

RESEARCH ARTICLE

Visual determinants of prey chasing behavior in a mudflat crab

Brian Gancedo^{1,2,*}, Carla Salido^{1,2,*} and Daniel Tomsic^{1,2,‡}

ABSTRACT

The crab *Neohelice granulata* inhabits mudflats where it is preyed upon by gulls and, conversely, preys on smaller crabs. Therefore, on seeing moving stimuli, this crab can behave as prey or predator. The crab escape response to visual stimuli has been extensively investigated from the behavioral to the neuronal level. The predatory response (PR), however, has not yet been explored. Here, we show that this response can be reliably elicited and investigated in a laboratory arena. By using dummies of three different sizes moved on the ground at three different velocities over multiple trials, we identified important stimulation conditions that boost the occurrence of PR and its chances of ending in successful prey capture. PR probability was sustained during the first 10 trials of our experiments but then declined. PR was elicited with high probability by the medium size dummy, less effectively by the small dummy, and hardly brought about by the large dummy, which mostly elicited avoidance responses. A GLMM analysis indicated that the dummy size and the tracking line distance were two strong determinants for eliciting PR. The rate of successful captures, however, mainly depended on the dummy velocity. Our results suggest that crabs are capable of assessing the distance to the dummy and its absolute size. The PR characterized here, in connection with the substantial knowledge of the visual processing associated with the escape response, provides excellent opportunities for comparative analyses of the organization of two distinct visually guided behaviors in a single animal.

KEY WORDS: Predatory behavior, Escape behavior, Pursuit, Capture, Crustacean

INTRODUCTION

Visually guided escape and predatory behaviors represent two of the most attractive animal actions for studying fundamental themes in contemporary behavioral neurobiology, such as visuo-motor transformations, decision-making strategies, and learning and memory processes (e.g. Schuster, 2012; Muto and Kawakami, 2013; Peek and Card, 2016; Ben-Tov et al., 2018; Evans et al., 2019). Considerable knowledge on these areas has arisen from studies performed in arthropods, mostly insects and decapod crustaceans (Card and Dickinson, 2008; Herberholz and Marquart, 2012; Gonzalez-Bellido et al., 2016; Tomsic, 2016). In these animals, prey capture and escape behaviors proved to be suitable paradigms for research because they can be easily elicited in

the laboratory. Additionally, the two types of behavior entail fast responses subserved by straightforward neural circuits containing large neurons amenable for neurophysiological analyses. Among classic arthropod models for studying the neurobiology of visual avoidance behaviors are locusts (Rind et al., 2016; Dewell and Gabbiani, 2019), fruit flies (Ache et al., 2019) and crabs (Tomsic et al., 2017). In contrast, models for investigating the neural control of visually driven predatory behaviors are dragonflies (Lancer et al., 2019), praying mantis (Nityananda et al., 2019; Rosner et al., 2019) and predatory flies (Wardill et al., 2017). Except for the praying mantis (Yamawaki, 2011; Yamawaki et al., 2011), studies of visually guided escape and prey capture behaviors are performed in separate animal models. Establishing a model where these two competing behaviors can be suitably investigated in a single animal at the neuronal level would provide opportunities for addressing new questions in behavioral neurobiology research.

The escape response of the crab *Neohelice* (previously *Chasmagnathus*) *granulata* to visual danger stimuli has been the subject of extensive research for nearly 30 years. The studies were aimed at investigating aspects as diverse as the visual processing of moving objects (Sztarker et al., 2005; Medan et al., 2007; Berón de Astrada et al., 2013; Scarano et al., 2018), the transformation of visual information into motor outputs (Medan et al., 2015; Oliva and Tomsic, 2014, 2016), the response modulation by different factors such as age, season, food presence, shelter availability or predation risk (Tomsic et al., 1996; Sztarker and Tomsic, 2008; Hemmi and Tomsic, 2015; Magani et al., 2016), and the acquisition and long-term retention of visual memories (Sztarker and Tomsic, 2011; Klappenbach et al., 2017). The studies involved field and laboratory studies and were performed combining a wide variety of methodologies including neuroanatomy, electrophysiology, pharmacology, molecular biology and calcium imaging. Therefore, there is substantial knowledge about central aspects underlying the visual control of behavior in this crab (for reviews, see Tomsic, 2016; Tomsic et al., 2017).

Recently, we discovered that *Neohelice* displays a robust visually guided chasing behavior (Tomsic et al., 2017). In fact, this crab preys on smaller crabs of its own species and also on sympatric fiddler crabs of the species *Leptuca* (previously *Uca*) *uruguayensis* (Daleo et al., 2003; Bas et al., 2019). Preliminary studies in the field have shown that the predatory behavior of *Neohelice* can readily be evoked by using a small dummy moved at ground level (Tomsic et al., 2017). This, in association with the previous knowledge on visual processing described above, makes this crab a good candidate to carry out investigations of prey capture and escape behaviors in a single animal model. However, the hunting behavior of the crab is yet to be described. To begin bridging the gap, we performed a characterization of the predatory behavior of the crab as well as the identification of stimulus visual parameters and contextual conditions that affect the probability of evoking the predatory response. Previous studies have shown that stimulus apparent size and stimulus retinal speed are two important parameters for eliciting the escape response of crabs (Hemmi, 2005; Oliva and Tomsic, 2012). Therefore, we tested the hypothesis that the same parameters

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would be decisive for eliciting the predatory response. As an alternative hypothesis, we evaluated the possibility that crabs might choose prey by their real size, for which they must be able to estimate the distance to the stimulus.

Here we show that: (a) the predatory behavior of *Neohelice* can be reliably elicited in the laboratory; (b) the behavior involves stages of evaluation (freezing) and decision (run after or not) that may have different outcomes (prey capture or failure); (c) the response probability is independent of the position in the crab's visual field from which the dummy is detected; (d) the probability of the crab engaging in a particular behavioral component is affected by stimulus parameters such as absolute size and velocity, and by contextual conditions such as dummy distance and trial repetitions.

MATERIALS AND METHODS

Animals

Animals were adult male *Neohelice granulata* (Dana 1851) crabs, 2.7–3.0 cm across the carapace, weighing approximately 17 g, collected in the rías (narrow coastal inlets) of San Clemente del Tuyú, Argentina. The crabs were maintained individually in glass jars filled to 2 cm depth with artificial seawater prepared using hw-Marinex (Winex, Hamburg, Germany), salinity 10–14‰, pH 7.4–7.6 and within a temperature range of 22–24°C. The holding and experimental rooms were kept on a 12 h light/12 h dark cycle (lights on at 07:00 h to 19:00 h) and the experiments were run between 08:00 h and 19:00 h, 4–10 days after the animals' arrival at the laboratory. The animals were not fed after their arrival at the laboratory.

