

## RESEARCH ARTICLE

# Flicker is part of a multi-cue response criterion in fiddler crab predator avoidance

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### SUMMARY

**Predator avoidance behaviour costs time, energy and opportunities, and prey animals need to balance these costs with the risk of predation. The decisions necessary to strike this balance are often based on information that is inherently imperfect and incomplete because of the limited sensory capabilities of prey animals. Our knowledge, however, about how prey animals solve the challenging task of restricting their responses to the most dangerous stimuli in their environment is very limited. Using dummy predators, we examined the contribution of visual flicker to the predator avoidance response of the fiddler crab *Uca vomeris*. The results illustrate that crabs let purely black or purely white dummies approach significantly closer than black-and-white flickering dummies. We show that this effect complements other factors that modulate escape timing such as retinal speed and the crab's distance to its burrow, and is therefore not due exclusively to an earlier detection of the flickering signal. By combining and adjusting a range of imperfect response criteria in a way that relates to actual threats in their natural environment, prey animals may be able to measure risk and adjust their responses more efficiently, even under difficult or noisy sensory conditions.**

Key words: sensory constraint, *Uca vomeris*, escape behaviour, vision, flicker, multi-cue response strategy.

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### INTRODUCTION

Prey animals constantly have to make life-or-death decisions. While ensuring escape from all real predatory threats, they also have to avoid costly false alarms. Because of the limitations of sensory systems, the information available to make these decisions is usually imperfect and incomplete (Hemmi, 2005a; Hemmi, 2005b; Koops, 2004; Koops and Abrahams, 1998; Lima, 1998; Luttbeg, 2002; Martin and Lopez, 1999; Sih, 1992). For instance, many animals cannot reliably determine important risk-related cues such as the distance, approach direction or speed of potential predators (Collett and Harkness, 1982; Hemmi, 2005a; Hemmi, 2005b; Hemmi and Zeil, 2005). Instead, they have to rely on simple rules-of-thumb to estimate predation risk (Bouskila and Blumstein, 1992; Koops and Abrahams, 1998; Welton et al., 2003).

These rules-of-thumb are not necessarily based on cues reflecting general properties of dangerous situations. Rather, the cues should be commonly available in the presence of a natural predator, and reliably detectable against unpredictable background noise. Differences in appearance and behaviour between commonly encountered dangerous and harmless animals, for example, can be reflected even in highly degraded signals or those viewed by comparatively simple sensory systems. Although these cues may not directly indicate risk, they can help determine a potential predator's identity or behaviour, and thus correlate with the relative risk it poses. By combining several such cues – some of which may be readily available but unreliable, while others may take longer to obtain but provide more risk-related information – prey animals can create robust

and efficient anti-predator strategies even with poor sensory information.

In a previous study (Smolka et al., 2011), we compared the signals that dangerous and harmless flying animals present to fiddler crabs in their natural habitat. The results showed that the spatio-temporal statistics of these signals, despite background noise, differ enough for the crabs to partially distinguish dangerous from harmless events. The cues they use to make this distinction include not only retinal speed and elevation (Hemmi, 2005b), but also flicker, which can be created, for example, by flapping bird wings.

The main goal of this study is to understand how flicker is used as part of a multi-cue response criterion to estimate the threat an object poses. We therefore aim to show (1) that flicker is used as a response criterion, (2) how flicker interacts with retinal speed and (3) that flicker does not trigger an immediate 'panic' response at the time of detection, but contributes to a more complex risk assessment strategy. Understanding how fiddler crabs weigh their response decisions against different criteria, and how these tie in with different stages of the escape response, will help us understand how prey animals in general might employ multi-cue, multi-stage escape strategies to respond to predators in an efficient and adaptable way.

### MATERIALS AND METHODS

#### Animals, apparatus and video analysis

Experiments were conducted in October 2006 with the fiddler crab *Uca vomeris* McNeill 1920 (Ocypodidae: Brachyura: Decapoda) on intertidal mudflats near Cunggulla (19°24'S, 147°6'E), south of

