex box and were required to reach toward a

103   target and fetch the food reward by inserting their arm through a hole in the box. All

104   animals were able to adapt to the physical constraint and used distinct strategies

105   during the reaching (Figure 1A) and fetching tasks (Figure 1B). Overall, 286

106   successful reaching movements and 382 fetching movements were observed.

107   Reaching

108   During reaching tasks octopuses used motions that were classified into two

109   strategies, a straight point-to-point reaching (please see supplemental movie clip

110   "Reaching.mov") and a seemingly undirected movement we termed waving-like

111   (please see supplemental movie clip "Waving.mov"). Straight reachings (n=148) are

112   linear point-to-point and goal directed bend propagation reachings as first described

113   by (Gutfreund et al., 1996), complemented by elongation of the arm. The octopus

114   positions the midsection of an arm over the hole of the Perspex wall and forms a loop

115   outside of the box (Figure 1 Aseconds 0.3 – 1). This loop initiates the new bend,

116   which will then travel toward the tip of the arm (see Figure 1A, seconds 1.4 – 2.4).

117   Next to loop-induced bend propagation movements, bend propagations were set up

118   freely outside the box in about 7% of all successful reachings. In these cases the arm

119   was put through the hole in a different manner (e.g. by stretching and pushing the tip

120   of the arm through the hole) and a bend was established outside the box without the

121   loop-building procedure at the hole.

122

123   In order to compare straight reaching motions in constrained situations to

124   unconstrained motions described by Gutfreund et al. (1996), the same analyzing and

125   normalization methods were used on ten random reaching movements, which

126   successfully hit the target. The normalized tangential velocity profiles of constrained

127   reaching movements showed typical invariant bell-shaped curves (Figure 2B) with

128   three corresponding phases, identical to reaching movements in an unconstrained

129   situation (Figure 2A). Phase I corresponds to the establishment of the bend and is the

130   most variable part of the movement. Phase II, the propagation of the bend along the

131   arm, corresponds to the steep velocity increase in the profile and is the most robust

132   part of the movement. The maximum and subsequent decrease of velocity in phase III

133   corresponds to a passive part of the movement in the vicinity of the object.

134   Waving-like movements (n=138) are seemingly undirected, explorative

135   movements outside the box with no bend propagation and random kinematic profiles

136   (Figure 3). In most cases the arm is put through the hole by using the loop-building

137   procedure similar to movements in the straight category.

138   The reaching strategies differed significantly in the duration until the object

139   was touched (Mann-Whitney U= 312, N= 272, p< 0.001, Figure 4), in which mean

140   duration for straight bend propagation reachings was short (2.4 ±1.3 sec) and longer

141   for waving-like motions (12.4 ±7.1 sec). While waving-like behavior was observed

142   more often than straight bend propagation reaching on average (N = 130 ±109 and 29

143   ±19), the success rate was higher for straight reachings (87% ±11.4) than for waving-

144   like motions (27.7% ±29.8).

145   Since straight reachings were more successful, learning in the octopuses might

146   mean a transfer of their strategy from a more undirected and waving-like movement

147   to an efficient point-to-point reaching. To test if a shift in reaching strategies

148   happened over time, strategy choices were compared between the beginning and the

149   end of the experiments. Successful reaching motions were split into three trial bins

150   for each animal and then compared between first and last bin (Figure 5). Two of six

151   animals significantly changed the strategy in the last third of the experiment

152   compared to the first; in the last third of the experiment Animal 5 increased the

153   amount of waving-like motions ($\chi^2(1)= 6.65$, N= 30, p= 0.01) and Animal 3 increased

154   the amount of straight reachings ($\chi^2(1)= 7.84$, N= 74, p= 0.005). The relative number

155   of fails did not change over the course of the experiment ($\chi^2(1)= 3.043$, N= 634, p=

156   0.081).

157

158   Fetching

159   All animals were able to pull the food reward through the hole in the Perspex

160   wall and only a few trials were marked as fails (food dropped n= 24, general

161   execution error n= 5). To test for differences in movement patterns, all movements

162   were subjectively categorized into two categories, straight (please see supplemental

163   movie clip "Fetching.mov") or deflected (please see supplemental movie clip

164   "Deflected.mov") movements. Movements that showed a general immediacy and an

165   overall straight and point-to-point shape were classified as straight movements and

166   movements that could not clearly be classified as straight movements formed the

167   deflected group. To differentiate the two categories in order to test if these

168   movements are discrete, a sample of 60 successful fetching trials (ten per animal)

169   were tested for general reliability of the classification into categories. First, the

170   movements were reevaluated by subjective categorization of a second observer and

171   then by a categorization based on 3D reconstruction of the movements' trajectories

172   and their tangential velocity profiles.

173   To test for inter-rater reliability of the subjective categorization,

174 Krippendorff's α (Hayes and Krippendorff, 2007) was calculated for two observers.

175 The classification was accepted with an agreement of α= 0.67 (95% CI, 0.443 to

176 0.851). The relatively vague criteria for classification justified the use of the

177 minimum recommended α-values (Hayes and Krippendorff, 2007).

178   Movements with generally straight trajectories were categorized as straight

179 (Figure 6A), as well as normalized tangential velocity profiles that showed stereotypic

180 bell shaped curves (Figure 6B). Trajectories and tangential velocity profiles that were

181 random and not stereotypical were categorized as deflected (Figure 6C and 6D). The

182 three ratings per movement, based on subjective categorization, tangential velocity

183 profiles and trajectories were tested for compliance and showed a general consent on

184 their respective categorization (Krippendorff α = 0.71). Overall 281 trials were

185 categorized as straight and 100 as deflected.

186

187   Mean fetching times also differed significantly between categories (Mann-

188 Whitney U= 21.5, N= 381 p< 0.001), with a mean duration of 2.7 ±1.66 sec for the

189 straight category and 5.81 ±4.82 sec for the deflected category.

190   The distribution of the strategies during the first ten trials was not

191 homogenous among the animals (Table 1). Four of the six animals showed straight

192 fetching in the first trial and the general distribution of strategies was found to be

193 random (One-sample Runs test, not significant; see Table 1).

194   To test if the animals changed their fetching strategies in the course of the

195 entire experiment due to an adaptation to the constraint, all trials were divided into

196 three trial bins for each animal and the respective movement categories were analyzed

197 (Figure 7). The relative number of straight and deflected fetches did not change

198 significantly from the first to the last third of the experiment (χ^2 (1)= 1.748, N= 254

199 p= 0.1869). Also the combined fetching time of all animals showed no significant

200 improvement (U= 8752, N= 253 p= 0.191), however, two individual animals

201 significantly changed their mean fetching time in the course of the experiment:

202 Animal 2 lowered the mean fetching time from 7.24 ±5.5 sec in the first third to 3.85

203 ±3.5 sec in the last third of the experiment (U= 69.5, N= 34, p= 0.009) but Animal 5

204 raised it from 1.71 ±0.75 sec to 2.45 ±1.1 sec (U= 1015, N= 75, p= 0.001). The two

205 opposed changes in reaching time point toward individual, rather than general effects.

206

DISCUSSION

208

209   A very promising perspective to explain movement generation and to

210 overcome the *motor equivalence problem* of increasing complexity with increasing

211 DOF's (Bernstein, 1967) is the modular approach. Movements result from the

212 combination of a finite set of stable motor primitives (Bizzi et al., 2008) or a

213 stereotypical co-activation of several muscles, called muscle synergies (d'Avella et

214 al., 2003). Several studies showed the use of robust motor primitives during reaching

215 (Gutfreund et al., 1996) and fetching movements (Sumbre et al., 2005) of unrestrained

216 octopuses. However, there are no studies on the plasticity of movements and

217 adaptivity of movement control. Our study is the first to manage to introduce a

218 physical constraint to the octopus arm. This enabled us to gain new insights into the

219 ability of the motor system to adapt and modify the motor primitives *bend-*

220 *propagation reaching* and *pseudo-joint fetching*.

Adaptation to constrains

222   All animals adapted to the physical constraint and were able to reach and fetch

223 through the hole in the Perspex wall. The animals showed flexibility in movement

224 control by adapting to the constraint and using an appropriate movement to get to the

225 food reward. In order to elucidate learning effects, movements of the reaching and

226 fetching tasks were categorized into variant and invariant movements. Invariant

227 movements had stereotypical kinematic profiles with straight trajectories and bell

228 shaped tangential velocity profiles. Variant movements were described as waving-like

229 reaching and deflected fetching and had no stereotypical trajectories, variable

230 tangential velocity profiles and were longer in duration.

231   As there is no significant change in the amount of these movements over the

232 course of the experiments, we assume that these movements are not transitional states

233 during an adaptation period (Arce et al., 2009). Only one animal changed its behavior

234 toward the more efficient straight reaching strategy, despite the higher success

235 probability. Likewise, during fetching tasks animals did not entirely change to the

236 faster pull-in movements. Interestingly, the relative number of fails, which

237 presumably represented explorative movements without coincidental target hits, did

238 not change over the course of the experiment per animal as well, which overall

239 suggests an absence of learning effects (Sosnik et al., 2004) or an insufficient

240 motivational state of the animal to trigger learning effects. The general absence of any

241 clear learning effect in terms of improvement in performance or in terms of time

242 taken to complete a task eludes toward an absence of the ability of octopus vulgaris to

243 shape motor programs due to learning. Since these behaviors must then be innate, the

244 variance in the strategies suggests that the animals switch between different

245 movement strategies during the same condition. In general, the waving-like reaching

246 and the variances in the fetching patterns showed that the octopus' movement

247 repertoire is probably not limited to a fixed set of movements. At least in the waving-

248 like movements the high number of observations (N = 130 ±109) and low success rate

249 (about 25%) compared to straight reachings (N = 29 ±19, about 85% success rate)

250 might explain the movement as an explorative movement, in which the animal

251 touched the target by accident.

