

Characterizing the sub-second timescale strategies of fighting in zebrafish

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December 11, 2017

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Abstract:

Most animals fight by repeating complex stereotypic behaviors, yet the internal structure of these behaviors has rarely been dissected in detail. We characterized the internal structure of fighting behaviors by developing a machine learning pipeline that measures and classifies the behavior of individual unmarked animals on a sub-second timescale. This allowed us to quantify several previously hidden features of zebrafish fighting strategies. We found strong correlations between the velocity of the attacker and the defender indicating a dynamic matching of approach and avoidance efforts consistent with the cumulative assessment model of aggression. While velocity matching was ubiquitous, the spatial dynamics of attacks showed phase-specific differences. Contest phase attacks were characterized by a paradoxical sideways attraction of the retreating animal towards the attacker suggesting that the defender combines avoidance maneuvers with display maneuvers. Post-resolution attacks lacked display-like features and the the defender was avoidance-focused. From the perspective of the winner, game theory modeling further suggested that highly energetically costly post resolution attacks occurred because the winner was trying to increase its relative dominance

29 over the loser. Overall, the rich structure of zebrafish motor coordination
30 during fighting indicates a greater complexity and layering of strategies than
31 has previously been recognized.

32 **1 Introduction**

33 Animals fight by roaring [1], lunging [2], circling [3], head-waving [4], head-
34 butting [5], biting [6], wrestling [4] and in a myriad of other ways [7]. While
35 we have good theories and measurements about why an animal might start
36 a fight with a fin-display and end the fight with mouth wrestling [8], we have
37 have much less information about what exactly happens during a lunge,
38 a circling display or a directed attack maneuver. Much of this may come
39 down to the problem of measurement. It is comparatively easy to count the
40 number of displays or time the duration of a wrestling bout, it is much harder
41 to accurately measure a multi-dimensional signal like a threat display. We
42 are therefore mostly confined to verbal descriptions of contest behaviors.

43 Yet the accurate measurement of within-behavior limb and body dynam-
44 ics has been a source of rich insight in many other systems. When researchers
45 were able to use high speed cameras to capture fly leg movements before
46 they jumped to dodge a moving stimulus, they uncovered a sophisticated
47 context-sensitive control system in what was previously believed to be a sim-
48 ple ballistic reflex [9]. Likewise, statistical descriptions of escape trajectories
49 have given us convincing experimental evidence of protean behavior- a strat-
50 egy where prey occasionally randomize their movement direction in order to
51 reduce the degree to which their behavior can be predicted [10, 11]. The
52 analysis of peregrine falcon attack trajectories has revealed a precise math-
53 ematical analogy between falcon prey capture and ballistic missile targeting
54 which can only be uncovered through precision measurement [12].

55 The last two examples are particularly relevant for the study of aggression,
56 because they illustrate cases where a complete understanding of strategic be-
57 haviors cannot be obtained unless we measure the dynamics occurring within
58 elementary behaviors. Next we will highlight some outstanding issues in the
59 study aggression which might similarly benefit from modern data capture
60 methods.

61 As a first example, let us consider how much is known about attack ma-
62 neuvers in zebrafish. During contests, zebrafish frequently engage in repeated
63 attacks, where one animal performs a rapid directed movement towards an-
64 other and the other animal sometimes responds with an avoidance/retreat
65 maneuver [6]. What has remained unclear is the quantitative relationship
66 between the attack maneuvers and the avoidance maneuvers. Does every

67 attack induce an avoidance maneuver? Are the locomotor costs of an attack
68 greater or smaller than the locomotor costs of a retreat?

69 One reason why answers to these questions matter concerns the theoret-
70 ical interpretation of zebrafish fighting. Animal conflict is partly structured as
71 a series of assessments of relative strength and different game theory models
72 of assessment postulate a different relationship between individual activity
73 levels and fitness costs. For example, WOA models postulate that individ-
74 ual acts of behavior induce fitness/energy costs only in the producer of the
75 behavior [13] whereas SA [14] and CA [15] models allow the behavior of the
76 producer to influence the fitness costs of the target of the behavior as well.
77 Target fitness costs might occur because the target suffers contact injuries
78 or alternatively, because it needs to perform costly avoidance maneuvers to
79 avoid suffering the injuries. The relevance of the aforementioned factors to
80 the interpretation of zebrafish contests is obvious: if attacks rarely end in
81 contact and the cost of an avoidance maneuver is small compared to the cost
82 of an attack, then a WOA model might potentially be a good description
83 of zebrafish fighting. However, if each attack nearly always induces a costly
84 avoidance maneuver in the target of the attack and in the absence of avoid-
85 ance bodily contact typically occurs, then only the CA and SA model remain
86 viable as descriptions of fighting.

87 A second utility to measuring the fine structure of fights stems from
88 the potential to expand domains in which evolutionary game theory can be
89 tested. As was already mentioned, it has been speculated that predator and
90 prey interactions during escape maneuvers are best characterized as a game
91 where the prey makes unpredictable maneuvers in order to avoid easy capture
92 [10, 11, 16]. Similar games might unfold within the multitude of elementary
93 interactions occurring during a fight. Analyzing games which occur on a fast
94 time-scale might be of interest not only because it provides opportunities to
95 expand the domain where game theory is applied, but also because payoffs
96 obtained in low-level games will determine the payoffs of various strategies
97 for the long time-scale assessment games in which they are embedded. A
98 similar methodology has already shown promise in the analysis of schooling
99 behavior [17].

100 In the last section of our results, we take a first step towards game-
101 theoretical analysis of movement rules with a particular focus on the struc-
102 ture of resolution phase attacks. The literature on game theory and dyadic
103 aggression is rich but appears to be primarily focused on the symmetri-
104 cal/assessment phase of the conflict (see for example Chapter 2 of [18]). In
105 addition to an assessment phase, zebrafish fights also have a structured post-
106 resolution phase, where both the winner and the loser engage in stereotyp-
107 ical behaviors. It has previously been shown that post-assessment behaviors

108 either serve the function of chasing the looser out of the territory or main-
109 taining dominance rank [19, 20, 21]. We show how insight from these studies
110 can be used to formulate a model of zebrafish resolution phase attacks which
111 provides a concise explanation of the main qualitative trends present in our
112 data.

113 Thirdly, analysis of elementary aggressive interactions can shed light on
114 multiple functions of a single behavior. When a boxer holds up his hands, it
115 is with the dual purpose of being ready to both attack and defend. Likewise,
116 a zebrafish attack may be shaped by multiple competing needs. The attack
117 intensity may need to be moderated in order to avoid overcommitment to
118 a single direction of assault which could be exploited by a responsive oppo-
119 nents. An attack might simultaneously carry out the function of damaging
120 an opponent and signaling to it, or the dual functions of the attack may be
121 somewhat separated in time. Without large-scale datasets, it is difficult to
122 experimentally address these subtleties of multi-functionality and variability.