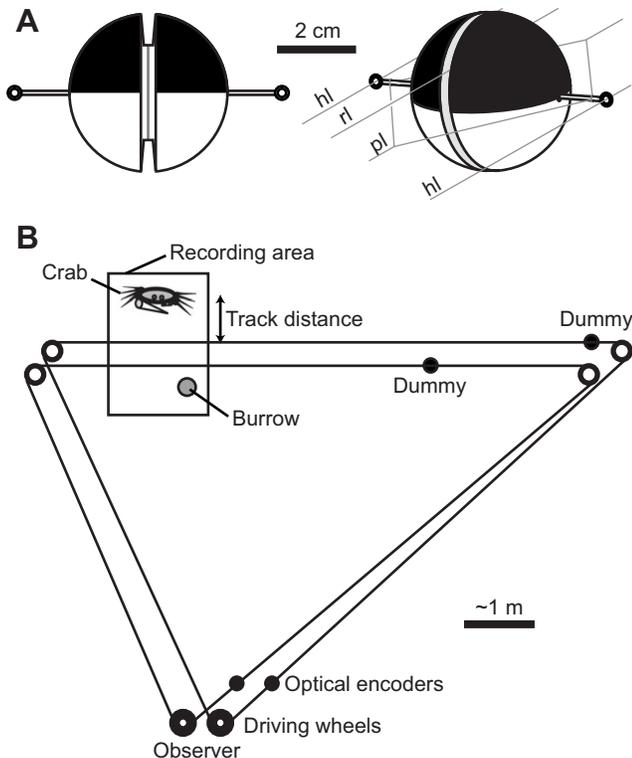


Fig. 1. Experimental setup. (A) Design of the flickering dummy. The loops on both ends were threaded onto two holding lines (hl). A third line [rotating line (rl)] was wrapped around the central groove and served to rotate the dummy while it was pulled by a fourth line [pulling line (pl)]. By halving the diameter of the inner groove, the dummy could be run at half speed and still rotate at the same frequency. (B) Schematic of the experimental setup from a bird's-eye view, showing the observer, a crab, the combined field of view of the two cameras and the stimulus apparatus (modified from Hemmi, 2005a).

Townsville, Queensland, Australia. Two camcorders (Panasonic NV-GS300, Kadoma, Osaka, Japan) were mounted on vertical steel poles approximately 1.6 m above the mudflat, monitoring adjacent areas of approximately 1 m<sup>2</sup> each within a crab colony.

Plastic spheres (4 cm diameter) with a narrow groove around their centre were used as dummy predators (Fig. 1A). Using two loops at the end of a metal axle through its centre, each dummy was suspended on two parallel monofilament lines (holding lines; Fig. 1A) that were strung between metal poles 6 to 8 m apart on the mudflat. The dummy was moved along this track, 20 cm above surface, by a non-stretch fishing line (pulling line; Fig. 1A). A fourth, stationary line (rotating line; Fig. 1A) was wound around the dummy's central groove and served to rotate the dummy while it was pulled along its track. The pulling line was wrapped around the poles at both ends of the track and around another pole near the operator (Fig. 1B), where it was moved by a motorised wheel, and its progress was recorded by an optical encoder. This made it possible to reconstruct the dummy's exact position even outside the cameras' field of view. To simulate the flicker of flapping bird wings, several dummies were painted white on one hemisphere and black on the other (Fig. 1A). Winding fishing line around the dummies' central grooves meant that all dummies rotated at a frequency that depends on their translational velocity and on the groove's inner diameter. Fully black or white dummies still rotated around the central axis, but produced no temporal variation in luminance, i.e. no flicker.

In each experiment, two dummies were present on their respective dummy tracks on the mudflat (Fig. 1B). The two dummies were then pulled individually towards the crabs in a randomised order, spaced such that the crabs were approached by one dummy every 2 to 3 min. Dummy presentations were randomised in the following way. Presentations were organised in blocks of three. Each block contained a random permutation of two repetitions of one condition and one presentation of the other condition. Consecutive blocks alternated in the repeated condition, resulting in a final design where no more than three consecutive repetitions of the same stimulus condition could occur and the total number of presentations was equal for each condition. Up to 12 blocks (=36 presentations) were included in a single experimental session.

Five sets of experiments were performed to test the influence of flicker on the predator avoidance decisions of fiddler crabs. First, the crabs' response distances to a black and a flickering dummy (Experiment 1) or a white and a flickering dummy (Experiment 2) were compared. Further, to test how flicker interacts with retinal speed, the crabs' responses to two dummies with different inner diameters were observed. When the dummy with the larger inner diameter was moved at twice the speed of the other dummy, both rotated and flickered at the same frequency, approximately 4.8 Hz, which is slightly higher than the wing-beat frequency of gull-billed terns, the crabs' main aerial predator (Land, 1999). This experiment was performed both with purely black dummies (Experiment 3) and with flickering dummies (Experiment 4). Finally, a control experiment tested whether the crabs actually saw the rotating dummies as flickering or whether they responded to the moving edges between the black and white hemispheres. For this purpose, responses to a vertically and a horizontally rotating dummy were compared (Experiment 5). The main experiments (1, 3 and 4) were each repeated in a new location on a separate day.