252 Stereotypical movements

253   Movements of the reaching and fetchings tasks were categorized according to

254 their kinematic profiles or movement patterns. Stereotypical movements were

255 generally immediate and goal directed movements with straight trajectories.

256   During reaching tasks the animals used propagating bends that were either

257 initiated by building up loops through the hole of the wall using approximately the

258 midsection of the arm, or were freely initiated outside the box. These bend

259 propagation movements showed linear trajectories and stereotypical invariant

260 normalized tangential velocity profiles and were identical to movements in freely

261 behaving animals (Gutfreund et al., 1996). The dynamic range of control over this

262 robust feed-forward motor program has not been shown before in octopus: The

263 animals were able to sequentially connect the motor primitive bend propagation

264 reaching and the loop building at the hole of the wall or could even be initiated

265 outside the box. Since loop building at the hole was also observed in most movements

266 of the waving category, it should be seen as an independent movement from the bend

267 propagation initiation. Our findings suggest the ability of the octopus to start the

268   motor primitive at any point along the arm and to subsequently hit the target. This is

269   an important finding as it stands in contrast with previous hypothesis that the

270   directional control of the reaching movement is determined by adjusting two DOF's

271   (yaw and pitch) at the base of the arm (Gutfreund et al., 1996).

272   Fetching movements categorized as straight consisted of a single linear

273   motion. They were done with straight point-to-point pull-ins of the arms, with straight

274   trajectories and bell shaped normalized tangential velocity profiles. These movements

275   differ from fetching movements in freely behaving animals, as in our experiments no

276   formation of stereotypical pseudo joints and quasi-articulated limbs could be

277   observed. Interestingly, the kinematic profiles of straight fetching movements were

278   very similar to the stereotypical bend propagation reaching movements in freely

279   behaving animals, suggesting that these fetching movements are complete and

280   uninterrupted movements. This suggests that this is either a modification of the

281   existing motor primitive or an so far unknown new motor primitive – arm pulling.

282   Visual examination of all fetching movements showed a commonality

283   between the two categories during fetching: In all trials the gripping shape of the arms

284   seemed to be preserved and showed an S-shape, formed by the attachment of the food

285   and an immediate second bend (see arrows in

286   **Figure 1**B, 0.8 s). This has been described before (Sumbre et al., 2005; Sumbre et al.,

287   2006) as "grasp of food item" and "distal joint". It is unclear, however, if the grasping

288   of the food item triggered pseudo-joint fetching, initiating for example the onset of

289   medial and proximal joints, which might then have been masked or cancelled by a

290   conflicting feedback signal triggered by the constrain on the arm. To clarify this

291   possibility a further kinematic analysis would be required.

292   The neuromuscular control of the movement generation is unclear. It was

293   hypothesized before, that the grip of the food item triggers two waves, which form

294   pseudo-joints at the point of collision, creating dynamic joints along the arm with

295   fixed ratios of inter-segment lengths (Sumbre et al., 2006). Although it is unclear if

296   these joints were masked or cancelled by higher-order control mechanisms in the

297   constraint situation, they did not interfere with the immediate switch to a straight pull-

298   in movement in some animals (see Table 1). Unfortunately the proximal part and the

299   base of the arm inside the box were not visible enough for a meaningful analysis of

300   the pull-in mechanism. The food items might have triggered the onset of a medial and

301   proximal bend at the very proximal part of the arm inside the box, which then were

302   dynamically altered by sensory information in terms of the length and stiffness of the

303   quasi-articulated structures.

304

305   Variant movements

306   Movements of each of the two stereotypical categories share similar motion

307   patterns and seem goal directed because of the stereotypical kinematic profiles.

308   However, the mechanisms underlying the movements in the variant category are

309   unclear. The variant movements of the reaching tasks, categorized as waving-like

310   movements, seemed to be fundamentally different from stereotypical bend

311   propagation movements. Waving-like movements had random kinematic profiles and

312   were seemingly undirected and the successful reaching to the target were lower than

313   the direct reaching thus less rewarding. The movement patterns of variant fetching

314   movements on the other hand differed only marginally from stereotypic point-to-point

315   fetching movements, although differences in the kinematic profiles and duration were

316   observed. The trajectories seemed to be random deviations from linear trajectories

317   and were thus labeled as deflected categories. A commonality of all fetching

318   movements seemed to be a pull-in motion pattern, controlled by the proximal segment

319   of the arm and by shortening the arm. In contrast to reaching movements the reward

320   gained by the two types of puling were simialr.

321   Point-to-point pull-in fetchings with their stereotypical kinematic profiles, that

322   is, linear trajectories and the bell shaped normalized tangential velocity profiles, could

323   present another motor primitive, for situations, where an arm is pulled through a tight

324   opening. It is reasonable to assume that the pull-in movement itself was controlled by

325   more proximal parts of the arm, which were inside the box and unfortunately not

326   visible enough for a meaningful analysis. A common mechanism for pull-in fetchings

327   could explain why the movement showed both, robust and variant forms and still

328   seemed to have the same motion mechanics: While the proximal part of the arm

329   controls the pull-in, the distal part is passive. Movement speed or immediacy of the

330   pull-in changes the kinematic profile of the tip of the arm, which was the reference

331   point during the kinematic analysis (see methods section). The animal would then be

332   able to switch between activating a pull-in motor primitive and active control of the

333   distal part of the arm. This switch between robust motor primitives and flexible

334   movements would be similar in principal to the dynamic linking of movement

335   patterns during reaching movements in the constrained situation.

336   Sensory feed-back

337   It has been discussed previously if octopuses are able to use sensory feedback

338   to control their movements (Wells, 1978; Gutfreund et al., 2006) and Gutnick et al.

339   (2011) presented evidence that animals use visual feedback from their arms during

340   three-choice-maze experiments. In our findings tactile sensors might collect

341   additional information on the arm. The restriction due to the hole should provide

342   sensory information to recognize the restricted mobility of the arm and thus this

343   information is used to generate appropriate movements to overcome the constraint.

344   The lack of systematic change in strategy choices between the variant and

345   stereotypical form of the respective movement implies that no trial-and-error learning

346   phase occurred in the course of the experiment. In the fetching task most animals

347   used point-to-point pull-in motions without an adaptation phase. In the reaching task

348   the animals initiated the loop of the bend propagation at the hole, which suggests that

349   they used sensory feedback to identify the dimension of the obstacle and the point at

350   which the initiation of the feed-forward motor program *bend propagation reaching*

351   was possible.

352   Since feedback-controlled movements are generally considered to be too slow

353   for fast online correction (Kawato, 1999), we propose that the octopus uses sensory

354   feedback to gather information about its environment and incorporate them in its

355   feed-forward inverse model to compute adequate actions and trajectories. While no

356   change in categories over the course of the experiment was recorded, which could

357   have been an indication for trial-and-error learning, all animals explored the box and

358   its opening extensively during the experiments.

359

360   Résumé

361   The results of this study suggest that the octopus higher motor control system

362   is flexible and adapts to novel situations mainly by choosing between two different

363   movements that solve the task albeit with different rewarding rates. Interestingly,

364   despite the difference in reward rate in the reaching movement no learning was

365 demonstrated. This suggests that the reward does not affect the decision between the

366 two type of reaching (the waving and direct). An intriguing finding that requires

367 further investigation, is the demonstrated the ability of the octopus to direct its arm to

368 the target even though the movement starts from the hole rather than for the base of

369 the arm. This proposes that the octopus uses sensory feedback to gather information

370 about its environment and incorporate them in its feed-forward inverse model to

371 compute adequate actions and trajectories. With respect to fetching it seems that the

372 octopus has two alternative behaviors to solve the task (direct and indirect pulling). In

373 this task there also seems to be a fixed decision ratio that also does not change over

374 time (but here the reward is equal for the two movements).

375

376

MATERIALS AND METHODS

378

Subjects and holding

380 Subjects were six wild-caught *Octopus vulgaris* (Lamarck, 1798) (2 females, 4

381 males; between 250-450g bodyweight) collected by fishermen from the Israeli coast

382 of the Mediterranean Sea. The animals were housed individually in 100 liter artificial

383 sea water tanks within a closed circulation system and held according to the

384 guidelines for the EU Directive 2010/63/EU for cephalopod welfare (Fiorito et al.,

385 2014). Tanks were enriched with clay-pot dens, gravel, rocks and green algae

386 (*Caulerpa prolifera*), temperature of the holding rooms was held constant at about

387 19°C. Day and night cycles were simulated by artificial illumination for 12 hours.

388 Animals were fed every other day with either dead shrimps or pieces of fish.

389 All animals acclimatized for at least 14 days in the holding tanks before they

390 were transferred to an experiment tank (400 liter), where they acclimatized for

391 another day before experiments started. Animals were preselected for motivation and

392 general health.

Experiments

394 Each animal was placed separately inside a custom made transparent Perspex

395 box (40×40×40 cm) with a hole (1.5 cm in diameter) at the center of one side that

396   allowed the insertion of only a single arm. The animal had to reach out through the

397   hole to retrieve a food reward and pull it back in. Success criterion for the reaching

398   task was the touching of a target (white Perspex disc on a transparent Perspex stick).

399   A piece of shrimp was placed on the tip of the arm, which had to be completely pulled

400   through the hole for a successful fetching task. The reaching task onset was marked

401   by the insertion of the target into the water. Fetching tasks followed successful

402   reaching tasks or were initiated by letting the animal grip the target and then being

403   pulled to stretch the arm to average fetching distance. The target was presented

404   approximately at the level of the hole and the distance varied between 2-40 cm to

405   motivate the animals to reach for it.

406   Kinematic Analysis

407   The experiment was constructed according to the publication by Gutfreund et

408   al. (1996). The sessions were recorded with two digital video cameras (SONY

409   Handycam HDR-XR550; Tokyo, Japan) in an angle of about 90 degrees and later

410   formatted, cut and transformed into picture sequences (25 frames per second) with

411   video editing software (Adobe Premiere CS5; San Jose, California, USA).