123 In order to measure zebrafish aggressive interactions at a level compat-
124 ible with making progress on solving the above mentioned issues, it was
125 imperative to create a new measurement system. We took inspiration from
126 several pre-existing machine learning tools to create a system which allows
127 for tracking and identifying unmarked animals as well as automatically an-
128 notating their behaviors [22, 23, 24]. The resulting system provides the user
129 with trajectory data containing information about velocities, accelerations
130 and relative positions of the fighting individuals as well as an automated
131 ethogram which identifies the behavior performed by any animals at any
132 given moment. Our set of tools provided us with the data necessary to ex-
133 amine aggressive behavioral interactions at the lowest possible level.

134 2 Methods

135 2.1 Staging of contests

136 The study used 68 male zebrafish of the AB strain approximately 1 year of
137 age. All rooms are ventilated through a centralized HVAC system and are
138 kept at controlled room temperature (25C), 50%–60% humidity. Fish holding
139 rooms are kept under a 14-h light10-h dark cycle with a light intensity of 200
140 300 lux at the water surface. The density of the fish in the tanks was 10
141 fish/L and in a typical cage we had 20-25 animals. Our general feeding
142 protocol consists of two types of live feeds, rotifers and *Artemia nauplii*, and
143 a processed dry feed (Gemma Micro, Skretting, Spain). Depending on the
144 fish age, the feeding frequency varies. In the months prior to experiments,

145 the fish were fed Gemma500 feed and live de-capsulated Artemia once a day.
146 Our study involved staging contests between zebrafish. We adapted a
147 procedure from [6] where a pair of males were removed from their home tanks
148 and kept in visual but not olfactory isolation for a period between 24 to 48
149 hours. In a slight departure from the previous procedure, the fight was staged
150 in an arena which was different from and larger than the arena used for pre-
151 fight isolation, because we wanted to avoid the confounding influence of walls
152 on swimming behavior which occurs too frequently in smaller arenas. The
153 fight was staged in a uniform rectangular arena with dimensions 32-by-24-
154 by-12 cm, slightly rounded corners and water depth of approximately 7 cm.
155 Care was taken to ensure a lack of sharp illumination gradients in the tank so
156 as to facilitate later tracking. Recordings began when the two animals were
157 simultaneously poured from the isolation tank to the fight arena. A typical
158 recording lasted for 1 hour and was continued for another hour in the rare
159 cases where the fight appeared unresolved after 1 hours time. After the fight
160 was terminated, both animals were returned to their home tanks. Video data
161 was acquired at 20 frames per second using MATLAB standard functions.

162 2.2 Tracking

163 Code and trajectory data are available on request:

164 <https://goo.gl/eGCp3q>

165 Aggressive contests in zebrafish pose three challenges. First, fighting is a
166 3D process and the maneuvers are facilitated by deep waters, which induces
167 appearance changes as the depth of the fish varies. Second, fish change their
168 appearance not only due to varying depth but also due to color changes dur-
169 ing the fight. Third, collisions are more frequent during fighting than during
170 schooling. This motivated the use of a hybrid system where a new version
171 of idTracker [22] (idtracker.ai, Romero-Ferrero, Bergomi et. al, in prepa-
172 ration) utilizing deep convolutional networks was used for tracking when
173 the animals were not colliding, because of the greater expressive capacity
174 of learned templates compared to the hand-engineered template of classical
175 idTracker. When the pair of fish collided, a Gaussian mixture model was
176 used to separate the colliding animals (as in [24]) and identity information
177 was propagated into the collisions by using a greedy acceleration minimiza-
178 tion principle along the trajectory with the constraint that identities of both
179 trajectories at the start and end of the collision had to be matched with the
180 predictions from idTracker (see [22] for an analogous algorithm for collision
181 resolution).

182 The greedy acceleration minimization was implemented step by step. At
183 each time step, two candidate coordinates (each representing the center of

184 mass of a fish with unknown identity) originating from the GMM algorithm
185 needed to be identified. We considered the identities of the coordinates at
186 the previous two time steps to be fixed and then we calculated the absolute
187 net linear acceleration along both trajectories for the two possible identity
188 assignments. Whichever assignment resulted in the lower total acceleration
189 was used for final identification and the cycle was repeated again and again
190 until end of collision. During collisions, we had an identification accuracy of
191 98%.

192 **2.3 Automated behavior classification and analysis**

193 To improve data efficiency, we used a preprocessing method which was de-
194 signed to reduce translational and rotational variance. For our four vectors
195 at each time point, we transformed them into a new coordinate system where
196 the zero was located at the joint center of mass of the pair of fish at time
197 $t - K$. The x axis was aligned with a vector which pointed from fish 1 towards
198 fish 2 at time $t - K$. All coordinates of the four vectors were converted into
199 this coordinate system. After the preprocessing, the four processed vectors
200 were then concatenated into a single vector and passed as input to the first
201 layer of a standard multilayer perceptron with a ReLu hidden layer activation
202 function, a cross entropy loss function. Using this preprocessing and a fairly
203 small amount of annotated data (small as compared to the total corpus of
204 data analyzed), we were able to train a perceptron with two hidden layers of
205 size 250 neurons to have a test set accuracy of 95%.

206 All further analysis was done using custom-written MATLAB code. The
207 forcemap technique was adapted from [25]. In order to avoid potential influ-
208 ences from walls, the symmetric phase forcemaps were analyzed only when
209 both fish were further than 5 *cm* away from the nearest wall. During the
210 asymmetric phase, the fish spent most of their time swimming very close to
211 the wall, but we excluded the influence of corners on turning by removing all
212 data when fish were closer than 5 *cm* to the nearest corner.

213 **3 Results**

214 We began our study by staging 34 contests between adult male zebrafish
215 (see Methods for details of contest staging). In order to analyze the fine
216 details of aggressive behavior in fish, we augmented the software idTracker
217 [22] (which allows tracking and identification of unmarked animals) with
218 a custom-written collision resolution system that enabled us to resolve the
219 identities of the animals while they were colliding as well (see methods for

220 details on this and all other machine learning procedures). The output of
221 the tracking system was a time series of trajectories for both contestants
222 (sampling rate 50 ms, 20 Hz). We annotated a small fraction of our video
223 data to indicate when attacks were taking place. These annotations were
224 in turn used to train a neural network which could detect the presence of
225 attacks from trajectory data with 95% reliability. Our behavior classification
226 system differed from similar systems [23] through the use of end-to-end deep
227 learning on trajectory data, which allowed us to eliminate an intermediate
228 feature engineering step. By combining several augmented and improved
229 machine learning tools into a common pipeline, we thus created a machine
230 learning software that automatically provided information about the move-
231 ment, behavior and identity of each animal on a subsecond timescale (Figure
232 1).