Experimental setup and recording procedures

The experimental arena (Fig. 1) consisted of a rectangular plastic box (65 cm long×45 cm wide×55 cm high), with the floor covered by a 5 cm layer of mud obtained from the crab's natural

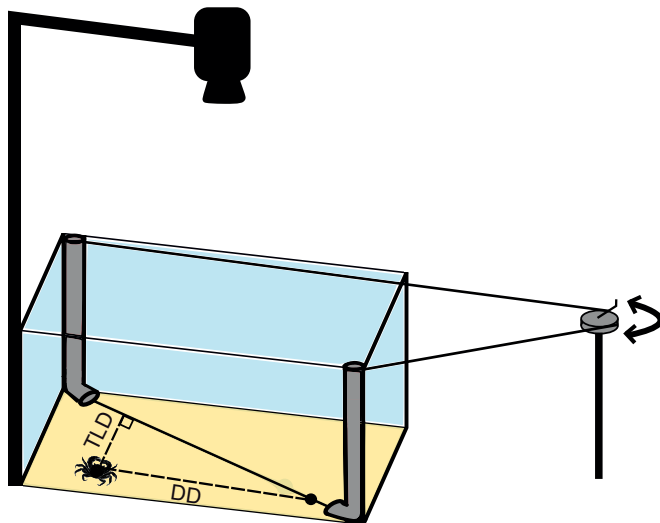


Fig. 1. The experimental arena. Experiments were run in a rectangular arena (65 cm×45 cm) with the floor covered with mud from the crab's natural environment. A fishing line that passed through two vertical pipes at the corners of the arena was used to pull an attached dummy, which was moved at ground level in either direction. The movement of the dummy was controlled by a manual steering wheel placed outside the arena. A video camera located 80 cm above was used to record the crab's behavior and dummy movement. TLD, tracking line distance; DD, dummy distance. For further details, see Materials and Methods.

environment. The arena had two vertical plastic pipes located in opposite corners. A fishing line passing through these pipes allowed an attached dummy to be pulled at ground level between the two corners of the arena. The line coming out from the top of the pipes was attached to a manual steering wheel placed outside the arena that was used to move the dummy in either direction.

A video camera (Sony Handycam HDR-CX440) located 80 cm above the arena was used to record the dummy motion and the behavior of the crab during trials. Accurate position of the crab and the dummy was calculated at 16.7 ms time intervals from calibrated video information. Lens distortion calibration and video footage analysis were made with the free software Tracker.

Visual stimuli and protocol

The dummy stimulus consisted of a black plastic sphere of three different diameters (small: 1 cm, medium: 1.8 cm and large: 3 cm) moved at three different relatively constant velocities (mean±s.e.m.: slow: 8.2±0.2 cm s⁻¹, middle: 18.5±0.4 cm s⁻¹, fast: 45.1±0.8 cm s⁻¹). These velocities were chosen to cover a wide range, including a velocity that surpasses the fastest running speed of *Neohelice*, but that is within the running speed of fiddler crabs, which *Neohelice* preys on. Each animal ($n=27$) was evaluated with all three dummy velocities presented in a pseudo balanced way across trials, but with only one dummy size ($n=9$ individuals per size). Experiments with each particular dummy size were regularly distributed across the days of study. Each animal was evaluated in 30 trials, with an inter-trial interval of approximately 3 min to curtail habituation. The initial trial started 10 min after the animal was installed in the arena. A trial always began with the dummy departing from one corner and ended when it reached the opposite corner. The motion direction of the dummy alternated between trials.

Response criteria and measurements

A variety of different responses to the moving dummy that included freezing, defense, and moving towards or moving away the target were readily observed. A response was considered to have occurred whenever a crab changed its behavior. In the vast majority of cases, the change consisted of starting or stopping moving (freeze). On a few occasions, however, the animal was moving and suddenly changed its speed or direction of motion; these changes were easily detectable. No crabs were excluded from the analyses. The criteria to start a trial, i.e. to begin moving the dummy, was twofold. First, we always waited 3 min after the end of the previous trial. Second, we checked whether the crab was at least 5 cm away from the tracking line; if not, we waited until the critical distance was exceeded. This was done by continually monitoring the activity within the arena through a mobile phone connected to the recording camera. During offline analyses, we determined dummy distance and tracking line distance (the shortest distance between the crab and the trajectory of the dummy) (Fig. 1). From the geometry of the situation, we could then calculate the apparent size (the angular size of the dummy as seen from the crab's point of view) and apparent speed of the stimulus (the angular speed of the dummy as seen from the crab's point of view).

Statistical analyses

The probability of a predatory response (coded as 1 for pursue or 0 for not pursue) and the probability of successful capture (1 for capture or 0 for failure) were modeled using generalized linear mixed models (GLMMs) assuming binomial error distributions and logit link functions. GLMMs are extensions of generalized linear models, particularly useful for non-independent data such as

repeated measurement and nested data (Zuur et al., 2009). The variable that we measured was binomial (pursuit or not; capture or not) and data corresponded to individuals that were measured repeatedly; hence, we used GLMMs. The models were performed to determine whether the behavioral responses of crabs (dependent variable) vary with the tracking line distance (TLD), dummy size and dummy velocity. These variables were incorporated into the model as fixed factors and crab number was considered as random factor. Crab number was nested within dummy size to minimize the disturbance to the crabs introduced when changing the dummy between trials. The Akaike information criterion (AIC; Akaike, 1973) was used as a measure of the goodness of fit to assess model performance. The model with the smallest AIC value was chosen as the one that better represented the data. We also applied the Hosmer and Lemeshow goodness of fit test to our models. The lack of patterns in the residue values and homogeneity of variance were checked by graphic methods. The significance of the parameters and their interactions was tested by likelihood ratio test and multiple comparisons were performed using Tukey's method (z -values). Circular distributions were analyzed using the Rayleigh test. Comparison of freezing distances, pursuit distances, stimulus angular size and angular speed were conducted using Mann–Whitney and Wilcoxon signed-rank test with Bonferroni correction. To compare the proportions of behavioral responses we used non-parametric repeated-measures Friedman tests. The reason for using non-parametric tests was the lack of normality of the data. All statistical analyses were performed with R software (version 3.4.4; <http://www.R-project.org/>). Packages lme4 (Bates et al., 2015) and lsmeans (Lenth, 2016) were used for GLMMs and Tukey's method for multiple comparisons, respectively.

RESULTS

Description of behaviors and general analyses

Observations of the videos from 27 animals tested with the three dummy velocities and sizes readily led us to the identification of four main behaviors, which were mutually exclusive. The ethogram of Fig. 2 represents these behaviors and Movie 1 exemplifies the observed responses. These we classified as: avoidance response (AR), when the animal moved away from the dummy or displayed a defensive reaction, raising its claws; freezing response (FR), when the animal stopped walking and remained still for the whole trial (note that this category does not include the transitory freezing that precedes other responses, as explained later); no response (NR), when the animal did not change its behavior (most often remaining still, as it was before the dummy began to move); predatory response (PR), when the animal moved towards the dummy and, in most cases, attacked it. From a total of 241 trials, NR occurred in nearly 11% of the trials, AR in 19%, FR in 33.5% and PR in 36.5%.

Animals performing PR displayed different outcomes (Fig. 2, blue boxes). These we named incomplete pursuit (IP), when the animal gave up its approach to the dummy before making contact with it, and complete pursuit (CP), when the animal continued running after the prey and attacked it. Nearly 80% of PR consisted of CP. Of the animals that performed CP, some succeeded in capturing the dummy, grasping it with the claws, while others failed. The first outcome, named successful capture (SC), occurred 56.5% of the time, while the second outcome, named unsuccessful capture (UC), occurred in 43.5% of cases. It should be noted, however, that all these percentages correspond to the total trials, and hence comprised all stimulus conditions. As described below, these percentages change greatly when particular stimulus sizes and velocities are taken into consideration.