412   For the 3D reconstruction of trajectories and tangential velocity profiles, the

413   visual information of the two cameras was transformed to 3D coordinates, applying

414   the direct linear transformation (DLT) method (Wood and Marshall, 1986; Woltring

415   and Huiskes, 1990). A calibration body was used to obtain 11 parameters that were

416   used to define the image coordinates of the two cameras in the following DLT

417   equations:

418     $$x_1 = \frac{P_1 X + P_2 Y + P_3 Z + P_4}{P_9 X + P_{10} Y + P_{11} Z + 1} \qquad (1),$$

419     $$y_1 = \frac{P_5 X + P_6 Y + P_7 Z + P_8}{P_9 X + P_{10} Y + P_{11} Z + 1} \qquad (2),$$

420   with x_1 and y_1 as image coordinates of a designated point of camera 1 and the

421   unknown 3D coordinates $X,\ Y$ and Z. The variables P_{1-11} represent the 11 parameters

422   obtained from defined points of the calibration body.

423   Three points of interest were then marked in the image sequences using

424   MATLAB (MathWorks; Natick, Massachusetts, USA.) to reconstruct arm movement:

425   two reference points and either the bend or tip of the arm during reaching tasks or the

426 food item, which was typically put on the distal quartile of the arm, during fetching

427 tasks. This positional data was then used to calculate the tangential velocity profile.

428 The data was smoothed by fitting a fifth order polynomial to the projections of the

429 points on the three axes as a function of time. The coefficients were obtained by

430 calculating the least-square equation, using the singular value decomposition

431 algorithm. Then V_{tan} was calculated from the derivatives of the smoothed coordinates

432 *X(t), Y(t)* and *Z(t)* with:

433 $$V_{tan} = \sqrt{\left(\frac{dX}{dt}\right)^2 + \left(\frac{dY}{dt}\right)^2 + \left(\frac{dZ}{dt}\right)^2} \qquad (3),$$

434 To account for invariances, the tangential velocity [V(t)] and time (t) were normalized

435 according to the maximum velocity (V_{max}) and travel distance (D), following

436 procedure after Atkeson and Hollerbach (1985) and Gutfreund et al. (1996):

437 $$V_{normalized} = \frac{V(t)}{V_{max}} \qquad (4),$$

438 $$T_{normalized} = \frac{V_{max} \times t}{D} \qquad (5),$$

439 $$D = \sum_t \sqrt{(X_t - X_{t-1})^2 + (Z_t - Z_{t-1})^2} \qquad (6),$$

440 with the smoothed coordinates *X* and *Z* and the index *t* as image number or time.

441 Further data analysis was done with SPSS 19 (IBM Software; Armonk, New

442 York, USA) and Microsoft Excel 2011 for Mac OS (Redmond, Washington, USA). A

443 inter-rater reliability test was done in order to calculate rating similarities between

444 two independent observers. For this purpose two observers categorized the same trials

445 according to the categorization rules and differences were calculated according to

446 Hayes and Krippendorff (2007).

447

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531

543 COMPETING INTERESTS

544

545 The authors declare no competing financial interests.

546

547 AUTHOR CONTRIBUTIONS

548

549 J.N.R. and M. J.K. designed the study and carried out the behavioral experiments,

550 J.N.R. analyzed the data, J.N.R, B.H. and M.J.K. discussed the results and drafted the

551 manuscript.

552
553 *Table 1: Distribution of categories among the first ten trials*

554

		Animal 1	Animal 2	Animal 3	Animal 4	Animal 5	Animal 6
Trial	1	Deflected	Deflected	Straight	Straight	Straight	Straight
	2	Deflected	Deflected	Deflected	Deflected	Straight	Straight
	3	Deflected	Straight	Straight	Straight	Straight	Straight
	4	Deflected	Deflected	Deflected	Straight	Straight	Straight
	5	Deflected	Deflected	Straight	Straight	Straight	Straight
	6	Deflected	Straight	Straight	Straight	Straight	Straight
	7	Deflected	Straight	Straight	Straight	Straight	Deflected
	8	Straight	Deflected	Straight	Straight	Deflected	Straight
	9	Deflected	Straight	Deflected	Straight	Straight	Straight
	10	Straight	Straight	Straight	Deflected	Deflected	Deflected
One-sample runs test							
r =		4	6	7	4	4	4
p =		1	1	0.287	1	1	1

555

556 Figure texts

557

558 **Figure 1** Picture sequence of typical straight reaching and fetching movements in a

559 constrained situation. Octopuses are behind a Perspex wall and reach or fetch through

560 a hole with a single arm (indicated in red). **A** Straight reaching toward a target is done

561 with a typical bend propagation, which is set up by building up an arm loop at the

562   hole. White arrow points at arm bend. Seconds 0.3 – 0.6 show building up of the arm

563   loop; seconds 1.4 - 1.8 show bend propagation toward the target; seconds 2.4 show

564   arm hitting the target. Blue ring highlights the hole; **B** Straight fetching of a food item

565   (white object). Frame at 0.2 seconds shows the arm attached to target; seconds 0.4 –

566   1.5 show linear point-to-point pull-in movement. Arrows at second 0.8 mark two

567   bends of the S-shape grip of the food item (white). Colors, brightness and contrast

568   were altered to highlight arm movements.

569

570   **Figure 2** Comparison of normalized tangential velocity profiles during reaching tasks.

571   **A** unconstrained animals (taken from Gutfreund et al., 1996) and **B** constrained

572   animals. Both graphs show bell shaped curves, aligned at peak velocity and with axes

573   normalized for time and velocity.

574

575   **Figure 3** Kinematic profiles of typical waving-like motions. **A** 3D reconstruction of

576   the trajectory of an arm. One circle represents the site of the attached food item on the

577   arm in a single frame of a picture sequence with 25fps. Red circle marks the site of

578   the target. The axes are in cm. **B** Normalized tangential velocity profile

579

580   **Figure 4** Comparison of reaching durations. Reaching durations (in seconds) for

581   reaching of the straight and waving-like category. Asterisk denotes significance $p<$

582   0.05

583

584   **Figure 5** Number of choices in respective reaching category waving and straight, split

585   in three trial bins for each animal. Significant differences between the first and third

586   trial bin were recorded in Animal 3 and Animal 5. Asterisks denote significance $p<$

587   0.05.

588

589   **Figure 6** Kinematic profiles of fetchings of the straight and the deflected category. **A**,

590   **C** 3D reconstruction of typical arm trajectories for each respective category. One

591   circle represents the site of the attached food on the arm in a single frame of a picture