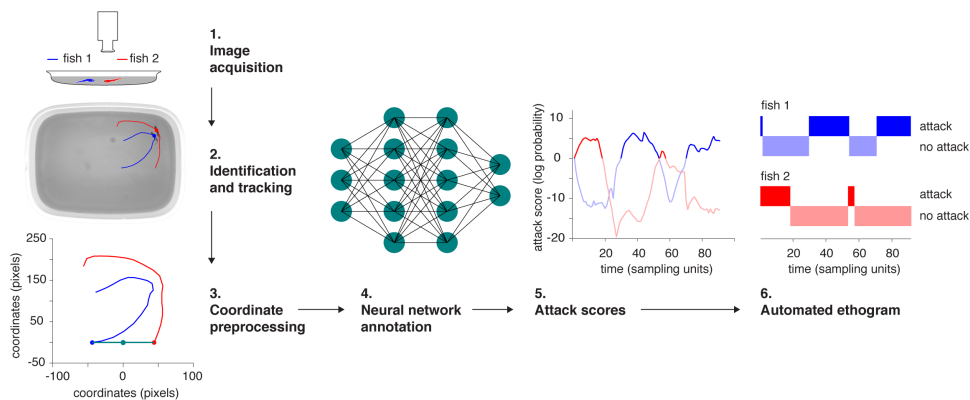


Figure 1: **The computer vision pipeline.** 1: the raw video. 2: unmarked animals after identification with idTracker and a short span of the trajectory of each animal overlaid. 3: preprocessing of a local chunk of trajectory for neural network analysis. 4: schematic of the neural network classifier which was trained to mimic human annotations. 5: a time series of attack scores for two animals as produced by the neural network classifier. High attack score values indicate a high internal confidence of the network that an attack is taking place. 6: an automatic ethogram calculated by thresholding the attack score.

233 **3.1 Analysis of activity correlations and assessment** 234 **models**

235 As mentioned in the introduction, one of the focal points of our study was to
236 achieve more precise measurements of locomotor activity in order to assess
237 the relative costs of attacks and retreats. A necessary preliminary to study-
238 ing activity correlations was to first characterize the large-scale patterns of
239 aggressive behavior in our dataset. We found clear signs of aggression in
240 27 of the 34 staged contests. When we examined the attack rates of our
241 contestants during individual contests, there was evidence that fights con-
242 sisted of two distinct types of phases (Figure 2A, see also supplementary
243 video S1). During what we called the symmetric phase (Figure 2A, 24-28
244 minutes), both individuals engaged in mutual attack behavior. During the
245 asymmetric phase, mainly one individual performed attack behaviors (Fig-
246 ure 2a, 34-60 minutes). When a symmetric phase was present (N=15 fights),
247 the most common pattern (N=8 of 15 fights) was for there to be a pre-fight
248 phase with very few attacks (Figure 2A 0-22 minutes), followed by a sym-
249 metric phase, which was in turn followed by an asymmetric phase where
250 only one individual engaged in attacks. It is thus likely that the symmetric
251 phase is similar to the contest phase described in many other model systems
252 of aggression, whereas our asymmetric phase resembles the resolution phase
253 [21, 18].

254 However, not all fights followed the aforementioned progression. In some
255 cases, the symmetric phase was not followed by an asymmetric phase and in
256 other cases, an asymmetric phase both preceded and followed the symmetric
257 phase. Interestingly, the individual who was dominant before the symmetric
258 phase was not necessarily the same one who engaged in attacks after the
259 symmetric phase (see Figure S1 for example plots of fight progression in the
260 more rare cases). In 12 fights, no symmetric phase was present and the only
261 phase present was the asymmetric one. In the next sections, our analysis will
262 focus on 14 of the 15 fights where the symmetric phase was present unless we
263 state otherwise (with 1 fight excluded from analysis since its long duration
264 posed a threat to animal welfare and had to be prematurely stopped).

265 We used the outputs of our machine learning pipeline to analyze coarse
266 kinematic parameters of attacks, namely velocity and acceleration. We fo-
267 cused on these variables first since they may be regarded as an approximate
268 individual level measure of energy expenditure [26]. Attacks in both the
269 symmetric and asymmetric phase were associated with high velocities com-
270 pared to the pre-fight phase. Pre-fight, the fish had an average speed of
271 5.3 ± 0.84 cm/s (N=13, mean \pm standard deviation), which during the sym-
272 metric phase rose to 10.3 ± 1.9 cm/s (N=14) for the attacker and 10.9 ± 1.4

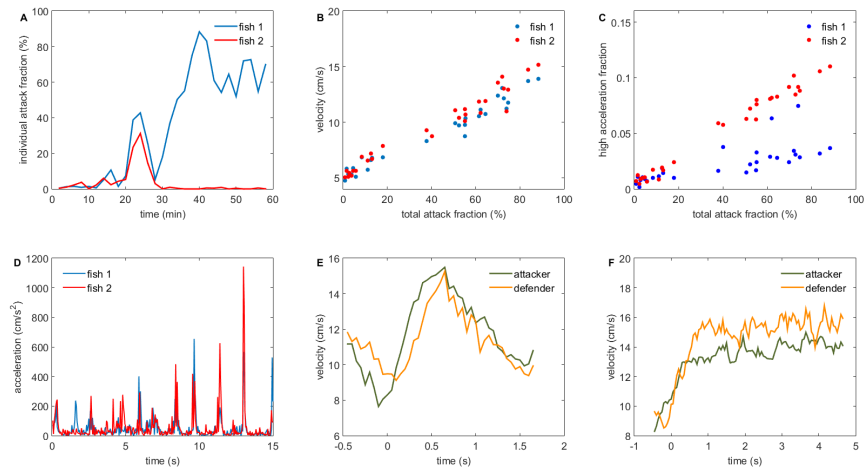


Figure 2: A kinematic characterization of a fight. A: The fraction of an animal’s time budget used in attacks (the individual attack fraction) over the course of the fight (blue and red curves mark the two different individuals here and elsewhere). Analysis is conducted in non-overlapping 2 minute time windows. Minutes 24-28 correspond to the symmetric phase. The asymmetric phase approximately spans the time from 34-60 minutes. B: correlation between total attack fraction (sum of individual attack fractions) and velocity. C: very high intensity acceleration bouts ($a > 128 \text{ cm/s}^2$) occur mostly during attacks. D: a time series of acceleration during the symmetric phase of the fight depict the occurrence of sudden acceleration bouts. E: the velocity waveforms of the attacker (green) and defender (orange) during an average attack ($N=114$) in the symmetric phase. Attacks begin at time 0. F: same as before but for the asymmetric phase ($N=116$).