Effect of stimulus repetition, dummy size and visual field location

Our experiments included 30 repeated trials for each crab. Fig. 3A shows that the probability of PR declined over trials, accompanied by an increase in FR and NR. Within the first 10 trials, however, the proportion of animals displaying each particular type of response remained rather stable. In fact, there were no differences between the first and second 5-trial blocks for each dummy size (Friedman tests, large $P=0.11$, medium $P=0.11$, small $P=0.12$). For this reason, the analyses throughout the present study (including the percentages described above) were performed on the results obtained in the first 10 trials. The differences in the probability of each response type elicited by the different dummy sizes over the initial 10 trials can be more clearly seen in Fig. 3B. The figure shows that the dummy size largely determined the type of response displayed by the animals. The large dummy elicited mainly AR or FR, while the most frequent responses evoked by the smaller dummy were PR and FR. In no case the small dummy elicited an AR. The medium size dummy was the most effective one in evoking PR. Fig. 3C completes the description by showing the variability in the probability of responses across individuals. The tendency observed in most individual profiles is well reflected by the collective analysis just described, although a few crabs behaved differently (e.g. large dummy, crab 1; medium dummy, crab 15).

The monocular field of vision of *Neohelice* encompasses 360 deg, but the sensitivity varies across different retinal regions (Berón de Astrada et al., 2012; Medan et al., 2015). Thus, some behaviors could be associated with a particular orientation of the crab relative to the dummy. For instance, NR could be assumed to be the dominant behavior when the crab faces the opposite direction from the dummy. Fig. 4 shows the azimuthal position (and distance) distribution of the dummy around the crab for each type of response. A cursory inspection of the polar plots shows in all cases an apparent homogeneous scattering. In fact, the statistical analyses of circular distribution did not disclose significant differences in the orientation of crabs for any behavior (Rayleigh test, AR $P=0.4$, NR $P=0.51$, FR $P=0.07$, PR $P=0.12$). Therefore, the response probabilities were not affected by the position of the dummy across the azimuthal visual field of the animal.

Because our interest in the present study was on PR, we focused our analyses on this particular behavior.

Effect of feeding state on PR

The experiments were performed between 4 and 10 days after the animals had been captured in the field and brought to the laboratory. To increase the motivation of the animals to perform PR, they were not fed. To avoid a confounding effect of the cumulative days of starvation on the behavioral probabilities, tests with each particular dummy size were regularly distributed across the whole experimental period. Additionally, this allowed us to evaluate whether the difference in the number of days of starvation affected the crab's motivation for chasing a dummy prey. A comparison of the probability of PR performed on data grouped into days 4–5, 6–8 and 9–10 (0.45, 0.48 and 0.51, respectively) showed that there was no significant change over the experimental period (Friedman test, $P=0.13$).

Stimulus parameters that affect the probability of PR

A preliminary inspection of our videos suggested that the effectiveness of the dummy for eliciting PR declined with the increase in tracking line distance. In our experimental arena, the tracking line distance ranged from 5 to 35 cm (see Materials and Methods). An initial

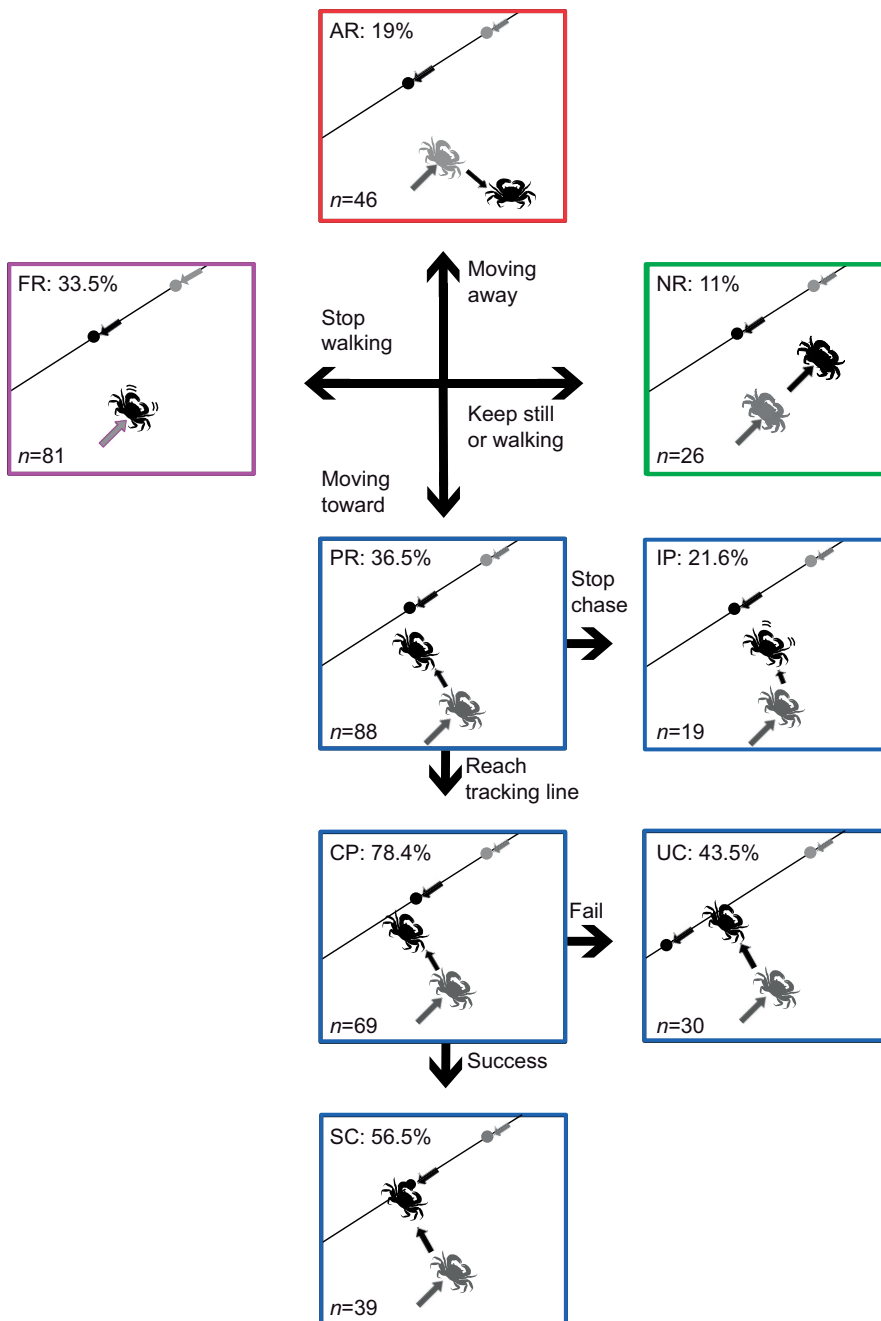


Fig. 2. Ethogram of responses to dummy stimulation. The ethogram represents the different responses and their probabilities to presentation of the dummy at three different sizes and velocities. Four main exclusive categories of behavioral response were observed: avoidance response (AR), no response (NR), freezing response (FR) and predatory response (PR). PR can end in an incomplete pursuit (IP) or a complete pursuit (CP). CP can conclude with an unsuccessful capture (UC) or a successful capture (SC). The drawings within boxes indicate the different behaviors. The gray crab and dummy represent the position of the animal and stimulus at the beginning of the trial. The black crab and dummy represent the response of the animal in association with the current position of the dummy. Further details are given in Results.