#### Video analysis and selection of responses

Videos were digitised, calibrated for perspective and optical distortion (Bouquet, 2010), and analysed at a sampling interval of 200 ms following procedures developed previously (Hemmi, 2005a). For the calculation of total response probability we included only dummy presentations during which (1) there was no interference by birds or other crabs, (2) the crab was more than 5 cm away from its burrow when the dummy started moving (to decrease the probability that a response was too short to be scored) and (3) the crab was inside the recording area when the dummy started moving. A total of 328 presentations met these criteria. For the analysis of response distance, crabs less than 5 cm away from their burrow were also included. To exclude unspecific crab reactions (e.g. to the movement of the operator or the fishing line), the analysis was limited to responses that occurred more than 3 s after the dummy started moving. The exact length of this interval has no influence on our main conclusions. Outliers – as shown in a box plot (R Development Core Team, 2011) – were removed from each experimental data set. Except for Experiment 4, this again had no effect on our conclusions (see Results).

The two days of experiment 1 showed different results. While the second day of this experiment shows a clear effect of the flickering dummy ( $P=0.008$ , see Results), the first day alone does not ( $N=110$ ,  $\chi^2=0.35$ ,  $P=0.55$ ). The combined data set of both days shows no significant effect of flicker, either ( $N=167$ ,  $\chi^2=2.54$ ,  $P=0.11$ ). We believe that this is because the first day was very early in the tidal cycle, a period when the crabs' responses often appear less specific and predictable (J.M.H. and J.S., personal observation). A pilot experiment conducted in 2005 ( $N=19$ ,  $\chi^2=6.79$ ,  $P=0.009$ )

clearly supports the result from the second day, and the full model combining all five experiments shows a very clear effect of flicker ( $N=368$ ,  $\chi^2=21.3$ ,  $P<0.001$ ). Whatever the reason for the difference found on the first day, we have decided to present data from the second day only, which appears to represent the crabs' normal behaviour. After these exclusions, a total of 257 crab responses (from 55 individual crabs, see Table 1) were included in the analysis.

### Statistical methods

For the statistical analysis, restricted maximum likelihood (REML) linear mixed models were calculated using the lmer function of the lme4 package in R version 2.13 (R Development Core Team, 2011). We took into account individual variance between crabs, between individual dummy presentations and between experimental days by treating them as random factors. Models were selected by sequentially fitting parameters and including those parameters that reached significance at a 5% level when added to the final model. Because burrow distance (the distance between a crab and its burrow at the time of response) and track distance (the distance between a crab and the closest point of the dummy track) are known to be important predictors of response distance (Hemmi, 2005a; Hemmi, 2005b; Hemmi and Merkle, 2009; Hemmi and Pfeil, 2010; Raderschall et al., 2011), they were included in all models even if they did not reach significance. This was the case in two instances (see Table 1), but it did not change the significance of other main effects and never changed the estimate of effect sizes by more than 7%. For higher reliability (due to larger sample size) and to be able to compare across experiments, we tested all two-way interactions in combined models that included data from several experiments. All REML models were graphically checked for a normal residual distribution.

### RESULTS

The crabs responded to all dummies following their typical multi-stage escape sequence (Hemmi and Pfeil, 2010; Hemmi and Zeil, 2005). At detection of the dummy they froze, i.e. they stopped all activity. Shortly afterwards, they started a sudden, fast home-run towards their burrow, where they again stopped and waited. Only when the dummy came even closer did they descend into their

burrows. The probability that a crab responded to a dummy with a home-run was so high (92.1% over all experiments) that it was impossible to identify which factors affected response probability. However, the response distance, i.e. the three-dimensional distance between dummy and crab at the time of response, did differ between the different treatments.

### Experiments 1 and 2: flicker triggers earlier home-runs

Crabs initiated their home-runs much earlier in response to a flickering dummy than to either a black (Hemmi, 2005a; Hemmi, 2005b; Hemmi and Merkle, 2009; Hemmi and Pfeil, 2010) or a white dummy, used here as an intensity control (Table 1, Fig. 2A,B). On average, crabs let the black dummy (Fig. 2A, black line) approach 46.5 cm closer than a flickering dummy presented in the same session (Fig. 2A, grey line). The difference between a flickering and a white dummy was even larger. The crabs reacted to the flickering stimulus when it was almost 1 m further away (Fig. 2B).