273 cm/s ($N=14$) for the defender. We note that here and elsewhere, the roles of
 274 attacker and defender were not fixed during the analysis of a fight but were
 275 calculated dynamically for each individual at each moment in time based on
 276 the outputs of our classifier. Fish swimming speed rose further during the
 277 asymmetric phase where the attacker attacked with speed $13.5 \pm 1.6 \text{ cm/s}$
 278 ($N=11$) and the defender swam with velocity $14.0 \pm 1.6 \text{ cm/s}$ ($N=11$). As a
 279 further check of our analysis, we binned data from each fight into consecu-
 280 tive non-overlapping 2 minute long segments and calculated the average speed
 281 and the total percentage of time that attacks were occurring (the total attack
 282 fraction) during each time bin. There is a strong linear correlation between
 283 average movement speed and attack percentage (Figure 2B, $r = 0.90 \pm 0.06$,
 284 $N=28$ individuals).

285 Fighting is associated not only with an increase in velocity but also with
286 the occurrence of bursts of high acceleration (Figure 2D). As with speed,
287 there was a strong correlation between the total attack fraction and the total
288 fraction of time each animal spent performing acceleration bursts (Figure
289 2C, $r = 0.88 \pm 0.15$, $N=28$).

290 From our analysis, it becomes clear that an attack induces a strong en-
291 ergetic cost not only for the attacker but also for the defender. This point
292 is further reinforced if we time-align individual attacks and calculate the av-
293 erage velocity waveform for both the attacker and the defender during both
294 the symmetric (Figure 2E) and the asymmetric (Figure 2F) phase. From
295 Figure 2E,F it is apparent how attacks begin with an increase in the velocity
296 of both the attacker and the defender. In fact, the locomotor costs for the
297 defender are on average even higher than those for the attacker as defenders
298 swim with a higher average speed in 20 out of the 25 conflict phases analyzed
299 ($p=0.004$, two-tailed binomial test). These findings are compatible with the
300 assumptions of the CA and SA models and violate the assumptions of WOA
301 models.

302 As a control, we compared the inferences derived from our method with
303 more established methods of analysis, which recommend disambiguating as-
304 sessment strategies by studying the covariation between resource holding po-
305 tential (fighting ability) and the duration of the contest phase (the symmetric
306 phase in our terminology). The first step involved finding an indicator of re-
307 source holding potential. In our dataset, size was a statistically significant
308 indicator of resource holding potential (RHP) as the larger animal ended up
309 as the dominant individual in 20 out of 25 fights where we could identify a
310 clear winner ($p=0.002$, one-tailed binomial test, analysis includes fights both
311 with and without a symmetric phase). In fights where a symmetric phase was
312 present, there was a statistically significant trend for large size differences to
313 be associated with longer fights ($r=-0.47$, $p=0.045$, one-tailed t-test for Pear-
314 son correlation coefficient). A linear regression analysis of the effects of the
315 sizes of both contestants yielded a model where the larger individual's size
316 had a negative effect on fight duration and the smaller individual size had a
317 weaker but positive effect of fight duration, although the latter value was not
318 statistically significantly different from zero ($c_{large} = -0.14$, $c_{small} = 0.04$,
319 $p_{large} = 0.02$, $p_{small} = 0.52$).

320 A negative relationship between body mass difference and fight time is
321 expected in all three models (WOA, CAM, SAM) [27]. A negative effect of
322 larger individual body size on fight duration is incompatible with a WOA
323 model of contest behavior. Our result, where the size of the larger individual
324 has a stronger effect on fight times than the body size of the smaller individual
325 is inconsistent with a pure sequential assessment game model, but as we show

326 in a mathematical addendum, it is in principle consistent with the CAM
327 model (see supplement, Mathematical analysis of the cumulative assessment
328 model).

329 Overall, our analysis of resource holding potential and body size cor-
330 relations yielded results which are consistent with the analysis of velocity
331 correlations and thus indicates that our method might be of use as a substi-
332 tute where the standard analysis is inapplicable or yields ambiguous results.
333 A particularly interesting use case for our method might occur when fight
334 times are found to be dependent only on the resource holding potential of
335 the loser. Such a result has sometimes been interpreted as providing un-
336 unequivocal support for WOA model [27], but other authors have held that
337 this result would be compatible with CAM as well [4]. Our supplementary
338 modeling agrees with the conclusions of [4] and thus motivates the need for
339 further testing when loser-only fight time scaling relationships occur. Since
340 our measurement methods allow discriminating between WOA and CAM,
341 they may prove to be valuable for those further tests.

342 In addition to size, another weak predictor of fight outcome was color. We
343 found that zebrafish exhibited a transient darkening which occurred specifi-
344 cally during the symmetrical contest phase (see Figure S2 and supplementary
345 methods). On average, the symmetric fight phase was accompanied by an
346 $8\% \pm 4\%$ (N=28) darkening of appearance in both fighters and this transient
347 largely disappeared irrespective of whether the fight ended with asymmetric
348 chasing or not. The eventual loser tended to darken more than the win-
349 ner. In 9 out of 10 fights, the eventual loser had a higher intensity change
350 relative to pre-fight intensity than the eventual winner ($p=0.02$, 2-tailed bi-
351 nomial test). However, color change was a weak predictor of how the fight
352 ended, since unequal changes in color were also associated with fights that
353 ended without a clear way to determine the winner because chasing behavior
354 was absent.

355 **3.2 Analysis of movement rules**

356 Zebrafish fight maneuvers have a complicated spatio-temporal structure, which
357 may potentially contain useful information about strategic incentives. In or-
358 der to analyze this structure, we utilized the tool of forcemaps which was origi-
359 nally developed to study cooperative movement coordination during school-
360 ing [28, 25, 17]. Forcemaps are useful for the study of aggression because they
361 allow an easy visualization of the way fish influence each others movement
362 during social interactions.