inspection of the videos also suggested that the dummy velocity had no obvious effect on PR occurrence. The GLMM analysis confirmed these observations. The model that better fitted the probability of eliciting PR builds on the effects of dummy size, tracking line distance and the interaction between these two factors, but not on dummy velocity (Tables 1 and 2). The graphic representation of the model in Fig. 5) shows that the medium dummy was the most effective for eliciting PR, but its effectiveness quickly fell at tracking line distances beyond 15 cm. The small dummy was less effective, with a maximal probability achieved at short tracking line distances, which was equivalent to that evoked by the medium dummy at intermediate distances. A possible interpretation of this result would be that a crab that is far away from the tracking line is unable to detect the small dummy. Yet, the efficacy of the small dummy declined more gradually with distance, in such a way that beyond 20 cm, the effectiveness of the

two dummies was similarly low. Finally, the large dummy did not elicit PR, with few exceptions at the longer tracking line distance denoted by the slightly positive slope of the modeled line. The effectiveness of the large dummy for evoking PR was so weak that we did not consider this dummy in further analyses.

Stimulus visual features at the initiation of PR

Following recognition of the conditions in which PR was most likely evoked, we looked at the possibility that a particular visual parameter of the dummy determines the animal's decision to initiate pursuit. We analyzed two stimulus visual parameters, the apparent size and the retinal speed, which have been shown to be used by crabs to initiate avoidance responses (Hemmi and Tomsic, 2012).

PR was always initiated with momentary freezing. This was observed in every single trial where the animal was walking before

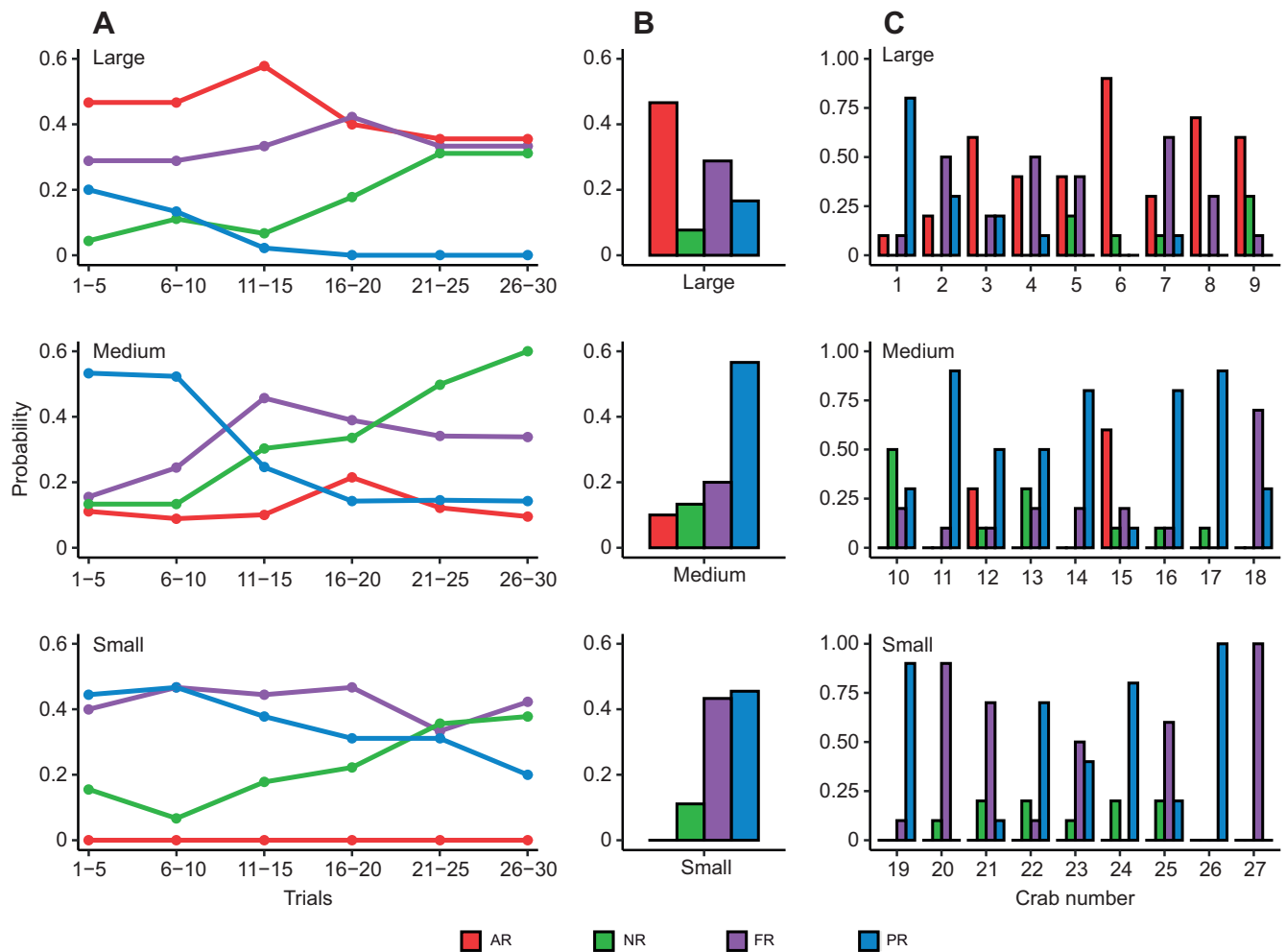


Fig. 3. Probabilities of the four mutually exclusive responses to each dummy size across trials and individuals. (A) The response probability over 30 trials is shown in blocks of 5 trials for each dummy size. (B) Behavior probabilities elicited by each dummy size in the first block of 10 trials. (C) Variability across individuals of behavior probabilities displayed for each dummy size during the first 10 trials. FR, freezing response; AR, avoidance response; NR, no response; PR, predatory response.

the dummy started to move (85.28% of trials). The presence of a freezing component suggests that immediately following detection of the dummy, the animal evaluated the situation in order to decide whether to run after the stimulus or not. This transitory freezing typically took place soon after the dummy began to move (see Movie 1); hence, in most cases when the dummy was approaching the crab (with the exception of those few trials when the crab was located close to the corner of the arena from which the dummy was departing). Consequently, when freezing occurred, the subtended angular size of the stimulus was smaller than when pursuit was begun. Fig. 6A shows the mean subtended angular size of the small and medium dummy at both freezing and pursuit response times. The statistical analyses disclosed a significant difference between the two dummies for both freezing and pursuit (Mann–Whitney tests with Bonferroni correction, freezing $P=0.004$, pursuit $P<0.001$). This shows that the criterion used by the crab to launch PR is not based on a particular value of the stimulus apparent size.