592   sequence with 25 fps. Red circles mark the site of the hole. The axes are in cm. **B**, **D**
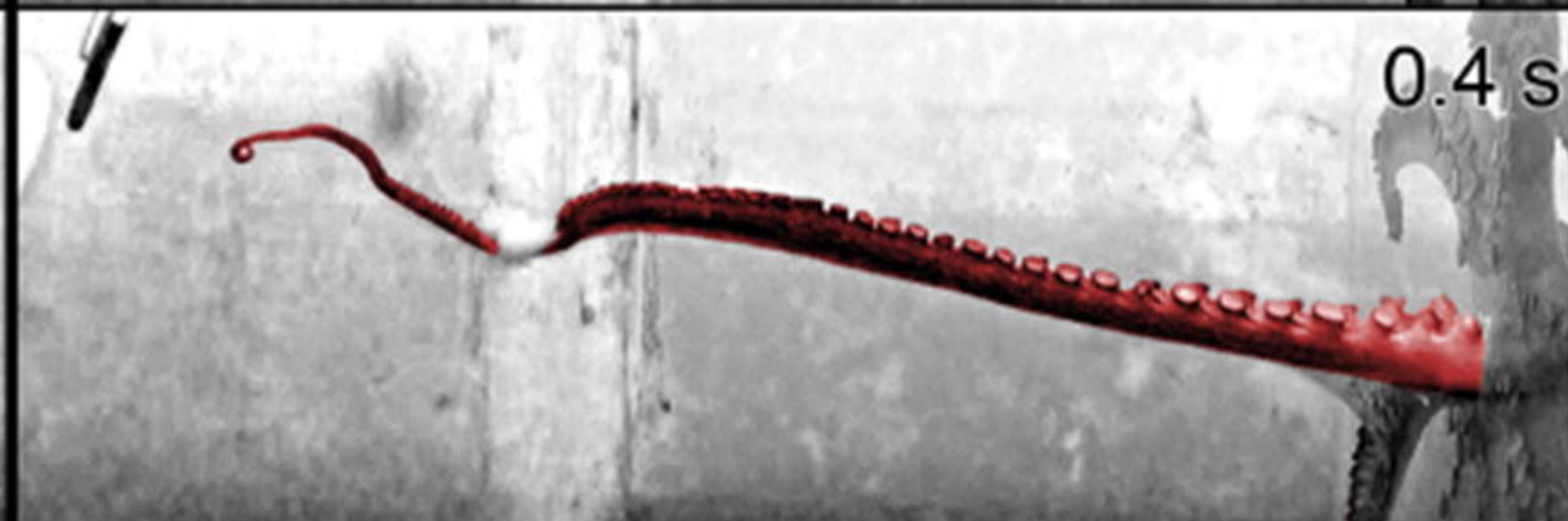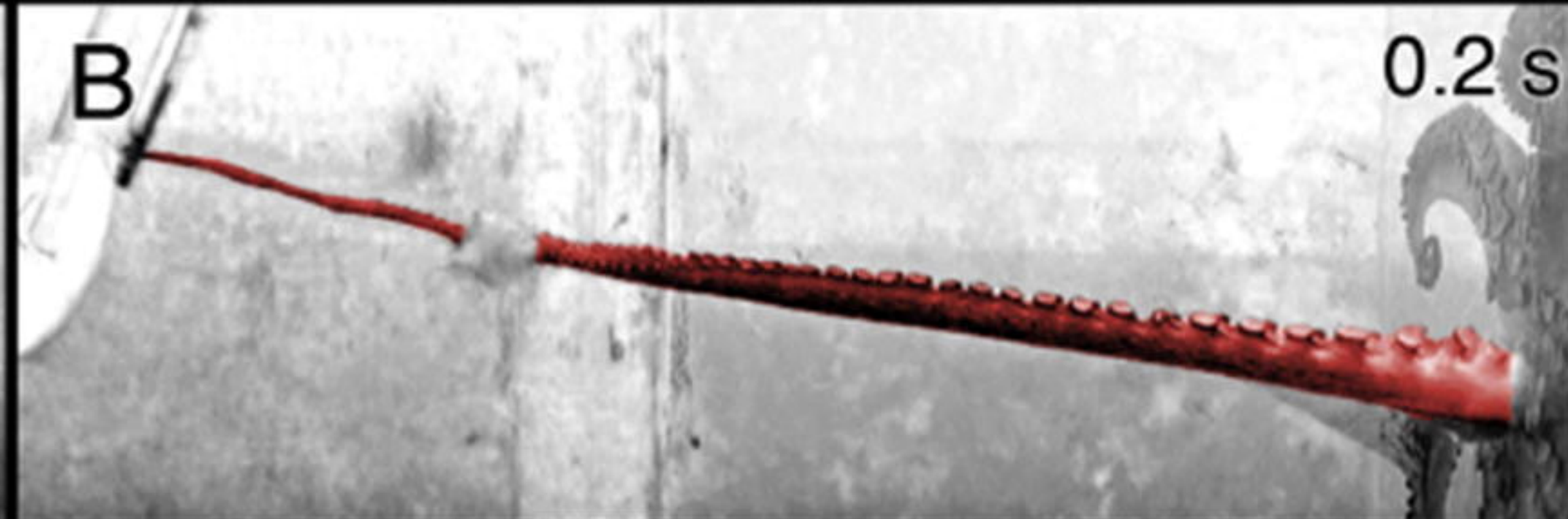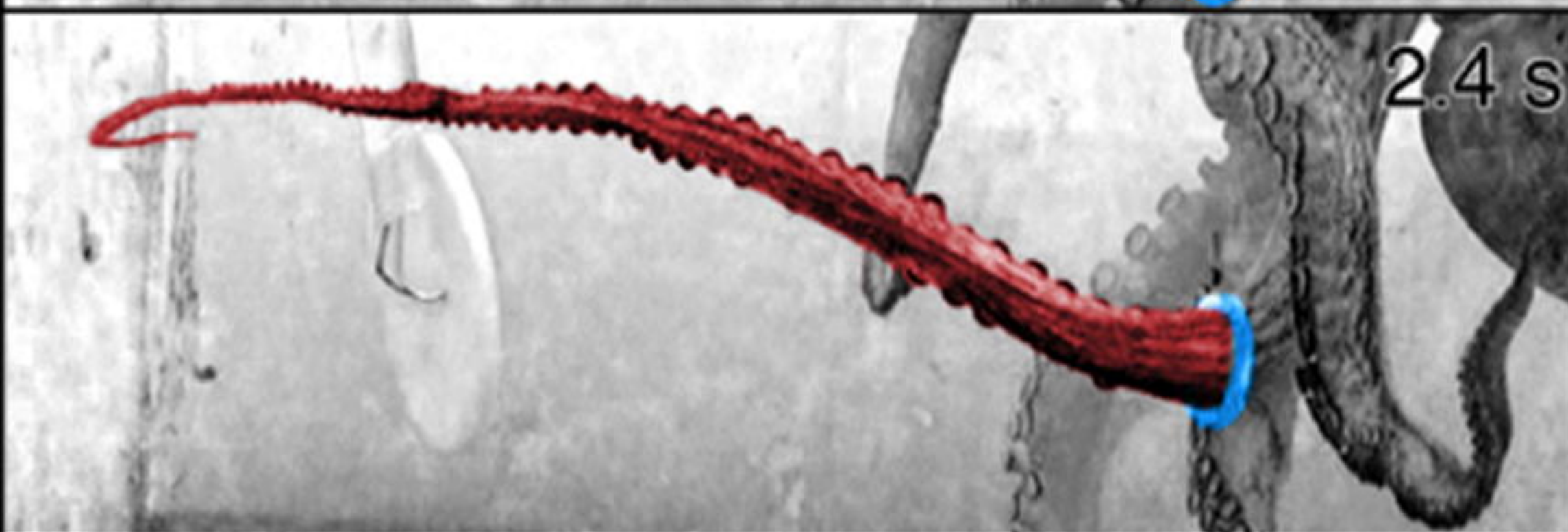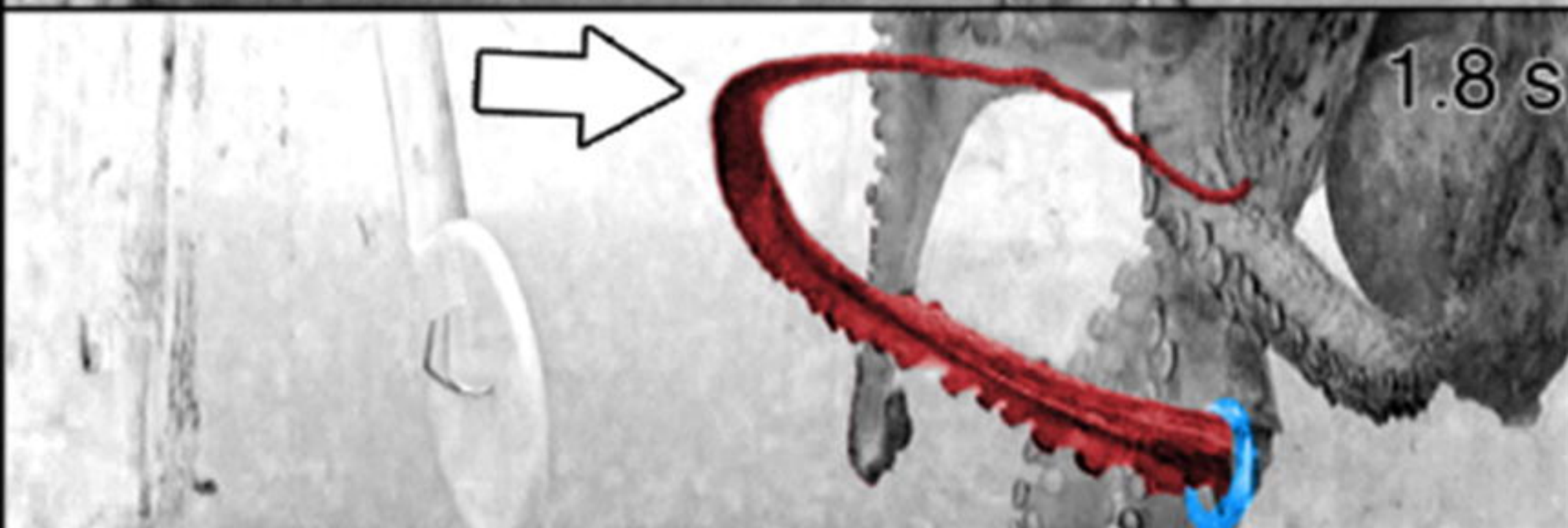