363 The central idea is to characterize the kinematic movements of a focal
364 individual from its point of view. As a brief description of the procedure (see

365 Methods for full details), during each moment in time, we transformed our
366 trajectory data into a coordinate system where a focal fish is located at the
367 center of the coordinate system and the y axis is aligned to the instantaneous
368 velocity of the focal fish (see panel 3A,E and panel 4A,E; direct attention
369 towards the orange and green dots). We then measured the distribution
370 of locations for the partner of the focal fish in this new focal fish coordinate
371 frame (see for example Figure 3B). We also calculated how the location of the
372 partner fish influenced the tendency of the focal fish to turn and to speed up.
373 As was the case with the analysis of velocity correlations, we separated our
374 data into four categories depending on whether the focal fish was attacking
375 or defending and whether the current phase of the fight was symmetric or
376 asymmetric (in Figures 3 and 4 which follow, the colored fish on the inset
377 images A,E always illustrates which fish is the focal fish for a given row of
378 the figure).

379 Previously, [6] had described zebrafish attacks as locomotion maneuvers
380 where the attacker orients its body towards the defender and then swims
381 rapidly towards it. The defender typically responds by swimming away from
382 the attacker in a maneuver named retreat. Additionally, the attacker some-
383 times veers to one side or the other of the defender in order to deliver bites
384 to the sides of the defender. Based on this description, we had four base-
385 line expectations. First, the attacker is expected to be located behind the
386 defender most of the time. Second, the attacker is expected to exhibit an
387 acceleration response towards the defender if the defender is in front of the
388 attacker. Third, the defender is expected to exhibit a repulsive speeding re-
389 sponse when the attacker is behind it (the running away response). Fourth,
390 when the attacker is located to one side (e.g. the right) of the defender, the
391 defender was expected to turn towards the other side e.g the left) in order
392 to dodge potential bites. To our surprise, all the hypothesis except the first
393 turned out to be partly incorrect to varying degrees.

394 We begin by considering the relative positions of the defender and the
395 attacker. The maps in Figure 3B,F depict the distribution of the locations
396 of the attacker relative to the defender during attacks in the symmetric (3B)
397 and asymmetric phase (3F). From the maps it is clear that as was antici-
398 pated, the attacker is typically located behind the defender. However, an
399 interesting elaboration on the baseline hypothesis was the finding of different
400 appearances of the maps between the two phases. During the symmetric
401 phase, the attacker is located about half a body length behind the defender
402 and is positioned to the left or to the right of the defender rather than staying
403 directly behind it (Figure 3B). In contrast, during asymmetric phase attacks
404 the attacker is typically located a whole body length behind the defender
405 (Figure 3F). Since a sideways location of the attacker was expected to be

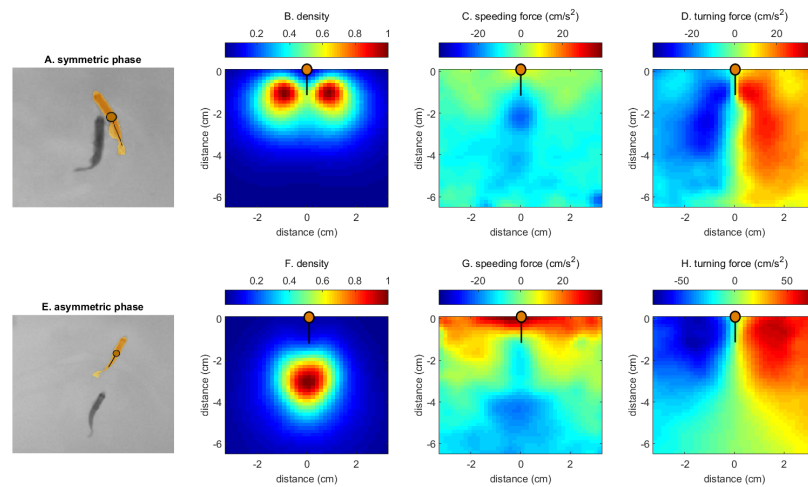


Figure 3: **Forcemaps of the defender in the symmetric (top row) and asymmetric (bottom row) phase.** Average forcemaps (N=14 fights, 230 000 time-points). The top inset image shows a typical configuration of the two fish during the symmetric phase (same for asymmetric phase at the bottom). In this figure, the focal fish is always located at the top middle of the map (orange dot, point 0,0) and its velocity vector is oriented up. A: a typical configuration of the two fish during the symmetric phase. B: a probability density map of the position of the attacker relative to the defender during the symmetric phase. Note that the negative numbers in the distance axis indicate that the attacker is behind the defender. C: the speeding force as a function of the relative location the attacker during the symmetric phase. Red color signals speeding up, blue color signals slowing down. D: the turning behavior of the defender as a function of the relative location of the attacker during the symmetric phase. Red colors signify turning to the right, blue colors signal turning to the left. E: a typical configuration of the two fish during the asymmetric phase. F-H: same as B-D for the asymmetric phase.

406 associated with attempts of biting, the phase differences initially suggested
407 a greater motivation on the side of the attacker towards delivering bites in
408 the symmetric phase. While this view is likely to be partly correct, we will
409 explore a further alternative explanation below.

410 Focusing on the speeding responses of the attacker next, we see that our
411 initial expectation of seeing acceleration responses was again partly fulfilled.
412 As can be seen in Figure 4C,G, if the defender is located far in front of the
413 attacker, the attacker does indeed have a tendency to accelerate towards the
414 defender as if it was attracted to the defender and was trying to chase it (the

415 red and yellow areas at the top of the maps in Figure 4C,G). However, the
416 expectation of pure attraction was violated at close range by the presence of
417 repulsion zones (blue areas at the bottom of Figure 4C,G). If the attacker
418 reached close to the defender, there was a tendency for the attacker to de-
419 celerate rather than accelerate. This deceleration response was present even
420 if we removed periods of collision from the analysis (see figure S3C bottom
421 panel). Therefore, the slowing down appeared to be a deliberate response by
422 the attacker and not the consequence of some direct physical interaction like
423 contact-driven repulsion.

424 Overall the speeding map of the attacker was consistent with a strategy
425 where the attacker tries to maintain a constant distance from the defender
426 by speeding towards the defender if the defender was far and by slowing
427 down and letting the defender escape if the defender was too close. This
428 finding was at odds with our initial expectation that the primary goal of the
429 attacks was to create bodily contact which would enable delivery of bites.
430 However, we found evidence for such a distance maintaining strategy on the
431 part of the defender was well. The speeding map of the defender in both
432 phases showed acceleration responses (running away) when the attacker was
433 too close (Figure 3C,G) and deceleration responses (permitting approach)
434 when the attacker was far.

435 When we examined the turning maps of the attacker, it gave us further
436 support for the idea that the attacker is using a distance maintaining strategy
437 during the symmetric phase. As can be seen in Figure 4D, if the defender
438 was far away, the attacker exhibited a turning response toward the defender.
439 However, at close range, the turning response once again changed to a repul-
440 sive response (notice the flipped polarity at the bottom of the turning map
441 when compared with the top in Figure 4D).