We then compared the values of stimulus retinal speed at PR initiation obtained with the three dummy velocities (see Materials and Methods). Because within each velocity there was no difference between the values obtained with the small and medium dummy, we pooled the data. Fig. 6B shows that PR elicited with the different dummy velocities occurred at significantly different stimulus retinal

speeds (Mann–Whitney test with Bonferroni correction, $P<0.001$ for all comparisons). Therefore, the crab's decision to start running after a dummy did not rely on a critical value of the stimulus apparent size or its retinal speed.

Dummy distance at freezing preceding PR and at the start of pursuit

It has been shown that fiddler crabs can measure the distance to a dummy moving over the ground, where they can use elevation in the visual field as an approximation of distance (Hemmi and Zeil, 2003). To evaluate the possibility that *Neohelice* may initiate PR when the dummy is at a particular distance, we analyzed the dummy distance at freezing and at the subsequent chase induced by the small and medium dummy separately. For both dummies, the mean freezing distance was more than twice the mean pursuit distance (Wilcoxon tests with Bonferroni correction, $P<0.001$). Yet, the freezing distance and the pursuit distance obtained with the small and medium dummy were very similar (Fig. 7A; Mann–Whitney test with Bonferroni correction, freezing $P=0.72$, pursuit $P=0.52$). The results show that following the detection and categorization of the stimulus as a prey, crabs initiated pursuit at a particular distance (around 15 cm), regardless of whether the dummy was of medium or small size. This indicates that crabs were able to measure the distance to the dummy.

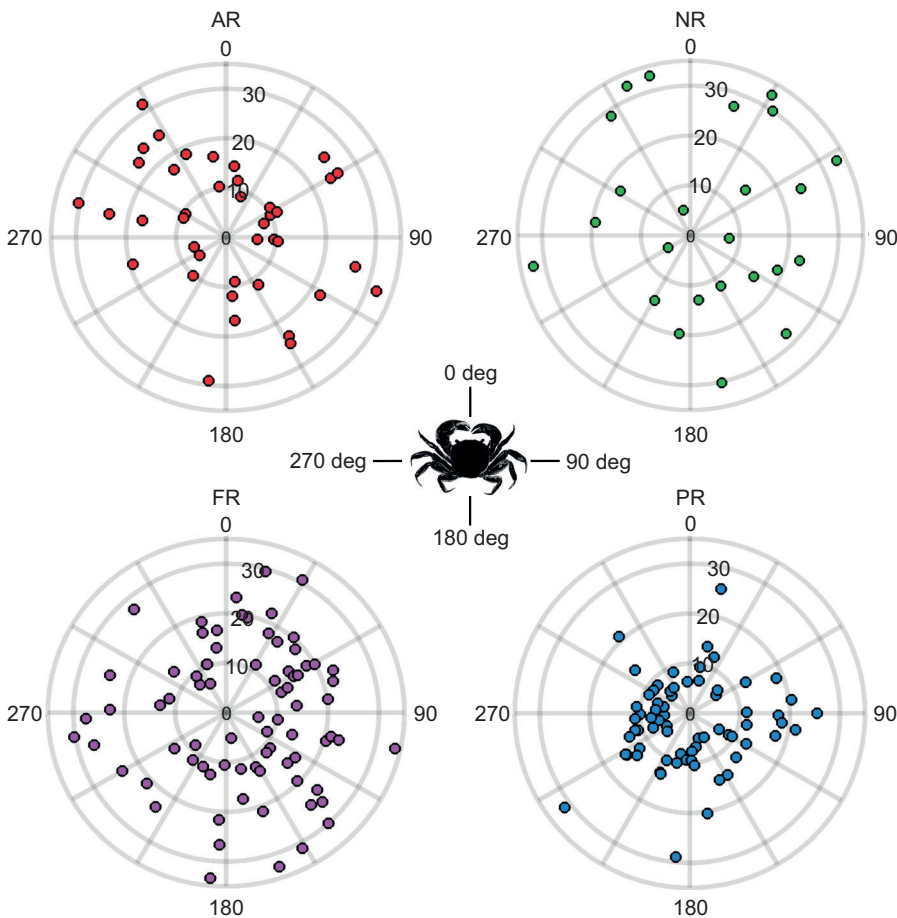


Fig. 4. Orientation and distance of the dummy with respect to the crab at the beginning of the trial for each type of response. Dummies in front of or behind the crab were computed as being oriented at 0 or 180 deg, respectively. Colored dots in the polar plots represent data from single trials. The four mutually exclusive responses show uniform distributions (Rayleigh test: AR $P=0.4$, NR $P=0.51$, FR $P=0.07$, PR $P=0.12$).

The results for freezing preceding PR show that crabs had no difficulty in spotting the small dummy at a relatively long distance and, therefore, preclude an interpretation of the difference in PR probability observed between the small and medium dummy (Figs 3 and 5) in terms of stimulus detectability.

We then distinguished between PR initiated when the dummy was approaching the crab from PR initiated when the dummy was getting away. In other words, between pursuits that occurred before the dummy reached the point of the shortest tracking line distance and those that occurred when the dummy passed this point. From a total of

77 PR events (45 obtained with the medium dummy and 32 with the small dummy), 51 were initiated when the dummy was approaching the crab and 26 when the dummy was departing (66% versus 34%, respectively). This difference may be partly explained by the fact that in some trials crabs were near the corner from which the dummy started to move, a situation in which the stimulus could only be seen moving away. Despite the fact that the dummy direction alternated between trials, it could be that each crab responded only when the stimulus was approaching or receding. Fig. 7B shows the number of PR elicited when the dummy was approaching or

Table 1. GLMM selection for predatory response probability and successful capture probability

Model	d.f.	AICc	Δ AICc	ω
PR probability				
TLD+DS+TLD:DS	7	167.3	0	0.78
TLD+DS+DV+TLD:DS	9	170.69	3.39	0.14
TLD+DS+DV+TLD:DS+TLD:DV	11	172.91	5.62	0.05
TLD+DS	5	173.54	6.25	0.03
SC probability				
DV	3	65.02	0	0.56
DV+DS	4	67.14	2.13	0.19
DV+TLD	4	67.26	2.24	0.18
DV+DS+TLD	5	69.48	4.46	0.06

GLMM, generalized linear mixed model; PR, predatory response; SC, successful capture; d.f., degrees of freedom; AICc, corrected Akaike's information criterion; Δ AICc, difference in AICc between the model and the model with the lowest AICc; ω , weight given to this model; TLD, tracking line distance; DS, dummy size; DV, dummy velocity. The best model is shown in bold.

Table 2. Parameter estimates for the GLMM predicting PR probability and SC probability

	Estimate \pm s.e.m.	Z-value	$P(> z)$
PR probability			
Intercept	6.24\pm1.99	3.132	0.001
TLD	-0.317\pm0.099	-3.198	0.001
DS (large)	-10.21\pm2.856	-3.576	0.0003
DS (small)	-4.85\pm2.34	-2.068	0.04
DV	-0.003 \pm 0.002	-1.814	0.07
TLD – large dummy	0.33\pm0.11	2.781	0.005
TLD – small dummy	0.19 \pm 0.11	1.675	0.09
Random effect (variance, s.d.); crab number (6.546, 2.559)			
SC probability			
Intercept	3.48\pm1.12	3.115	0.002
DV	-0.15\pm0.05	-3.226	0.001
Random effect (variance, s.d.); crab number (1.28, 1.13)			

GLMM, generalized linear mixed model; PR, predatory response; SC, successful capture; TLD, tracking line distance; DS, dummy size; DV, dummy velocity. Significant results with $|z|>2.0$ are shown in bold.