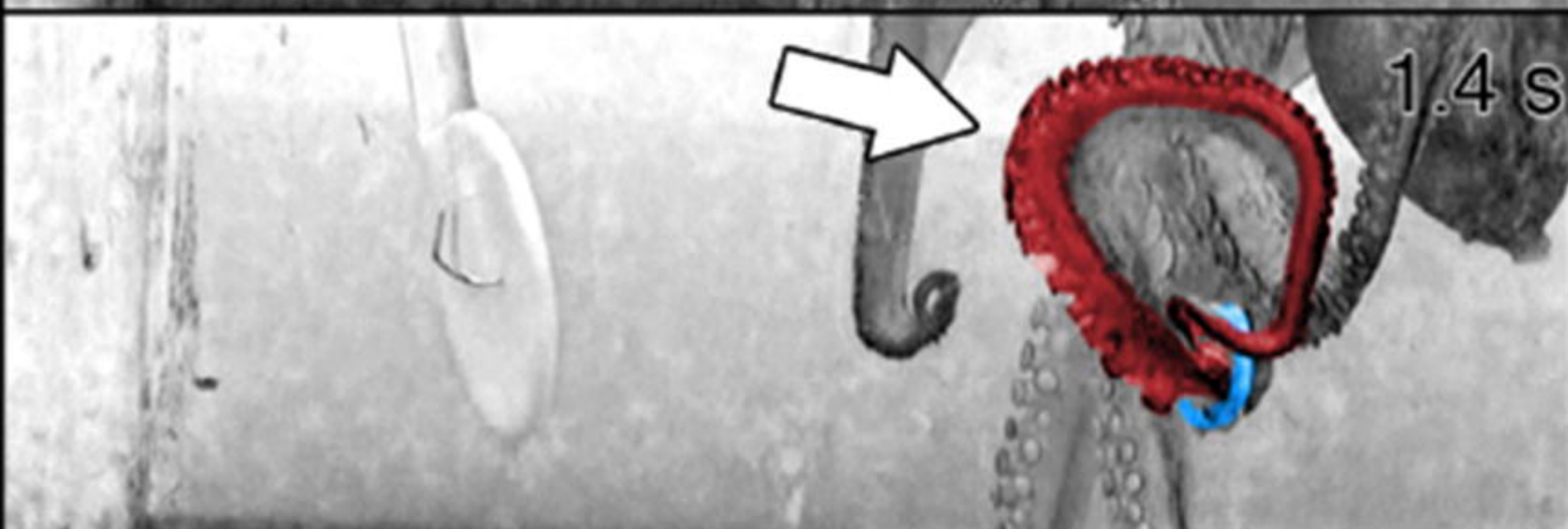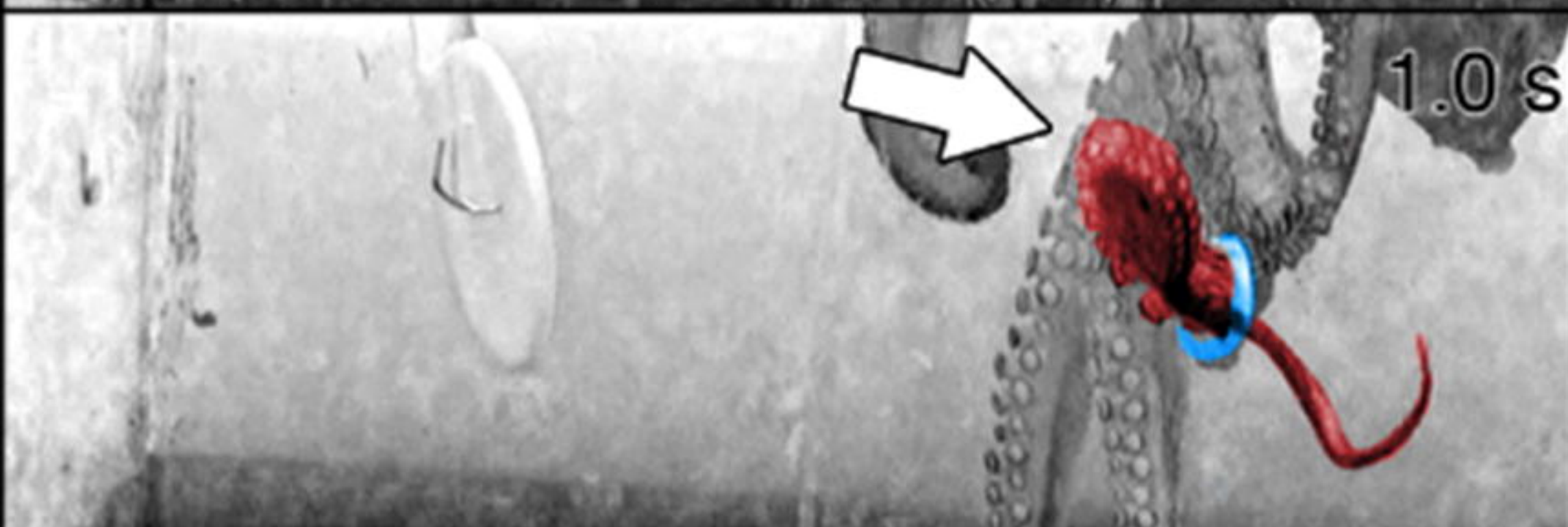
593   Normalized tangential velocity profiles. One trial is shown for clarity in the deflected
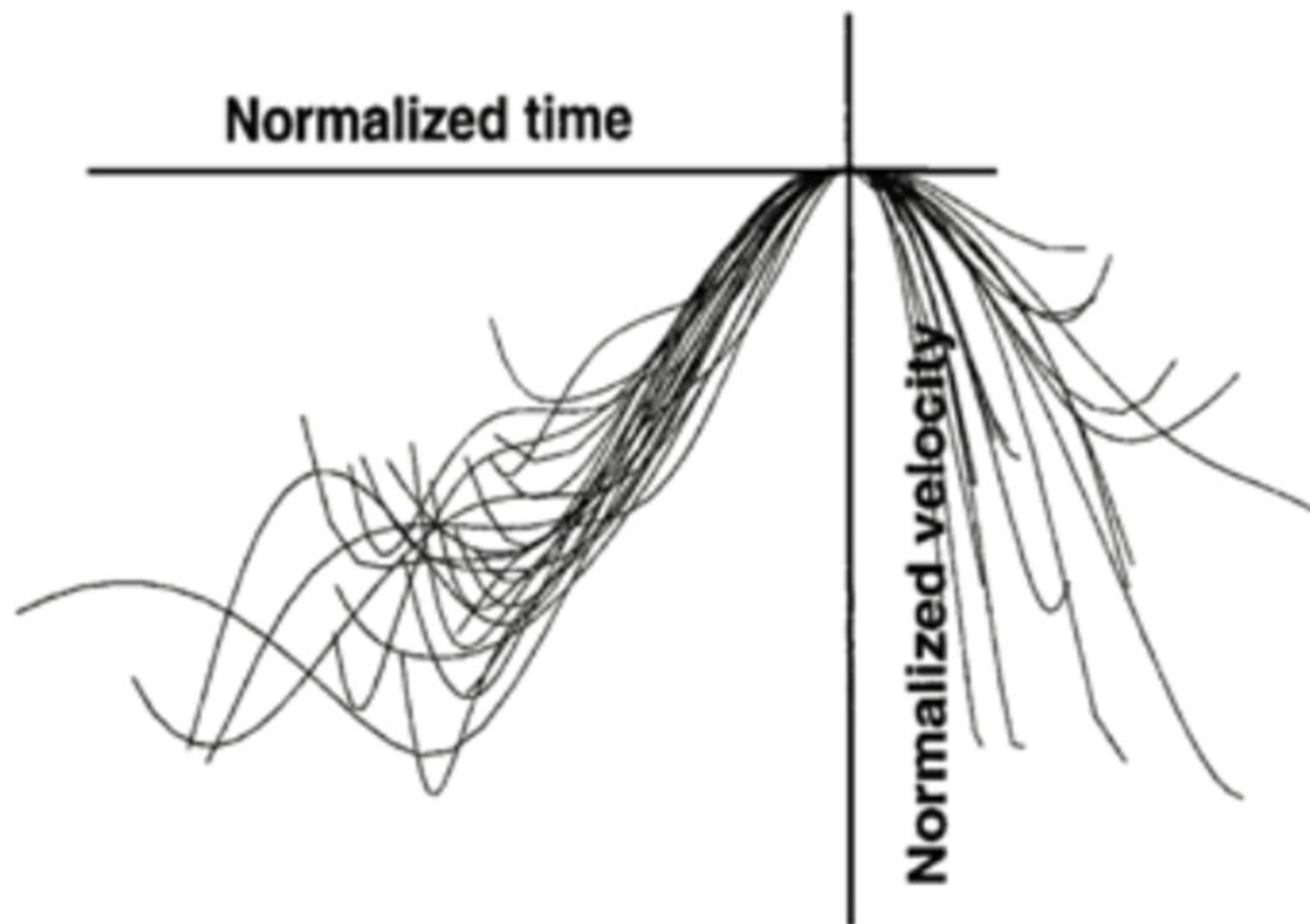
594   category.