442 Examining the turning map of the attacker during the symmetric phase
443 gave evidence of a more complex pattern than a simple distance-maintaining
444 strategy on the part of the defender. We remind the reader of our initial
445 expectation, which was for the defender to turn to the opposite side from the
446 location of the attacker as an avoidance response. What we found was the
447 exact opposite. If the attacker was to the left of the defender, the defender
448 turned to the left towards the attacker.

449 The above response by the defender probably contributed to the stable
450 maintenance of the T-like configuration (Figure 3A) which was often evident
451 during the symmetric phase. Our initial hypothesis attributed the generation
452 of the T configuration to efforts by the attacker to swim to this position
453 so he could deliver biting attacks to the vulnerable sides of his opponent.
454 Examination of social forces revealed the opposite was true. The defender
455 appears to actively contribute to the maintenance of the T configuration by

456 exhibiting a statistical tendency to turn towards the attacker thus exposing
457 the sides of its body even further. Contact appears to be avoided because
458 of a distance-maintaining strategy by the attacker instead. We emphasize
459 again that this effect is not the result of physical contact forces because the
460 maps have the same qualitative features even if we exclude from analysis the
461 periods where the bodies of the two fish are in physical contact (see Figure
462 S3).

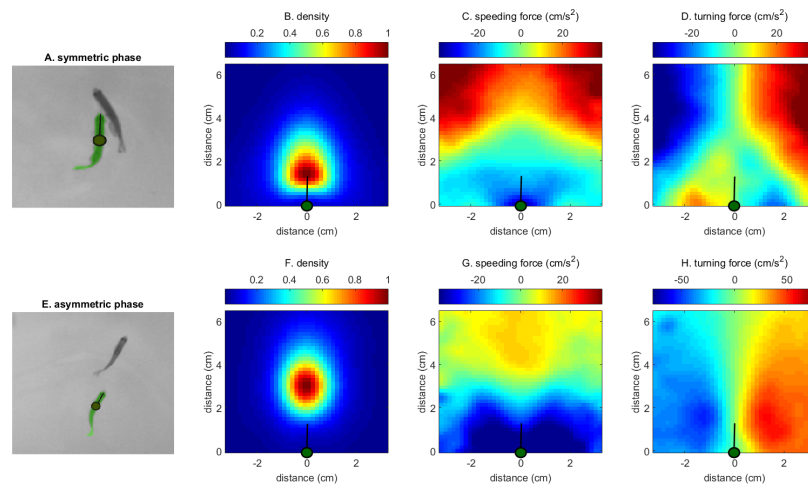


Figure 4: **Forcemaps of the attacker in the symmetric (top) and asymmetric (bottom) phase.** Average forcemaps (N=14 fights, 140 000 time-points). The focal fish for each row is marked in color on an inset image (A,E). On these forcemaps, the focal fish is always located at the bottom middle of the map (marked as a circle with a tail on the maps) and its velocity vector is oriented up. A: a typical configuration of the two fish during the symmetric phase. B: a probability density map of the position of the defender relative to the attacker during the symmetric phase. The positive numbers on the distance axis indicate that the defender is in front of the attacker. C: the speeding force as a function of the relative location the defender during the symmetric phase. Red color signals speeding up, blue color signals slowing down. D: the turning behavior of the attacker as a function of the relative location of the defender during the symmetric phase. Red colors signify turning to the right, blue colors signal turning to the left. E: a typical configuration of the two fish during the asymmetric phase. F-H: same as B-D for the asymmetric phase.

463 We conclude that during symmetric phase attacks, at close range there is
464 a paradoxical tendency for the defender to turn towards the attacker and for

465 the attacker to avoid turning towards the body of the defender. Although we
466 do occasionally observe contact and biting attacks between the contestants,
467 the statistically typical behavior is towards mutual short-range avoidance.

468 The strongly peaked nature of the position histogram (Figure 3B) pro-
469 vides quantitative confirmation of the persistent nature of the T-like config-
470 uration. The persistence of the configuration in time in conjunction with the
471 aforementioned evidence of repulsive interactions when the two fish are in the
472 T-like configuration further supports our description of the T-configuration
473 to be a metastable state. Such evidence also speaks against our initial hy-
474 pothesis, which saw the T-like configuration as a non-persistent state arising
475 either as a preamble to biting attacks or as a result of counter-maneuvers de-
476 signed to avoid the bites. The balance of evidence seems to indicate that the
477 T-configuration during symmetric phase attacks may instead be a ritualistic
478 configuration which is maintained by mutual efforts and may thus function
479 partly as a mutual display.

480 Crucially and consistently with the display hypothesis, the T configu-
481 ration did not appear during post resolution attacks- presumably because
482 display behaviors are superfluous after the winner has been resolved. As can
483 be seen from Figure 3E,F, the typical configuration during post resolution
484 attacks had the attacker located precisely behind the defender and the de-
485 fender running away from the attacker in a straight line. This pattern is
486 maintained due to the mutual presence of a distance maintaining strategy
487 in the speeding maps (see above). Furthermore, if we look at the turning
488 response of the defender in the region where the attacker is most likely to
489 be located, we see a green zone of neutrality (Figure 3H, green triangle-like
490 area at the bottom of the map) rather than an attractive turning response
491 as was seen in the symmetric phase. The data therefore supports a notion
492 where post-resolution decision maps help the defender simply to avoid the
493 attacker rather than engaging in a more complex strategy.

494 One final feature of the forcemaps is worth noting. The maps can often be
495 reliably calculated from data gathered only during individual fights. These
496 individual maps have a structure that is qualitatively very similar to the plots
497 we show in the main paper, where we pooled data across all 14 conflicts which
498 exhibited a symmetric phase (see Figure S4,S5). These movement maps thus
499 appear to be a very reliable feature of zebrafish aggression.

500 In addition to detailed analysis of attack bouts, we also found evidence
501 for a heretofore undocumented type of aggressive maneuver which we termed
502 the splash (Figure 5 top panels). We named the behavior splash after the
503 characteristic wave-like ripple pattern which occurred on the water surface
504 after the maneuver was performed. The splash behavior typically occurred as
505 one zebrafish approached another. As the two zebrafish made contact (Figure

506 5B), one or both of them responded with a sudden acceleration maneuver
507 (Figure 5A) which resulted in the orientations of the two fish being completely
508 reversed and the two fish being propelled apart by a distance of a few body
509 lengths or more (Figure 5C). Typically, a 180 degree change in orientation
510 (Figure 5D) was completed in less than 50 ms. We believe the splash may be
511 a crucial behavior which helps stabilize the previously mentioned display-like
512 attacks and we will comment more on this hypothesis in the discussion.