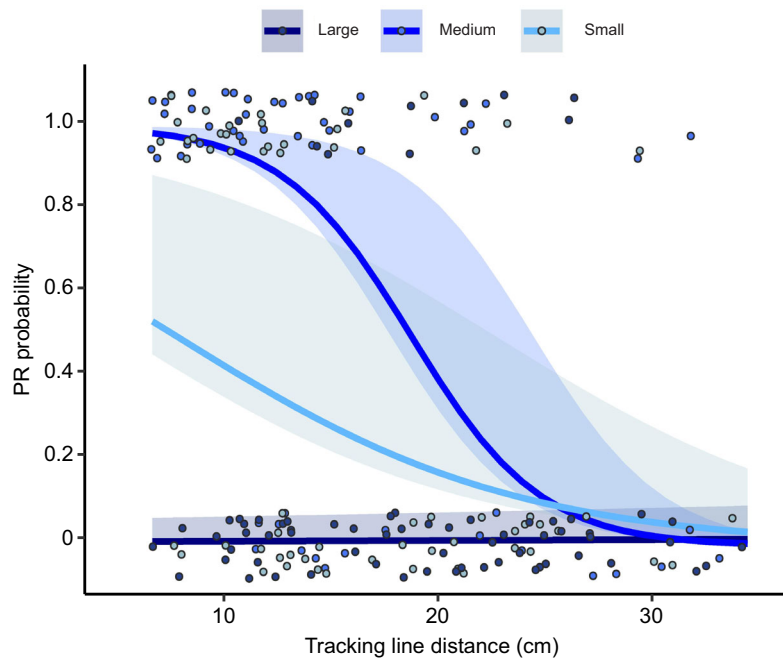


Fig. 5. Probability of PR as predicted by the statistical model. Solid lines represent the probability of response to each dummy size as a function of the tracking line distance. Shaded areas represent interquartile ranges. Colored dots represent individual data for each dummy size on which the model was based. Further details are given in Results and Tables 1 and 2.

departing across 10 trials (5 in each direction) for each crab. This individual analysis shows that most crabs responded to both approaching and departing dummies. We then analyzed the response distance for these two conditions (Fig. 7C). The mean dummy distances at which the pursuits were launched during approach or departure of the dummy were similar (mean \pm s.e.m. approach 14.9 \pm 1.1 cm, departure 17.3 \pm 2.4 cm; Mann–Whitney test, $P=0.75$).

Stimulus parameters affecting the chance of a successful capture

As shown in the ethogram of Fig. 2, PR could result in IP or CP and, in turn, CP could have two possible outputs: SC and UC. We wonder what factors may affect the rate of SC. For this, we examined the CP dataset using GLMM analysis. The results are shown in Tables 1 and 2, and in Fig. 8. The analysis indicates that

the factor that significantly affected the probability of SC was dummy velocity. As velocity increased, the probability of SC decreased. In fact, few attempts culminated in SC when the dummy moved at velocities greater than 30 cm s⁻¹ (Fig. 8).

We then analyzed whether the probability of SC was affected by the time when pursuit was initiated, i.e. if it was initiated when the dummy was approaching or departing from the crab. From a total of 39 SC events (24 obtained with the medium dummy and 15 with the small dummy), 32 were initiated when the dummy was approaching the crab and 7 when it was getting away (82% versus 18%, respectively). Therefore, the chances of achieving a SC were reduced when PR started late.

DISCUSSION

In a recent review, Tomsic et al. (2017) briefly described that in the field, *Neohelice* displays a robust chasing response to a small object

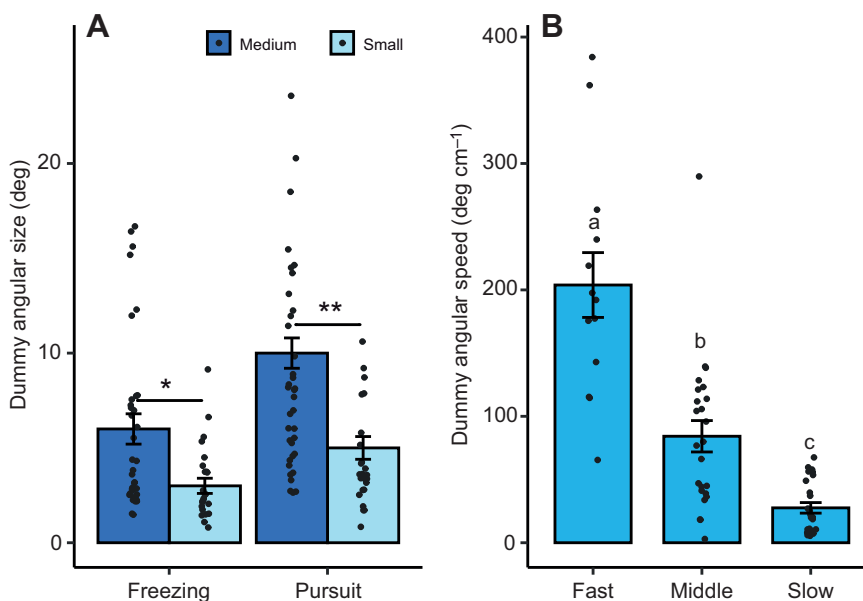


Fig. 6. Dummy visual parameters when crabs initiate PR. (A) Dummy angular size at the occurrence of the transitory freezing and the subsequent pursuit for responses obtained with the medium ($n=36$) and small ($n=24$) dummy. Crabs initiated both the freeze and the following pursuit at significantly larger angular sizes with the medium dummy than with the small dummy (Mann–Whitney tests with Bonferroni correction, freezing $*P=0.004$, pursuit $**P<0.001$). (B) Stimulus retinal speed at the time of pursuit for each of the three dummy velocities (fast $n=13$ trials, middle $n=25$ trials, slow $n=24$ trials). Responses were initiated at significantly different angular velocities (Mann–Whitney test with Bonferroni correction, different letters indicate significant differences; $P<0.001$ for all comparisons). Bars show means \pm s.e.m. Dots represent individual data.