595

596   **Figure 7** Number of choices in respective fetching category straight and deflected,

597   split in three trial bins for each animal. No significant differences were recorded

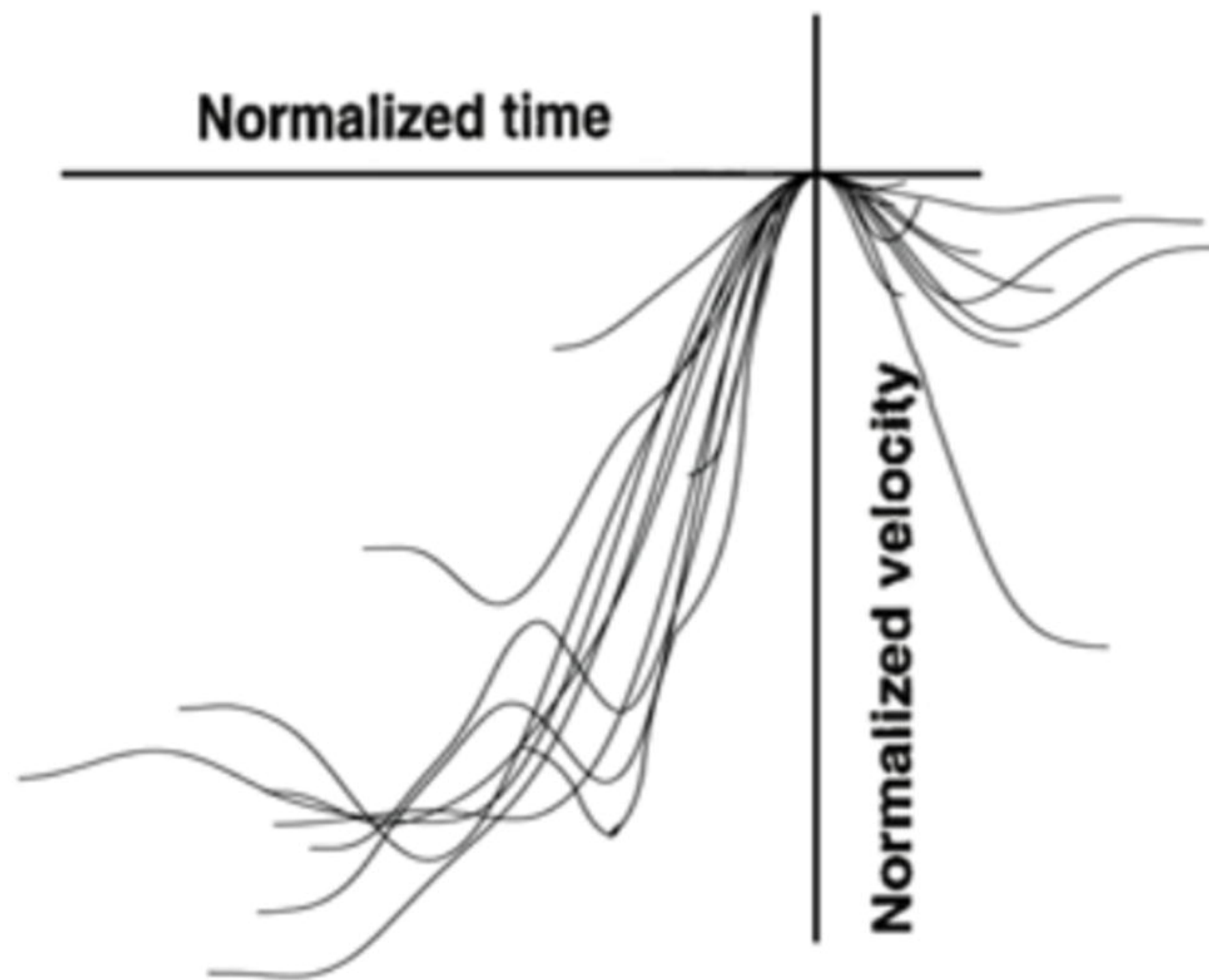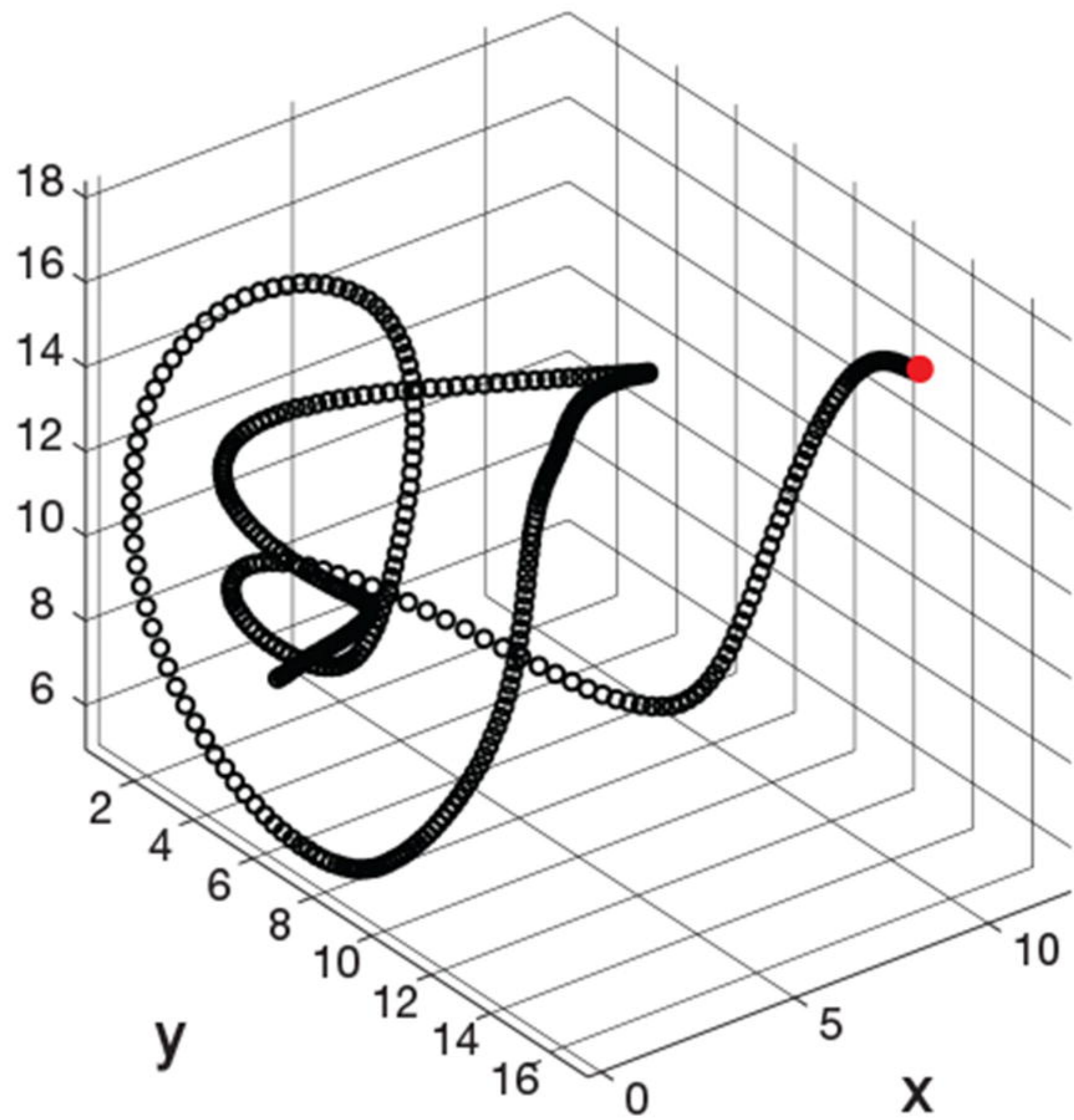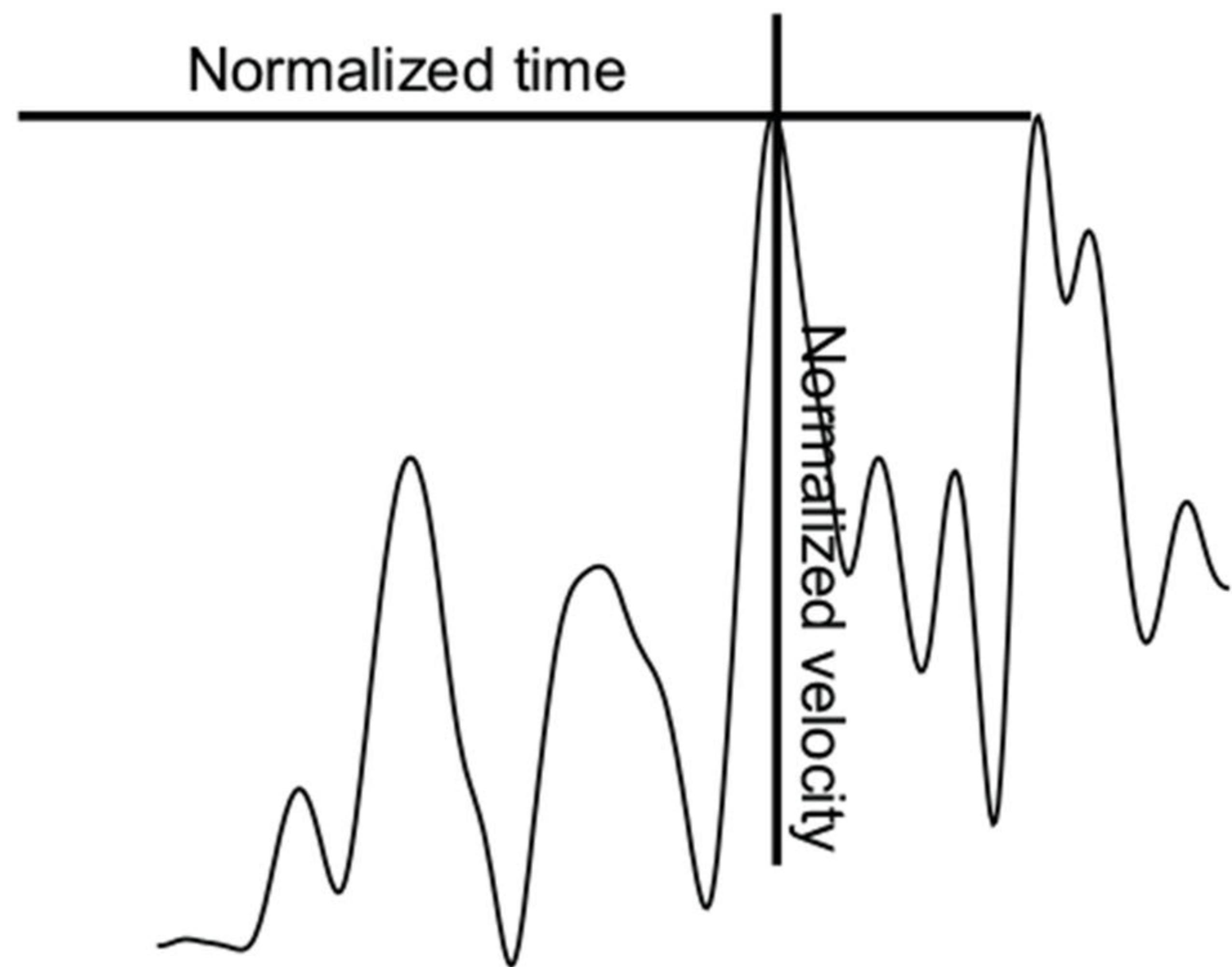598   between the first and third trial bin in each category per animal.
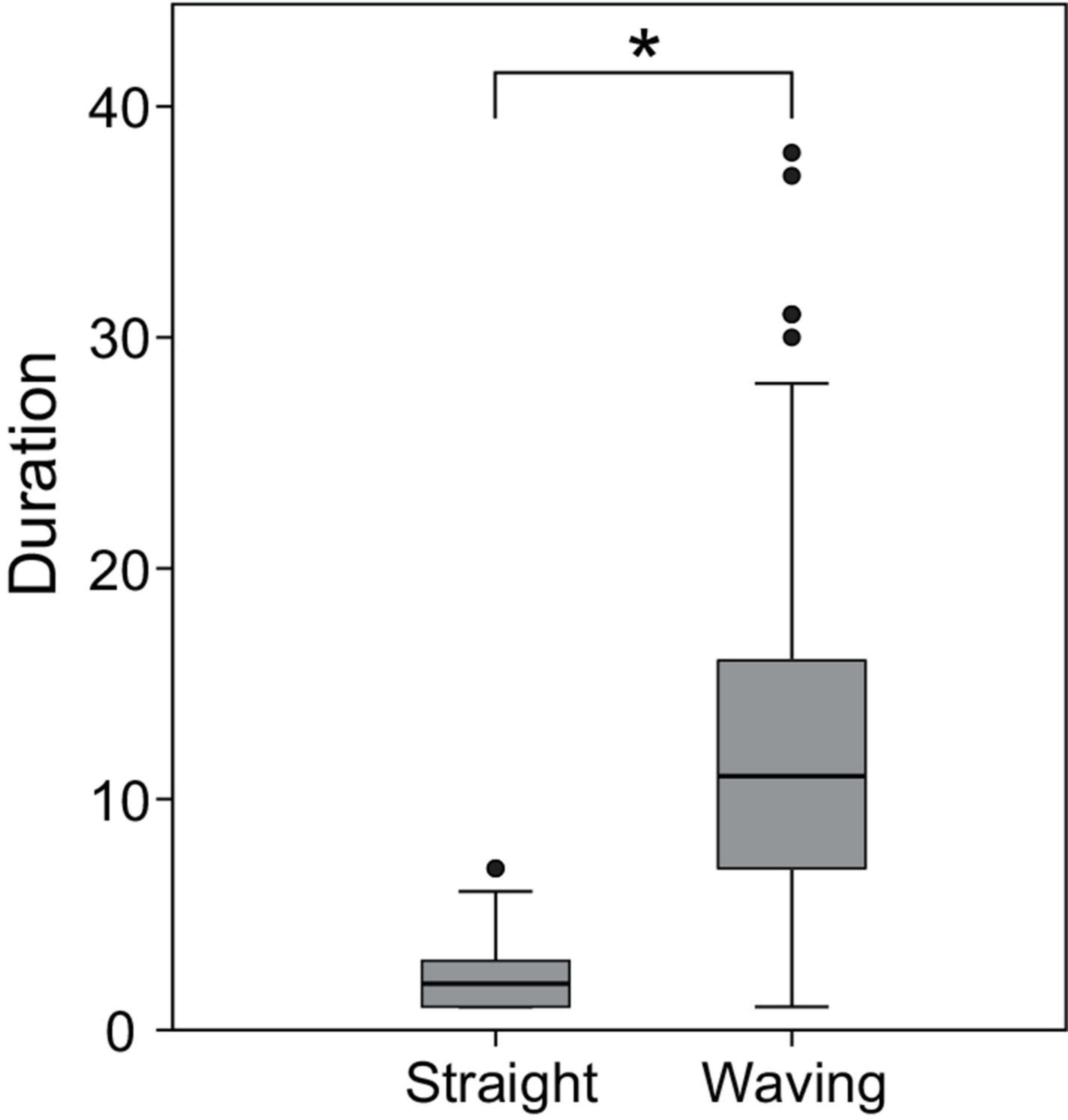
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A. Unconstrained animals