Crabs also responded earlier when they were further away from their burrow (Table 1, burrow distance; slope of fitted lines in Fig. 2). This observation held true for all five experiments. For every centimetre in distance to the burrow, the response distance increased by 1.8 or 3.3 cm in Experiments 1 and 2, respectively. Crabs also responded later to dummies that approached more directly, as is evident from the effect of track distance (Table 1).

### Experiments 3 and 4: flicker and dummy speed

In accordance with earlier studies, crabs responded significantly earlier to the faster of two non-flickering, black dummies (Table 1, Experiment 3; Fig. 2C) (Hemmi, 2005a; Hemmi, 2005b). A change of average dummy speed from 18.5 to 33.7 cm s<sup>-1</sup> increased the average response distance by 52.6 cm.

Crabs were still sensitive to speed while experiencing a flickering signal. We compared their responses to two dummies that flickered at the same frequency, but moved at different speeds. Again, the crabs reacted earlier to the faster dummy (Table 1, Experiment 4; Fig. 2D); they started their home runs when the faster dummy was on average 35.2 cm further away than the slower dummy. Experiment 4 was the only experiment where the inclusion of outliers

Table 1. Results of the REML linear mixed model analyses (random model: crab identity + trial identity)

Experiment	<i>n</i> ( <i>N</i> )	Model parameters/fixed effects ( $x_i$ )	Effect ( $b_i$ )	d.f.	$\chi^2$	<i>P</i>
1. Black vs flicker	57 (12)	Intercept	114.0	1	–	–
		Flicker	46.5	1	7.00	0.008
		Burrow distance	1.82	1	5.98	0.015
		Track distance	1.20	1	8.96	0.003
2. White vs flicker	54 (6)	Intercept	17.4	1	–	–
		Flicker	98.8	1	15.2	<0.001
		Burrow distance	3.24	1	6.83	0.009
		Track distance	2.82	1	10.2	0.001
3. Black fast vs slow	77 (16)	Intercept	97.6	1	–	–
		Speed (fast=1, slow=0)	52.6	1	21.3	<0.001
		Burrow distance	1.86	1	7.00	0.008
		Track distance	0.38	1	0.55	0.46
4. Flicker fast vs slow	45 (12)	Intercept	72.7	1	–	–
		Speed (fast=1, slow=0)	35.2	1	6.15	0.013
		Burrow distance	3.44	1	5.88	0.015
		Track distance	2.38	1	7.77	0.005
5. Horizontal vs vertical flicker	24 (9)	Intercept	137.1	1	–	–
		Flicker direction (horizontal=0, vertical=1)	–	1	0.57	0.45
		Burrow distance	6.61	1	18.7	<0.001
		Track distance	–0.28	1	0	1

Burrow distance and track distance were measured at the time of response. Total number of crab responses and number of individual crabs are given as *n* and *N*, respectively. The model predicts the response distance in cm as  $d=\sum b_i x_i$ .

made a significant difference. Although only a single outlier was present in the data set (Fig. 2D, black circle), no significant speed effect was found when the outlier was included ( $N=46$ ,  $\chi^2=1.31$ ,  $P=0.25$ ). There is no evidence that the magnitude of the speed effect is different from the black dummy experiment (Fig. 2C) – there is no interaction between speed and flicker in a combined model of Experiments 1, 3 and 4 ( $N=180$ ,  $\chi^2=0.946$ ,  $P=0.33$ ).

In both speed experiments, the crabs' response distances again strongly depended on their distance from their burrow. For every centimetre away from their burrow, they responded at a 1.86 cm longer distance to the black dummy, and a 3.44 cm longer distance to the flickering dummy. There was no effect of track distance in Experiment 3 ( $P=1.00$ ; Table 1). In Experiment 4, this effect was significant and similar in size to the effects in Experiments 1 and 2 ( $2.37 \text{ cm cm}^{-1}$ ). Again, this indicates that crabs responded later to a dummy that approached them more directly.

#### Experiment 5: crab responses are independent of the dummy's rotational axis

To examine whether the crabs react to the dummy's internal motion or to flicker (an oscillating change in the whole dummy's luminance), we exposed the crabs to dummies rotating around either their horizontal or their vertical axis (Table 1, Fig. 2E). Because the crabs show much earlier escape responses to a vertically moving object than a horizontally moving one (Hemmi, 2005a; Smolka et al., 2011), we would expect them to respond earlier to the dummy rotating around its horizontal axis if indeed the internal motion was the critical cue. We found no such difference between the crabs' responses to these two dummies (effect size 13.7 cm,  $N=24$ ,  $\chi^2=0.57$ ,  $P=0.45$ ). Response distance increased by 6.61 cm per 1 cm distance to the burrow, and there was no significant effect of dummy track distance ( $P=1.00$ ; Table 1).