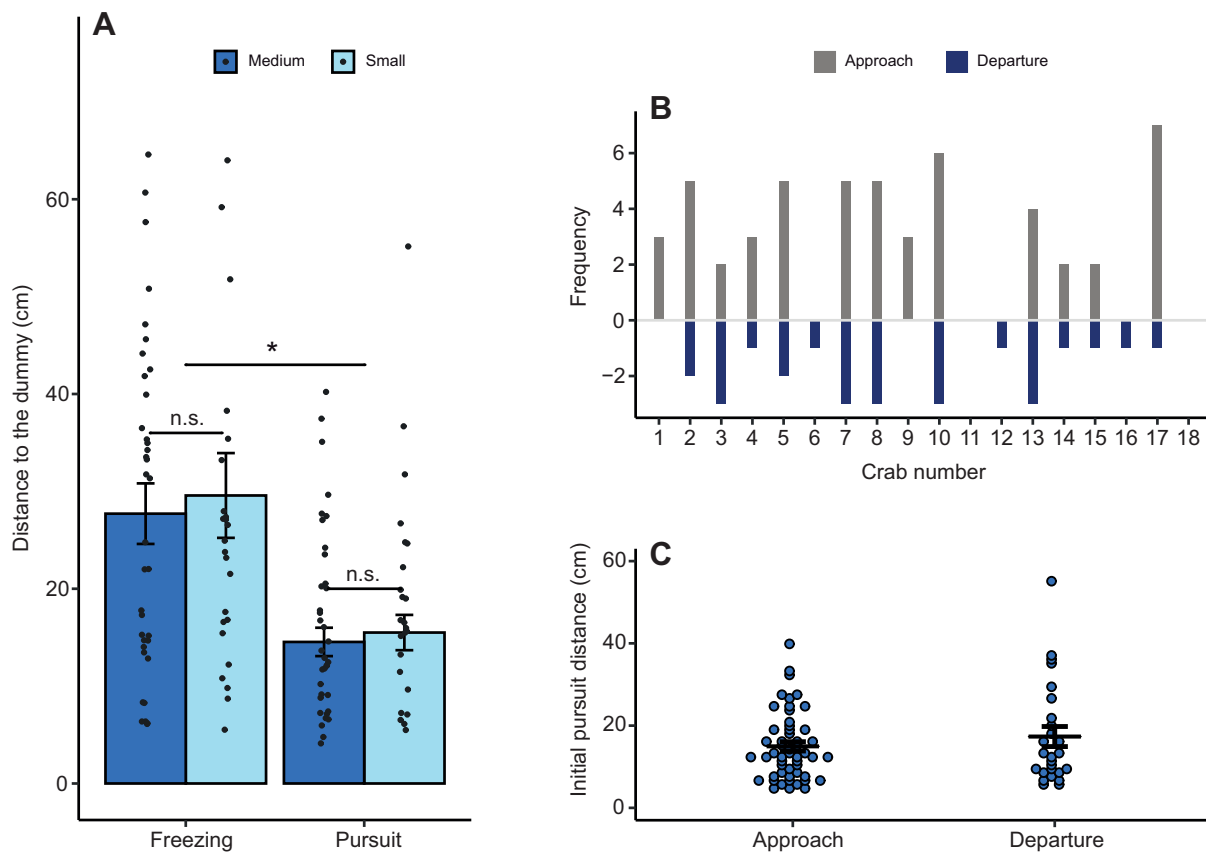


Fig. 7. Response distances that elicited crab predatory behavior. (A) Dummy distance at the occurrence of the transitory freeze and subsequent pursuit for the medium ($n=36$) and small ($n=24$) dummy. The freezing distance was significantly greater than the pursuit distance (Wilcoxon tests with Bonferroni correction, $P<0.001$), but there were no significant differences between the two dummies for the freezing or pursuit distances (Mann–Whitney test with Bonferroni correction, freezing $P=0.72$, pursuit $P=0.52$). (B) Number of predatory responses for each crab elicited when the dummy was approaching or departing. Data include responses initiated in still animals, i.e. when pursuits were not preceded by freezing. Crab numbers 1–9 and 10–18 were stimulated with the medium and the small dummy, respectively. (C) Pursuit distances of responses that were initiated before the dummy (either small or medium) reached the closest point to the crab (approach, $n=51$) and those that started when the dummy was already getting away from that point (departure, $n=26$). The two distances were not significantly different (Mann–Whitney test, $P=0.75$). A and C show individual data and the mean \pm s.e.m.

moving nearby on the ground. Here, we showed that the chasing response can be consistently induced and systematically studied in the laboratory. Interestingly, when confronted with an object moving

inside the artificial arena, the crab is capable of displaying different behaviors. It could just ignore the motion stimulus, freeze and remain frozen, freeze and then move away from the object or display a defensive reaction against it, or freeze and then run after it (Fig. 2). The freezing component may reflect the time it takes the animal to gain enough information about the stimulus in order to decide how to react. By using three dummy sizes moved at different velocities, we identified a set of conditions that prompts the occurrence of PR and that enhances the chances of ending with a successful prey capture.

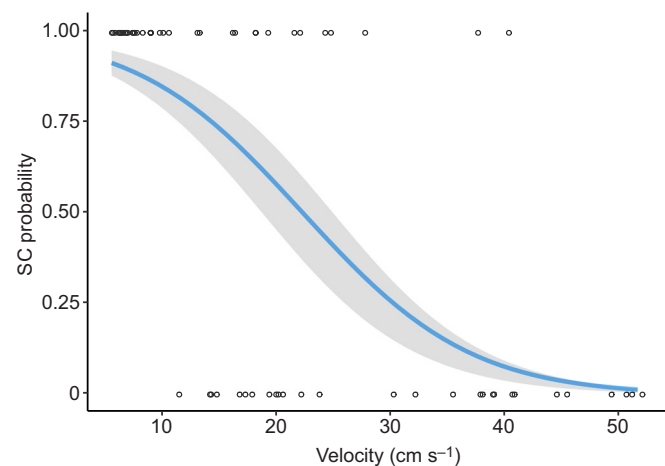


Fig. 8. Probability of SC as predicted by the statistical model. The solid lines represent the probability of SC as a function of dummy velocity. Shaded areas represent interquartile ranges. Circles represent data points on which the model was based. Further details are given in Results and Tables 1 and 2.

Dummy size as determinant of AR or PR

Mudflat crabs are preyed on by gulls and other seabirds; that is why they run away from or defend themselves against objects moving overhead (Zeil and Hemmi, 2006; Hemmi and Tomsic, 2015). Remarkably, the same small object moved above or below the horizon elicits two opposite behaviors, an avoidance response or a chasing response, respectively. Therefore, stimulus elevation appears to be used by the animal as a simple rule to distinguish prey and predators (Tomsic et al., 2017). In our experiments, when facing the large dummy, crabs mostly performed AR (Fig. 3). On the few occasions when PR was observed, the crab was rather far from the stimulus. The initial approach was stopped early and in no case did a crab perform a successful capture. From the crab's perspective, as it approached the dummy, the upper part of the dummy rose above the horizon. Thus, the

change of behavior occurring during the approach towards the large dummy was probably due to the apparent change in stimulus elevation.

The most effective dummy for eliciting PR was the medium-sized dummy. In fact, before stimulus repetition started to affect behavior, the proportion of PR was far larger than AR, FR or NR (Fig. 3). Because crabs are taller than the medium dummy, in a flat environment no matter the distance they always saw this dummy at the level of or below the horizon, fulfilling one important requisite for considering this stimulus as potential prey.

The small dummy was also effective at eliciting PR, though less so than the medium dummy. A considerable proportion of responses consisted of just freezing, suggesting that the animal detected the dummy but decided not to run after it. AR was never elicited by the small dummy, showing the crab did not consider this object size as a threat.