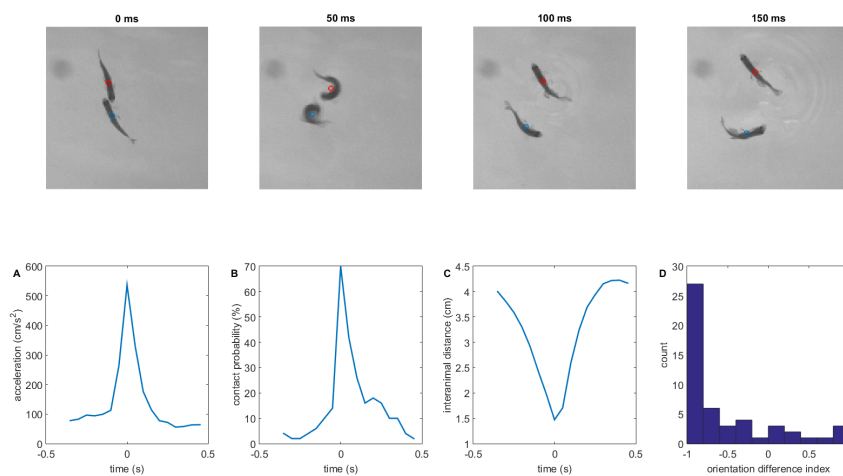


Figure 5: **The splash behavior.** Top panels: a time-lapse series of 4 consecutive frames (sampled 50 ms apart in time) during an example splash behavior. Bottom panels: A: the average acceleration of an individual during a splash. The splash takes place at time 0. B: The probability of contact during a splash. C: The average time evolution of inter-animal distance during a splash. D: A histogram of the orientation change index during 50 acts of splash. An index of -1 corresponds to a 180 degree change in orientation, an index of 1 corresponds to orientation being unchanged (see methods for details). For all plots, $N=50$ splash behaviors. Due to their short duration and comparatively rare occurrence, the splash behaviors were found by manual annotation.

513 3.3 Modeling of the asymmetric phase

514 We were motivated to seek a theoretical treatment of the post-conflict phase
515 by the observation that both the winner and the loser engage in a contact-
516 free but high-velocity chases, which are costly for both the winner and the

517 loser. Why does the winner use a strategy which results in a waste en-
518 ergy on attacks even after it has established its dominance in the symmetric
519 phase? Based on previous studies (see [19, 20, 21] as well as introduction) we
520 hypothesized that the winner implements a strategy which simultaneously
521 damages the loser without risking the possible loss of dominance.

522 We can therefore think of the post-resolution fight as a zero-sum game,
523 where the reward of the winner is $r_w = C_l - C_w$ and the reward of the loser
524 is $r_l = C_w - C_l$ (C_w and C_l designate the costs incurred by the loser and the
525 winner respectively). What are the possible ways that two fish can impose
526 costs on one another? Zebrafish incur costs either through rapid swimming
527 or by receiving bites from the opponent. During the post-resolution phase,
528 the dominant engages in rapid swimming with an approximately constant
529 velocity (Figure 2F) while staying a constant distance away from the sub-
530 ordinate (Figure 3F). Our analysis must explain why the dominant never
531 accelerates enough to touch and deliver bites to the opponent, which would
532 certainly help to selectively reduce subordinate fitness.

533 In order to maintain a stable velocity v , the winner fish must generate a
534 force $F(v)$ which carries a cost $C(F)$. If the loser also swims with velocity v ,
535 it will also incur a cost $C(F)$. If the winner engages in biting, it will deliver
536 to the loser an additional cost C_b . However, it is reasonable to expect that
537 the opportunity to deliver bites at velocity v will not come without a cost to
538 the attacker as well. It must produce extra force in order to generate some
539 pressure between his own mouth and the body of the loser. In addition,
540 extra energy may be needed for moving the jaws and potentially suffering a
541 less streamlined posture because of the bending needed to deliver the bites.
542 The extra force needed δF will induce a greater cost of $C(F + \delta F)$, while the
543 loser incurs a cost of only $C(F)$.

544 For real fish, the functions $F(v)$ and $C(F)$ are obviously not completely
545 generic. $F(v)$ is monotonically increasing, because higher velocities require
546 higher forces in order to overcome increased drag. The function $C(F)$ is likely
547 to be not only monotonically increasing, but also convex, since maintaining
548 higher forces requires recruitment of more energetically inefficient muscle
549 groups [29]. For convex functions, $\Delta C = C(F + \delta F) - C(F)$ is an increasing
550 function of F as well. At equilibrium, it must be the case that the winner
551 cannot increase his reward by switching from steady chasing at velocity v_e
552 and force $F(v_e)$ to a biting attack at velocity v_e and force $F + \delta F$. Therefore,
553 at equilibrium, $\Delta C(F) = C_b$. Since $\Delta C(F)$ is an increasing function of F , it
554 is a mathematical inevitability that there exists a value of F high enough for
555 this to condition to be true. Another solution to the model involves limits
556 on the range of possible values of F . If the value F has a biological maximum
557 (F_{max}) which is smaller than the value of F where biting costs become equal

558 to attack costs, then the equilibrium value v_{eq} is given by $F(v_{eq}) = F_{max} - \delta F$.
559 In both cases, the equilibrium involves a stable value of v_{eq} .

560 From our theory, we conclude that it is necessary for the looser fish to
561 maintain the high velocity v_{eq} as well because otherwise biting attacks be-
562 come profitable for the winner and the looser will further descend in relative
563 capacity. The winner in turn must maintain a high velocity and a close dis-
564 tance from its opponent or else the looser may respond by slowing down since
565 the dominant is too far away to attack. The caudal deceleration zones ap-
566 parent in the speeding map of the defender in the asymmetric phase (Figure
567 3G) may well be a mark of such strategic responses. The analysis thus indi-
568 cates a plausible link between game theory equilibria, well-known features of
569 fish biomechanics/physiology and the observed long duration chasing which
570 often concludes zebrafish fights.

571 4 Discussion

572 We have introduced a machine vision pipeline for the study of aggression in
573 zebrafish which allows both automated identification and tracking (see Meth-
574 ods) of unmarked animals by use of idTracker [22] as well as individual-level
575 automated classification of ethologically relevant behaviors on a sub-second
576 timescale (compare with the lack of identification and end-to-end deep learn-
577 ing in [23, 24]). The pipeline allows for reduced human workload by elimi-
578 nation of the marking stage and the annotation stage as well as reducing
579 the need for controls comparing marked and unmarked animals. Our meth-
580 ods also have the additional advantage of allowing for some parallelization.
581 Though we focused here on experiments in large arenas to avoid confounding
582 influence of walls on our analysis, it is possible to fit up to 4 smaller fight
583 arenas into the field of view of our camera. The tracking can also be done
584 in parallel without modifications to the code. Hence, it is feasible for certain
585 experiments to increase the setup throughput by a factor of 4 if needed.