#### Burrow distance and approach direction

Over the five experiments, the most robust predictor of response timing was a crab's distance to its own burrow ( $x$ -axis, Fig. 2A–E). Interestingly, this dependence becomes stronger as the crabs are approached more often by flickering dummies (Fig. 2F). In Experiments 1 and 2, where flickering and non-flickering dummy presentations were interspersed, the effect of burrow distance was stronger than in Experiment 3, in which only non-flickering dummies were presented. The effect in Experiments 1 and 2 was also stronger than in previous studies, which all used non-flickering dummies (Hemmi, 2005a; Hemmi, 2005b). In Experiments 4 and 5, both containing only flickering dummies, the effect was stronger yet. We tested this dependence statistically by demonstrating an interaction between the proportion of presented dummies that flickered (0, 50 and 100%) and the effect of burrow distance in a combined model of all experiments ( $N=258$ ,  $\chi^2=9.08$ ,  $P=0.011$ ). Like all other models, this combined linear model was adjusted for differences between individual crabs, runs and days. A similar interaction with the proportion of flickering dummies was not found for track distance ( $N=258$ ,  $\chi^2=3.95$ ,  $P=0.14$ ).

## DISCUSSION

### Flicker as a response cue

The results show that fiddler crabs use visual flicker as part of a complex multiple-cue response criterion in predator avoidance. Crabs responded earlier to flickering black-and-white dummies than to purely black or white dummies (Fig. 2A,B). Both black and flickering dummies elicited earlier responses when they moved faster (Fig. 2C,D). These results indicate that flicker is used in conjunction

with other visual cues such as retinal speed and presumably also size and elevation (Hemmi, 2005b). In all experiments, the crabs responded earlier when further away from their refuge. This effect was stronger when the crabs were exposed to flickering dummies (Fig. 2F). Finally, crabs reacted similarly to horizontally and vertically flickering dummies (Fig. 2E). As the crabs are far more sensitive to vertical motion (Hemmi, 2005a; Smolka et al., 2011), this indicates that they are truly perceiving the dummies as flickering (i.e. they see an oscillating change in object luminance) rather than reacting to the dummies' internal motion. This result is not surprising considering the crabs' visual acuity (Smolka and Hemmi, 2009). At typical response distances, dummies only occupied a visual angle of approximately 0.6 to 2.3 deg (at approximately 4 and 1 m, respectively). The crabs would thus have seen them with just one or two ommatidia, making it unlikely that they could perceive the dummy's internal motion.

The results very clearly support the notion that the crabs respond earlier to a flickering dummy than to a non-flickering dummy. As stated in detail in the Materials and methods, there was one day for Experiment 1 where this was not the case. This particular day was the very first day of the workable tidal cycle, when the site was sufficiently exposed during low tide. During those early days, crabs often appear more nervous and respond in a less specific way (J.M.H. and J.S., personal observation) than during later parts of the tidal cycle. The relevance of this behavioural difference is currently unknown. As none of our published studies on fiddler crabs has ever included results from this early period, we omitted this day from the final analysis.

Fiddler crabs use flicker in predator avoidance because it probably provides one of the earliest cues to detect the crabs' main predators in a noisy natural environment. Flicker, i.e. rapid changes in intensity, can be evaluated by a single ommatidium. This makes it an excellent early cue for predator avoidance. Moreover, flicker is closely correlated with the behaviour of gull-billed terns, the crabs' main predators in the study area (Land, 1999). These birds trawl the mudflats 2–3 m above the ground. When they have spotted a crab, they stop in mid-air and swoop down to catch it, a manoeuvre that creates a high-contrast flicker signal (Smolka et al., 2011).

In addition to carrying specific predator-related information, flickering may also increase the salience of the approaching dummies. However, it is important to realise that the crabs do not simply react earlier because they detect the potential predator earlier. If the crabs responded to the dummy as soon as they detected it, there would be no effect of crab–burrow distance because, on average, the dummy does not change its visibility when the crab moves away from its refuge. Crab–burrow distance, however, was significant in all five experiments and has been shown to be significant in all previous experiments (e.g. Hemmi and Pfeil, 2010). This indicates that the crabs do not respond immediately when they first detect the dummy, but that they delay their response when they are close to the safety of their refuge. It is still possible, though, that the crabs respond to an object based on its salience, whether that is through increased speed, contrast or flicker. Comparing results from different experiments actually shows that the effect of burrow distance becomes stronger, i.e. crabs are generally more cautious in the presence of flickering dummies (Fig. 2F). This might be a consequence of the extremely limited information content of flicker cues. Although a flickering signal can only be created by a moving object, it provides little information about that object's distance, speed, heading, identity or, most importantly, time to contact. Thus deprived of reliable information to determine a safe escape time, the crabs have to 'play it safe' and respond earlier. This might also