Normalized time

Normalized velocity

B. Constrained animals

Normalized time

Normalized velocity

A

B

Normalized time

Normalized velocity
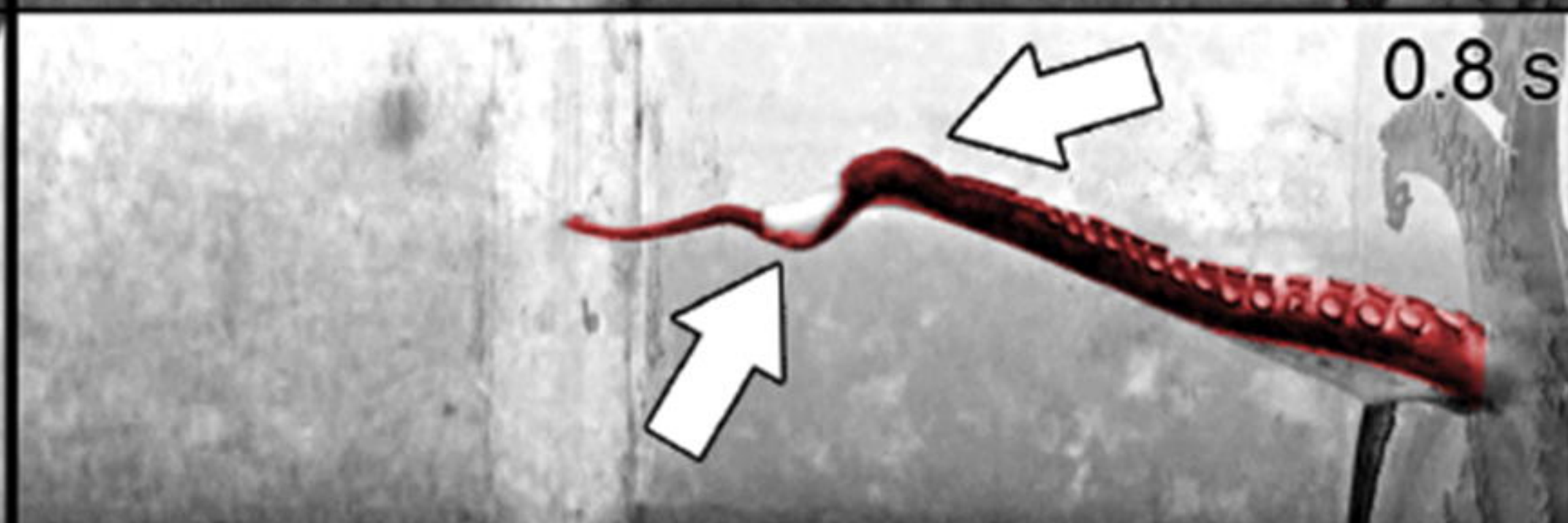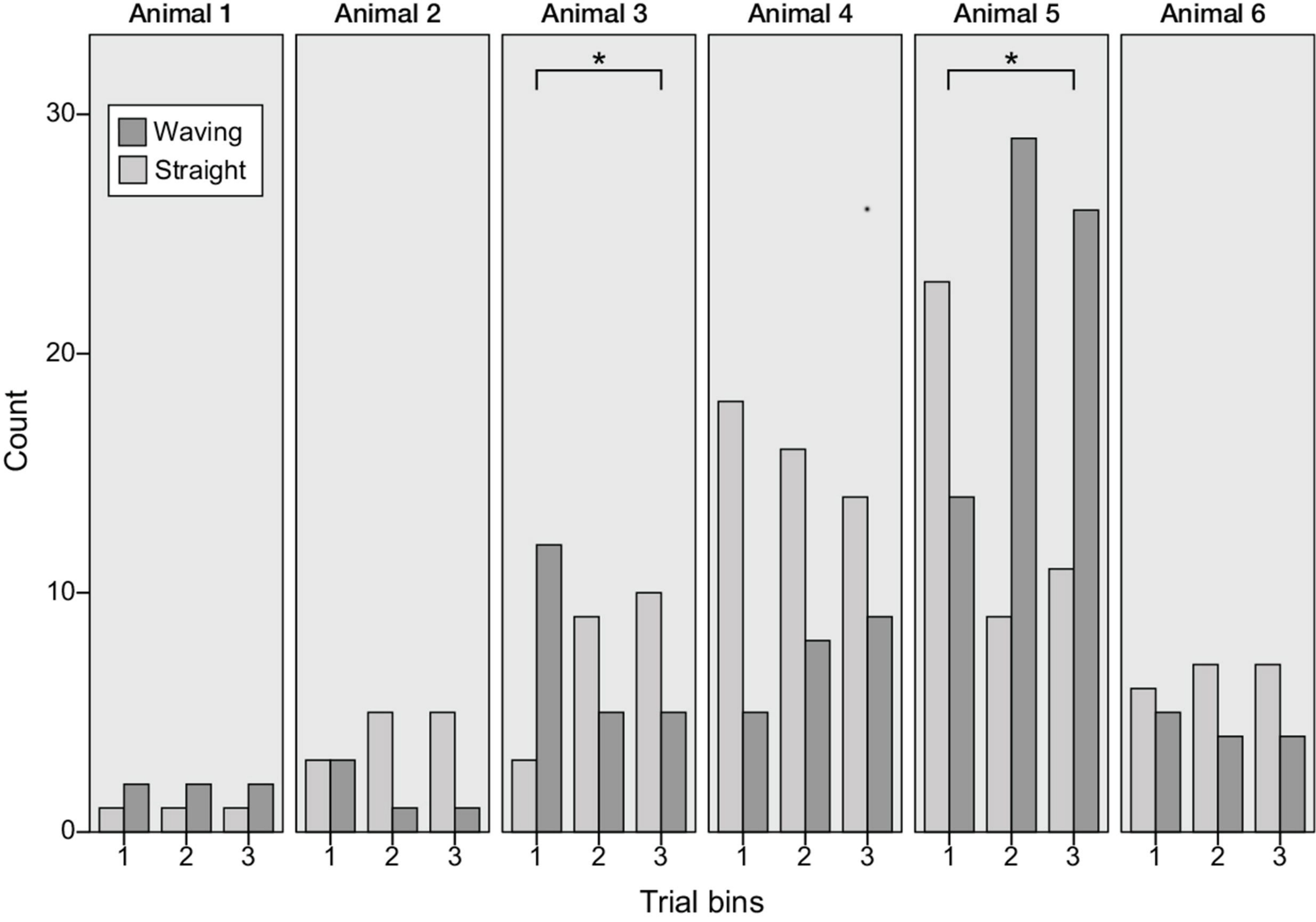
Straight category fetchings