586 In our work, we have also demonstrated how the ability to gather high
587 resolution trajectory data can be of aid in the process of deciding which of
588 the many assessment models provides the best description of the fight. For
589 example, we observed a strong correlation between the velocity of the attacker
590 and the defender during individual attacks. The observation of strong mutual
591 correlation in activity levels during individual acts of behavior gives evidence
592 that in zebrafish, approximately equal locomotor costs are borne by both the
593 producer of the attack as well as its target. This observation rules out WOA
594 models of contests as good descriptions of zebrafish aggression. We reach the
595 conclusion because these models posit individual behavioral acts to have an

596 effect on the energy budget of only the one who is producing the signal and
597 not on the target of the signal [13]- a hypothesis clearly violated in our data.

598 Based on our results, the standard sequential assessment game also ap-
599 pears ill-suited as a description of zebrafish aggression, because we were
600 unable to detect statistically significant positive relationship between the
601 fight time and the RHP of the loser [27]. Having ruled out both the self-
602 assessment and the sequential assessment models, we were left by elimination
603 with the cumulative assessment game as the only suitable description of ze-
604 brafish fighting and our supplementary modeling supported this conclusion
605 as well.

606 As stated before, we speculate that our technology may become a valu-
607 able complement to the current standard methodology of game theory model
608 testing in two contexts. First, as others have argued [4] and as we showed in
609 our supplementary modeling, the distinction between the CAM and WOA
610 in terms of fight time scaling relationships is not as clear-cut as is sometimes
611 stated [27, 30]. In such cases, the use of machine learning tools to infer
612 activity budgets and correlations from video data may become a valuable
613 complement to the standard toolkit as it will occasionally allow resolution
614 of the ambiguities. Secondly, since our analysis does not require knowledge
615 of the resource holding potential, it can be used in cases where the RHP is
616 unknown or RHP differences are small.

617 Beyond the falsification of game theory models, analysis of trajectory level
618 data also proved useful in clarifying the nature of certain behaviors. In the
619 beginning we believed that the primary function of attacks in the symmetric
620 phase was to maneuver the attacker into a position where he might be able
621 to elicit further damage through direct contact and biting. We were surprised
622 to find in our forcemaps that rather than avoiding such attacks, the defender
623 had a statistical tendency to turn its flank towards such attacks. Even more
624 surprisingly, the attacker had a tendency to incompletely exploit the resulting
625 vulnerable configuration as evidenced by the presence of weak repulsion zones
626 in the turning rule of the attacker. The willingness of the defender to expose
627 its flank may thus be at least partly a display behavior intended to signal its
628 ability to maneuver and/or withstand damage.

629 The potential risk of the display may be mitigated by the opportunity
630 to engage in the splash behavior. The splash behavior may enable one fish
631 to halt or perturb the approach of another as it is becoming too dangerous.
632 In support of this, notice how the splash is usually deployed right as the
633 attacker is making first contact with the defender (Figure 5B). The potential
634 option to engage in the splash behavior may also mitigate the risk associated
635 with engaging in the display-like attacks which leads the defender into a
636 vulnerable configuration. The vulnerable configuration which occurs during

637 the displays may be stabilized because the attacker knows that any attempt
638 to exploit the vulnerability can be countered with a splash maneuver by the
639 defender.

640 One of the novelties in our paper was the introduction of movement rules
641 [25] to the analysis of contests. The ability to quantify the fine structure of
642 aggressive attacks through movement rules is useful not only for the insight it
643 provides about typical fighting tactics, but also because it enables quantifi-
644 cation of change in those tactics. There is now much evidence for the role
645 of cognition and learning in shaping animal fighting ability [31]. Fighting
646 ability of animals changes with experience [32, 33], but exactly how experi-
647 ence makes fighters more competent and skillful has not always been clear
648 from the studies. It may be that changes in fine motor dynamics play an
649 important role and our measurement toolbox could be helpful in clarifying
650 some of these unresolved issues. For example, evidence from sticklebacks has
651 established a role for learning in the development of displays [34]. If the same
652 is true for zebrafish, then there is an expectation that early in development,
653 contest phase attacks might lack some of the display-like features we see in
654 adults. The force map technique we have introduced could be straightfor-
655 wardly applied to address this hypothesis, which might prove more difficult
656 to test with traditional methods.

657 Finally, we hope that the study of trajectory level data will open up a
658 new frontier in the study of strategic conflict. With the ability to record high
659 resolution data, we may be able to get a better handle on the biomechanical
660 determinants [17] of movement during contests. This may finally allow us to
661 study the long-ago stated goal of examining not just how displays are used,
662 but what factors determine the form and the fine dynamics of the displays as
663 well [35]. Or in other words, we may eventually be able to study the move-
664 ment subgames taking place within the larger assessment games. We took a
665 small step in that direction by explaining the qualitative patterns of locomotion
666 during the chasing phase through a game theory analysis, but there is
667 also a clear need for better theoretical methods to analyze the extended games
668 which occur when acceleration decisions influence inter-individual distances
669 over time. The recent merging of techniques from game theory and deep
670 reinforcement learning represents a promising avenue for further research in
671 this regard. In particular, the use of self play, which has allowed humanoid
672 robots to teach each other wrestling in an unsupervised way, is a technology
673 which should be immediately applicable to the study of fish aggression as
674 well [36].

675 **Author Contributions**

676 Designed project: MJ AL GP. Performed the experiments: MJ AL. Wrote
677 code: AL. Analyzed the data: MJ AL GP. Obtained models: MJ AL. Con-
678 tributed to the writing of the manuscript: MJ AL GP.

679 **Conflict of interest statement**

680 The authors declare no conflict of interest exists

681 **Acknowledgements**

682 We wish to thank Francisco Romero-Ferrero and Mattia Bergomi for sharing
683 an early version of idTracker.ai as well as for advice on how to best utilize the
684 software. We thank Hanna Kokko and members of the Collective Behavior
685 Lab for discussions.

686 **Funding**

687 We acknowledge funding from the Champalimaud Foundation (to GdP) and
688 from Fundação para a Ciência e Tecnologia PTDC/NEU-SCC/0948/2014 (to
689 GdP) and FCT fellowships (to AL and MJ).

690 **Supplementary video link**

691 <https://drive.google.com/open?id=0Bz9JP7PG5u41S1phejlyWU5Wb3M>

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