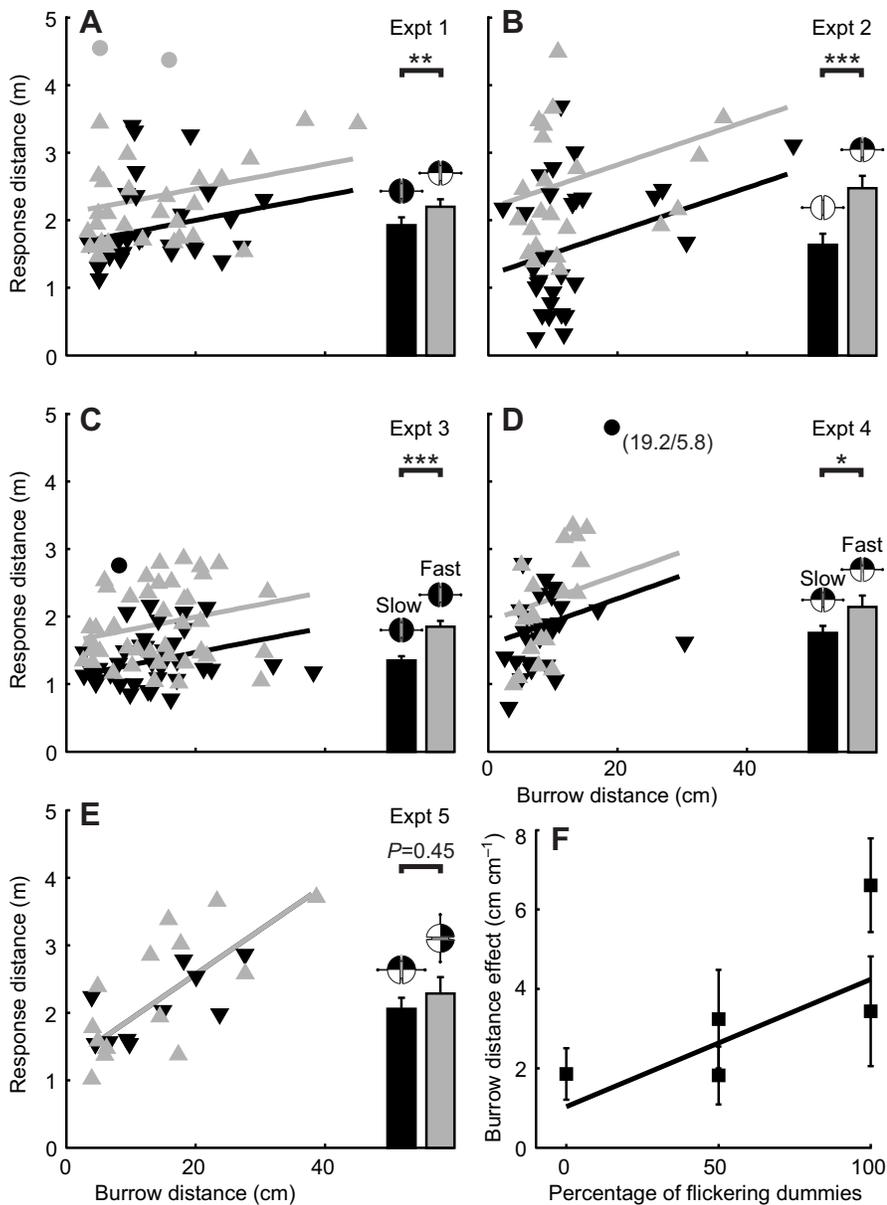


Fig. 2. (A–E) Home-run response distances in response to different dummy predators, shown as raw data (triangles), outliers (circles), model predictions (lines) and bar graphs of means ( $\pm$ s.e.m.). The outlier in D lies outside the plot area, so coordinates are given. Track distance was set to its mean to calculate model predictions. Crabs respond earlier to flickering dummies than to black (A) or white (B) dummies. When approached by black (C) or flickering dummies (D) of different speeds, crabs respond to the faster dummy earlier. There is no difference between responses to a horizontally and a vertically flickering dummy, indicating that crabs react to the flicker, not the internal motion of the dummy (E). The effect of burrow distance (slope) is stronger in experiments where only flicker dummies were presented (D,E) than in experiments where they were interspersed with non-flickering dummies (A,B) or where only non-flickering dummies were presented (C). This effect of flicker, as estimated by the linear model is shown in F. Error bars denote  $\pm$ s.e.m.

be the reason for the large number of false alarms observed in natural responses to the swoop of a distant tern or the passage of a fast, dark (harmless and distant) bird in front of a bright cloud (Smolka et al., 2011). Both of these signals flicker strongly and, without unambiguous additional information, the crabs have to assume that the threat is real.