A

B

Normalized time

Normalized velocity
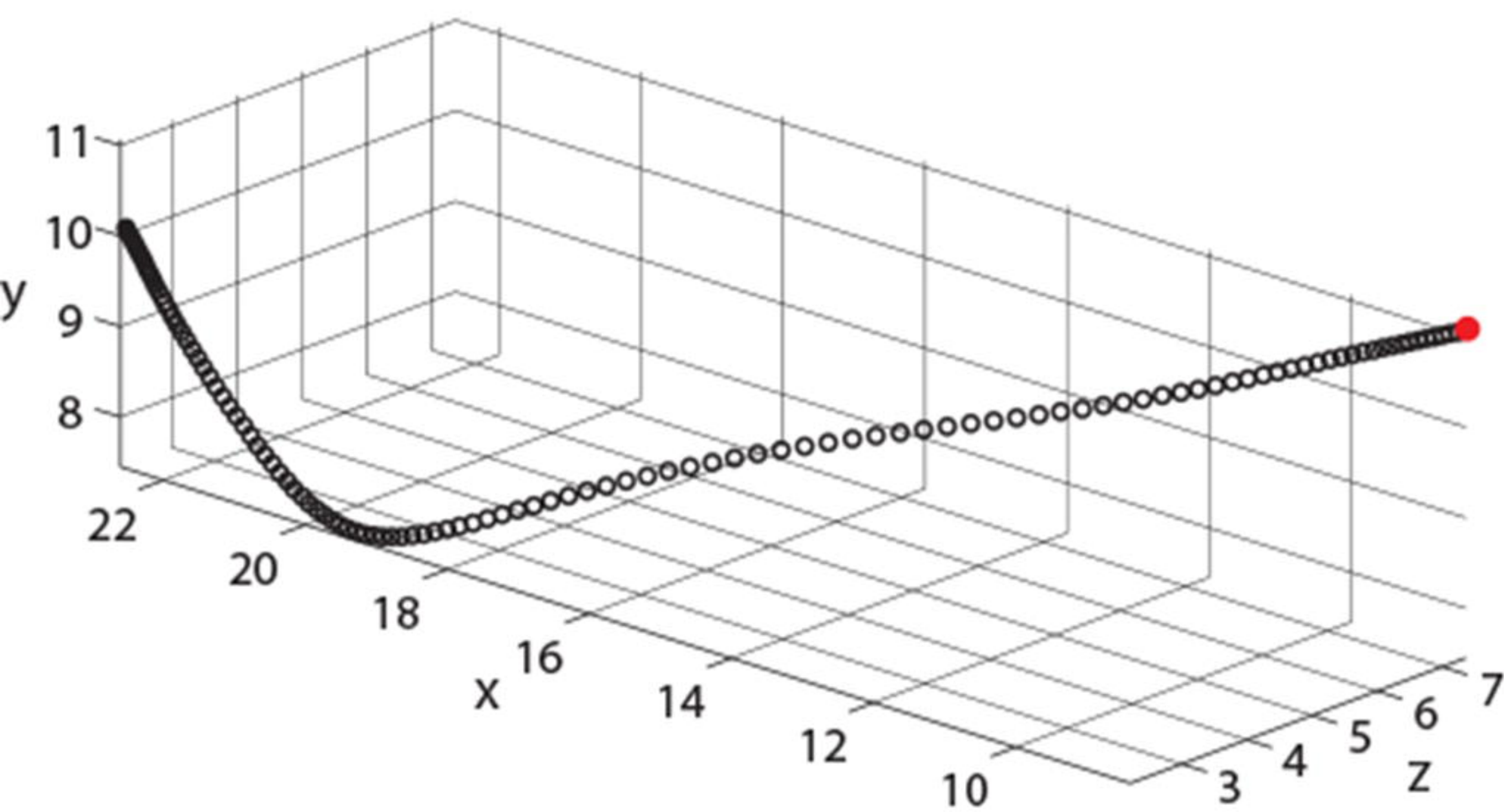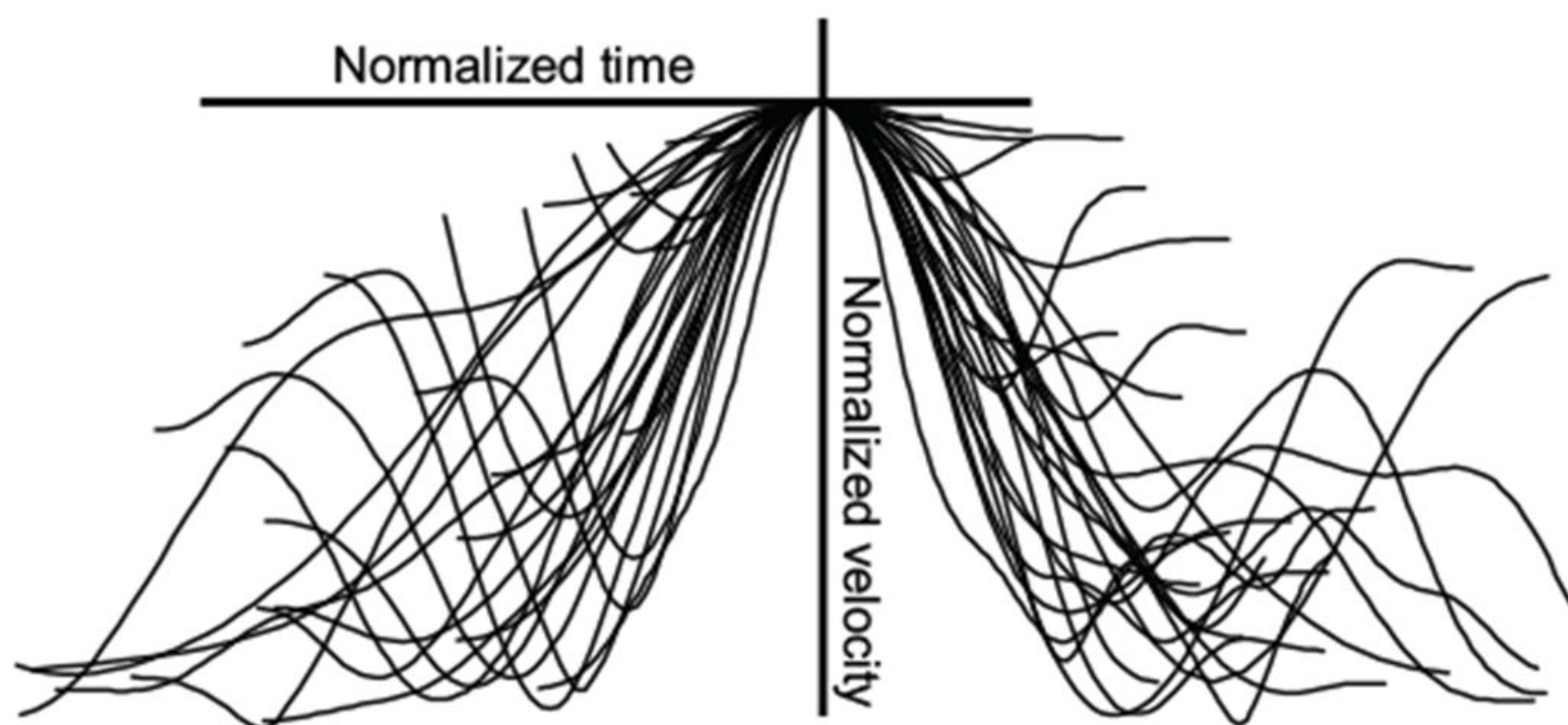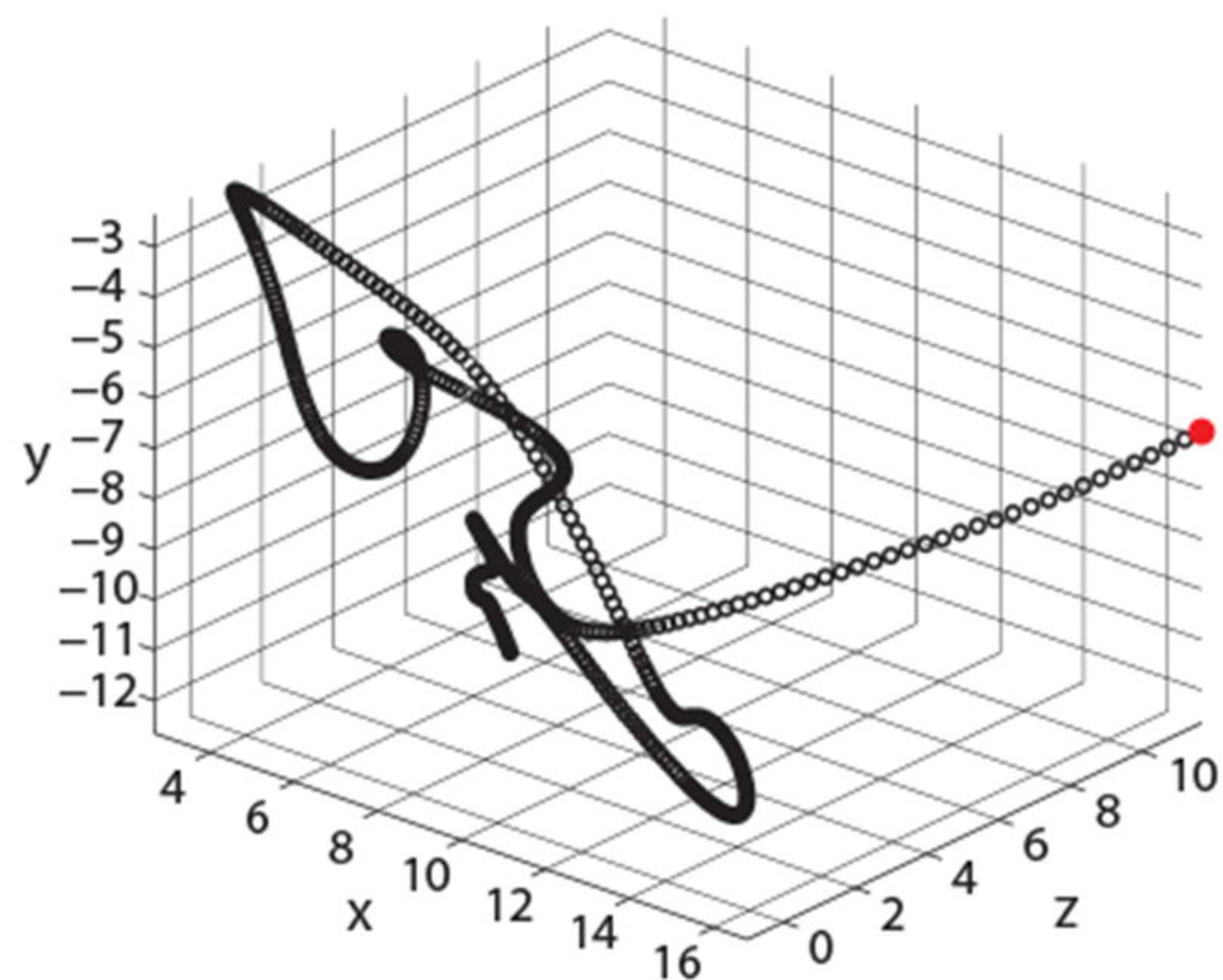
Deflected category fetchings

C

D

Normalized time

Normalized velocity