Tracking line distance and dummy distance

The probability of launching PR was also affected by the distance of the crab to the tracking line. The shorter this distance, the higher the PR probability. Within the range of effective distances (i.e. shorter than 20 cm; Fig. 5), the medium dummy was always more successful than the small dummy. It could be argued that this difference is simply because it is easier for an animal to visually detect the medium dummy. However, if that were the reason, it should be reflected by a parallel shift (or even a greater difference at larger distances) in the probability profiles of the two dummies, which was not the case. Besides, when we calculated the actual distance to the dummy, the mean values obtained for the two dummies were very similar (Fig. 7A). Moreover, the mean distance for the freezing component that preceded PR, which was initiated at a much greater dummy distance, was also similar between the two dummies (Fig. 7A). Therefore, the difference in probability for eliciting PR between the medium and the small dummy is unlikely to be caused by sensory limitations. We find more tenable that the difference reflects a bias in the preference of the animal based on an assessment of the stimulus reward value. In fact, prey size selection of bivalves is well documented in crabs (Micheli, 1995; Smallegange et al., 2008), although the involvement of visual information has not been particularly investigated.

Absolute dummy size preference and distance estimation

Olberg and colleagues (2005) investigated whether dragonflies can assess the distance to a potential prey and therefore its absolute size when deciding to take off after a moving object. They found that neither apparent size nor retinal speed was associated with takeoff. Because dragonflies preferred a certain stimulus size range, and the size of the stimulus cannot be determined without reference to distance, the authors concluded that dragonflies are able to estimate the distance to a prey. The range over which they estimated distance was about 1 m, which is a long distance considering the eye resolution and eye separation in these animals. The authors acknowledged that the mechanism of distance estimation was unknown, but suggested it may include a combination of stereopsis and motion parallax (Olberg et al., 2005).

The results in Fig. 6 show that, as for dragonflies, crabs do not use apparent dummy size or its retinal speed as a criterion for deciding to run after the dummy. Instead, within the range of absolute sizes explored in our experiments, crabs clearly preferred to prey on the medium dummy. A requisite for recognizing the absolute size of an object is to know at what distance it is located. The fact that crabs initiated pursuit of the medium and small dummy at identical distances (Fig. 7A) indicates that they were able to perform a rather

precise distance estimation. Within the range of distances analyzed in our experiments (<65 cm), there are several ways in which crabs can perform a robust visual estimation of the distance to an object. For an object on the ground, as in our experiments, crabs can use angular declination below the horizon (Ooi et al., 2001; Hemmi and Zeil, 2003) or stereopsis. So far, stereopsis has only been conclusively demonstrated in a single arthropod, the praying mantis (Nityananda et al., 2016). In *Neohelice*, we have recently shown that a large number of motion-sensitive neurons from the optic lobe are binocular (Scarano et al., 2018). These neurons are good candidates for distance estimators, as has been shown for neurons of the mantis (Rosner et al., 2019). Thus, the robust binocular neural network of *Neohelice*, in combination with our present results indicating that the crab is able to assess the distance to the dummy, offer good possibilities for discovering the use of stereopsis in a second arthropod. Further experiments using PR are being planned for this purpose.

Successful prey capture

Following the identification of dummy absolute size and distance as relevant features for the animal to decide to initiate PR, we investigated the factors that affected the rate of successful captures. The GLMM analysis identified that dummy velocity plays a major role. At velocities below 10 cm s⁻¹, the probability of SC was above 0.8, whereas for velocities beyond 30 cm s⁻¹, it decayed below 0.25. The maximum running speed of *Neohelice* is about 35 cm s⁻¹ (Oliva and Tomsic, 2012). When the crab is very close to the prey, it can jump towards it, reaching a much higher momentary speed. However, unless it is very close to the tracking line (a condition that was precluded in our study), there is no reason for a crab to run after an object that is moving faster than its own running speed. The reduction in the rate of SC with the increase in dummy velocity is because crabs missed the attack (see Movie 1) or the dummy reached the opposite corner before the crabs were able to get it. Both factors contribute to the low rate of SC obtained for those PR that were initiated when the dummy was already getting away from the crab.

Starvation period

Studies on different crab species have shown that the rate of predation increased after a few days of starvation and then stabilized or even declined (Sun et al., 2015). Prey size selectivity, however, was not significantly affected (Micheli, 1995; Smallegange et al., 2008). Our results showed no difference in PR probability across experimental days. One possible explanation is that the 3 days of starvation preceding the beginning of our experimental period led to a ceiling effect on the animal's motivation for hunting, such that no further differences could be discerned between days 4 and 10. Another, perhaps more interesting explanation is that the studies describing the effect of starvation on the predation rate were performed on motionless prey, mainly bivalves like clams, mussels or scallops. In contrast, the PR of *Neohelice* described here implies chasing a moving dummy. It is possible that motion stimuli override the effect of starvation observed in other crabs with immobile prey on the motivation to feed.

The effect of stimulus repetition

The reduction in PR probability observed across trials (Fig. 3A) could be due to a habituation learning process. Habituation of the escape response to repeated visual stimulation has been a subject of extensive investigation in *Neohelice*. Indeed, there is substantial knowledge on the behavioral, neural and molecular mechanisms underlying the short- and long-term habituation of the escape

response (Tomsic et al., 2009; Berón de Astrada et al., 2013; Tomsic and Romano, 2013; Tomsic and Maldonado, 2014). The waning of the PR observed across trials might entail habituation, offering an excellent opportunity for evaluating the mechanisms involved in two visual habituation processes of the same animal. However, further experiments using different intertrial intervals and long-term retention tests are required to be certain that the PR reduction is due to habituation.

Final remarks

Vision allows early detection, which gives time for evaluating the information available and making decisions about the most convenient strategy to be implemented in a particular situation. Investigations have demonstrated that in arthropods even apparent reflex behaviors, such as escape or chase responses to a visual stimulus, usually comprise different stages, each of which entails particular assessments and decisions (Hemmi, 2005; Lin and Leonardo, 2017). The use of single stimulus parameters, such as apparent size, retinal speed or combinations of these, as a criterion to initiate a response, has been shown in rather simplified experimental conditions. With the caveat of dealing with oversimplified situations, this approach proved to be successful for identifying central neurons involved in particular behaviors (Santer et al., 2012; Oliva and Tomsic, 2014, 2016; McMillan and Gray, 2015; von Reyn et al., 2017; Fabian et al., 2019). Studies under more naturalistic conditions, in contrast, revealed that animals make their decisions by computing multiple stimulus parameters as well as contextual information (Liden et al., 2010; Domenici et al., 2011a,b; Smolka et al., 2011; Hemmi and Tomsic, 2012). The complexity of such a reality imposes a serious limit for the identification of neural elements involved in a particular behavior using current technologies. The results of the present study tell us that the crab's decision to pursue a prey does not depend on a single factor. However, we identified a combination of main factors that increased the chances of eliciting the chasing response. From this, we predict that there must be neurons highly tuned to small targets (<2 cm), moving near the horizon slower than 25 cm s^{-1} and at less than 15 cm from the crab. We can now systematically search for such types of neurons.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: D.T.; Methodology: B.G., C.S., D.T.; Software: B.G., C.S.; Validation: D.T.; Formal analysis: B.G., C.S., D.T.; Investigation: B.G., C.S., D.T.; Resources: D.T.; Writing - original draft: D.T.; Writing - review & editing: B.G., C.S., D.T.; Supervision: D.T.; Project administration: D.T.; Funding acquisition: D.T.

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Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.217299.supplemental>

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