As in previous studies, crabs reacted earlier the less directly a dummy approached them (i.e. the larger the track distance; Fig. 1). The reason for this paradoxical effect is that less direct approaches create higher retinal speeds (Hemmi, 2005a; Hemmi, 2005b; Hemmi and Zeil, 2005). In contrast to the effect of burrow distance, the effect of track distance does not change in the presence of flickering dummies. Although larger track distance decreases flicker contrast (which may indicate decreased risk) because the dummies are seen more from the side, this effect is negligible compared with the increase in retinal speed (which indicates increased risk). If, for instance, the approach angle (0 deg being a direct approach) changes from 7.9 to 15.4 deg (the lower and upper quartile, observed at the time of response), flicker contrast decreases by 2.7%. At the same

time, retinal speed increases by 37–85% depending on the distance to the dummy (calculated here for 1 and 4 m). In short, the effect of track distance is due mainly to an increase in retinal speed, and is unaffected by the presence of flickering dummies.

#### Flicker as part of a multi-cue response criterion

If animals had perfect sensory information, they could use a few simple criteria to make decisions about their escape responses. If, for example, the distance and translational speed of the predator were known, a prey animal could calculate a safe escape time at which it would have just enough time to reach its refuge (e.g. Kramer and Bonenfant, 1997; Ydenberg and Dill, 1986). For fiddler crabs, like for many other animals, this information is not available. Therefore, decisions have to be based on noisy and unreliable sensory cues, which are only weakly correlated with risk. To deal with this problem, fiddler crabs combine several visual cues, which, on their own, are poor predictors of risk, into a complex decision criterion that could be described as the visual signature of an approaching object.

One advantage of such a multi-cue response criterion is that different parameters can reflect different balances between risk-sensitivity and the prevention of false alarms. Flicker, for example, can be measured in one individual ommatidium and therefore provides possibly the earliest, safest, but least-specific response criterion. The information contained in this cue confounds retinal speed with an object's contrast change and cannot distinguish between vertical and horizontal components of speed. Vertical retinal speed is a better indicator of risk for fiddler crabs, because their main bird predators fly at a constant height and are therefore seen at increasing elevations as they approach (Hemmi and Zeil, 2005). Directional speed measurements, however, which could differentiate between horizontal and vertical components, can only be performed when the signal is seen by at least two neighbouring ommatidia. Later yet, when the predator is much closer and its image larger, the crabs may acquire even more risk-related cues such as angular size or looming. While this may be too late for the home-run decision, crabs appear to use these cues when deciding whether to continue their escape underground (Hemmi and Pfeil, 2010; Hemmi and Tomsic, 2012). Combining several cues can thus provide an adaptable and sensitive response system.

An added advantage of the combination of multiple cues is that it is extremely adaptable to changes in predator strategies or the appearance of a new predator, and makes it more difficult for predators to develop counter-strategies. Additional cues in effect constitute additional 'lines of defence'. If, for instance, crabs relied solely on a speed threshold, predators could develop a strategy of approaching in slow, straight paths directly towards their target to minimise the retinal motion they create. The prey animal would be forced to reduce its thresholds and increase the risk of false alarms. The same is of course true for most visual cues when taken on their own, with the possible exception of looming (Hemmi and Pfeil, 2010; Hemmi and Tomsic, 2012).

Finally, a multi-cue strategy might be more adaptable in an environment with frequent motion noise and diverse predator types. It allows for selective habituation of individual cues while still remaining responsive (Hemmi and Merkle, 2009; Hemmi and Zeil, 2005; Raderschall et al., 2011). If, for instance, the crabs experience strong constant flicker due to jittering leaves of a nearby mangrove tree, they can safely choose to ignore flicker in this part of the visual field and identify predators by their strong motion signature.

### Conclusions

Fiddler crabs rely strongly on flicker as a pragmatic criterion for the early identification of potential threats. When approached by a flickering dummy, crabs respond earlier. Far from being a 'panic' response, however, the timing of this escape response is also modulated by other, more risk-related factors such as retinal speed and the crab's distance to its own burrow. The fiddler crab example demonstrates how multi-cue signal processing, combined with a multi-stage response strategy (Hemmi and Zeil, 2005), can create a flexible and efficient predator avoidance system despite sparse and noisy information. By combining several early and unspecific cues with more complex ones that take longer to obtain, prey animals

can adjust their escape responses to their natural predators and thus flexibly optimise the trade-off between risks and costs of predator avoidance behaviour. The future study of natural predator signals and their relevance to crabs and other animals will show how widespread these strategies are in the animal kingdom, how exactly they are implemented, what makes a 'good' predator-related cue, at what level criteria are combined, and how easily their hierarchy can be changed.

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### REFERENCES

- Bouquet, J. Y. (2010). Camera calibration toolbox for Matlab. Available at <http://www.vision.caltech.edu/bouquet/>.
- Bouskila, A. and Blumstein, D. T. (1992). Rules of thumb for predation hazard assessment: Predictions from a dynamic model. *Am. Nat.* **139**, 161-176.
- Collett, T. S. and Harkness, L. I. K. (1982). Depth vision in animals. In *Analysis of Visual Behaviour* (ed. D. J. Ingle, M. A. Goodale and R. J. W. Mansfield), pp. 111-176. Cambridge, MA: MIT Press.
- Hemmi, J. M. (2005a). Predator avoidance in fiddler crabs. I. Escape decisions in relation to the risk of predation. *Anim. Behav.* **69**, 603-614.
- Hemmi, J. M. (2005b). Predator avoidance in fiddler crabs. II. The visual cues. *Anim. Behav.* **69**, 615-625.
- Hemmi, J. M. and Merkle, T. (2009). High stimulus specificity characterizes anti-predator habituation under natural conditions. *Proc. Biol. Sci.* **276**, 4381-4388.
- Hemmi, J. M. and Pfeil, A. (2010). A multi-stage anti-predator response increases information on predation risk. *J. Exp. Biol.* **213**, 1484-1489.
- Hemmi, J. M. and Tomsic, D. (2012). The neuroethology of escape in crabs: from sensory ecology to neurons and back. *Curr. Opin. Neurobiol.* **22**, 194-200.
- Hemmi, J. M. and Zeil, J. (2005). Animals as prey: perceptual limitations and behavioural options. *Mar. Ecol. Prog. Ser.* **287**, 274-278.
- Koops, M. A. (2004). Reliability and the value of information. *Anim. Behav.* **67**, 103-111.
- Koops, M. A. and Abrahams, M. V. (1998). Life history and the fitness consequences of imperfect information. *Evol. Ecol.* **12**, 601-613.
- Kramer, D. L. and Bonenfant, M. (1997). Direction of predator approach and the decision to flee to a refuge. *Anim. Behav.* **54**, 289-295.
- Land, M. F. (1999). The roles of head movements in the search and capture strategy of a tern (Aves, Laridae). *J. Comp. Physiol. A* **184**, 265-272.
- Lima, S. L. (1998). Nonlethal effects in the ecology of predator-prey interactions: what are the ecological effects of anti-predator decision-making? *Bioscience* **48**, 25-34.
- Luttbeg, B. (2002). Assessing the robustness and optimality of alternative decision rules with varying assumptions. *Anim. Behav.* **63**, 805-814.
- Martin, J. and Lopez, P. (1999). When to come out from a refuge: risk-sensitive and state-dependent decisions in an alpine lizard. *Behav. Ecol.* **10**, 487-492.
- R Development Core Team (2011). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Raderschall, C. A., Magrath, R. D. and Hemmi, J. M. (2011). Habituation under natural conditions: model predators are distinguished by approach direction. *J. Exp. Biol.* **214**, 4209-4216.
- Sih, A. (1992). Prey uncertainty and the balancing of antipredator and feeding needs. *Am. Nat.* **139**, 1052-1069.
- Smolka, J. and Hemmi, J. M. (2009). Topography of vision and behaviour. *J. Exp. Biol.* **212**, 3522-3532.
- Smolka, J., Zeil, J. and Hemmi, J. M. (2011). Natural visual cues eliciting predator avoidance in fiddler crabs. *Proc. Biol. Sci.* **278**, 3584-3592.
- Welton, N. J., McNamara, J. M. and Houston, A. I. (2003). Assessing predation risk: optimal behaviour and rules of thumb. *Theor. Popul. Biol.* **64**, 417-430.
- Ydenberg, R. C. and Dill, L. M. (1986). The economics of fleeing from predators. *Adv. Stud. Behav.* **16**, 229-249.