

The neuroethology of escape in crabs: from sensory ecology to neurons and back

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A major challenge in neurobiology is to understand how brains function in animals behaving in the complexity of their natural environment. Progress will depend on our ability to correctly interpret results from laboratory experiments in the light of information processing demands identified by studying the organization of behaviour and the flow of information in naturally behaving animals. Predator avoidance responses of semi-terrestrial crabs offer an excellent opportunity for such an approach. We review here findings from two distinct lines of research: (1) Field studies which have characterized the structure and context of escape behaviour to real and dummy predators, and (2) Laboratory studies which have used computer-simulated images and *in vivo* intracellular recordings to identify and characterize individual neurons implicated in the control of escape. The results of both approaches highlight the influence of behavioural and environmental context in structuring escape. In order to understand how context and the complex flow of signals are processed and translated into behaviour in natural environments it is imperative that future studies take electrophysiology outdoors.

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Introduction

Understanding the neural control of behaviour requires detailed knowledge of the brain and its neural circuits. It also requires an appreciation for how animals operate in the complex natural conditions in which they move, interact and learn. Studying freely roaming animals outdoors,

however, adds several challenges. It becomes difficult to monitor neural activity and measure and control the information animals have available to make decisions. We are therefore forced to take animals into controlled laboratory settings, restrict their movements and simplify their sensory input. As a consequence, even when we know how neurons respond to certain stimuli, it remains difficult to interpret these responses in relation to the natural conditions under which the neural circuitry has evolved.

Context has a powerful influence on behaviour and neural processing [1^{*}]. In the visual domain, for instance, increasing evidence shows that neurons respond differently to natural or naturalistic stimuli compared to the simplified abstract versions commonly used in laboratory experiments [2,3^{*},4,5^{*}] and that environmental conditions, such as ambient light, temperature and behavioural context dramatically affect neural processing [6^{••},7,8].

Context is unlikely to affect neural processing like the flipping of a simple set of switches. Contextual cues, most probably, lead to more complex changes in neuronal response patterns, which are difficult to predict or understand in isolation. The stomatogastric nervous system, for example, contains only 30 cells, but is affected by at least 20 modulators that all lead to different motor patterns [9]. Context is not always well defined and, under natural conditions, animals are often exposed to a myriad of dynamically changing, and sometimes competing, contextual cues. Neuronal circuits have evolved to deal with such uncertainty and the resulting solutions should be reflected in the information processing mechanisms of contemporary animals. The challenge is to find ways to integrate neurobiological and ecological analyses to characterize the temporal dynamics of contexts, stimuli and behaviour and to identify the precise information processing demands associated with natural tasks.

Here we review work on the escape response of semi-terrestrial crabs that have been studied using two complementary approaches. The first approach is primarily concerned with identifying the visual information available to fiddler crabs (*Uca spp*) and the responses they make to predators under natural conditions. The second approach analyses escape behaviour in the grapsid crab *Neohelice granulata* (previously *Chasmagnathus granulatus*) [10] in the laboratory and records from interneurons involved in processing predator-related visual information in restrained, but intact and behaving animals. We compare the results of these studies in an attempt to

combine them into a single framework and highlight the extent to which escape responses and the underlying neural processing mechanisms are modified by context and experience. At this point it is not always clear to what extent the differences we find reflect species differences, but preliminary experiments suggest that these are not the main cause of response variation.

Crab escape behaviour as a model system for the neural control of behaviour

The escape response of crabs lends itself particularly well to complementary laboratory and field research. It is easy to record intracellularly from awake crabs and since they have low visual resolution and their main predator, birds, provide only visual cues [11], escape responses can be reliably triggered with relatively simple dummy predators or computer simulations [12,13]. Long-term observations of natural behaviour with video cameras are straightforward because these crabs are central place foragers that live in simple, unobstructed environments (Figure 1) [14,15]. It is also possible to measure the sensory information crabs have available while making decisions [16,17] because we know the sampling array of their compound eyes [18*,19–21] and the way they hold and move their eyes [22].

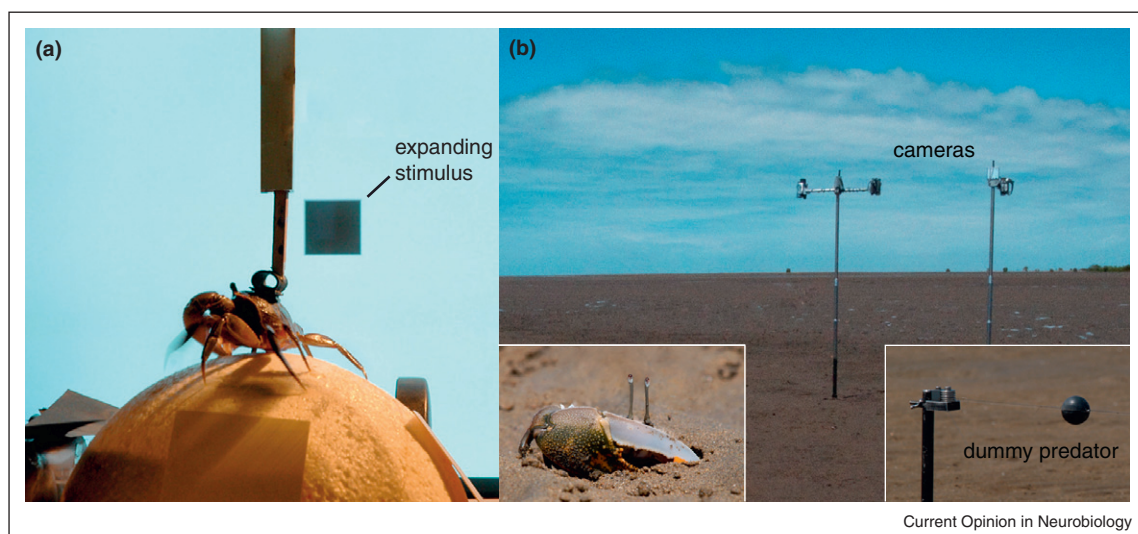
Field experiments provide information on the detailed behavioural organization the brain has evolved to produce, which allows us to predict the computations neural circuits must be able to perform. This informs the

interpretation of neural mechanisms discovered in physiological experiments in a behavioural, ecological and evolutionary context. Laboratory experiments in turn provide the mechanistic understanding of the neural circuitry underlying escape responses. There are also undoubtedly many extraneous variables influencing the escape response, such as an animal's history as burrow owner and its social or mating status, that cannot easily be controlled or measured under natural conditions, but can be regulated in the laboratory.

Predator avoidance in crabs

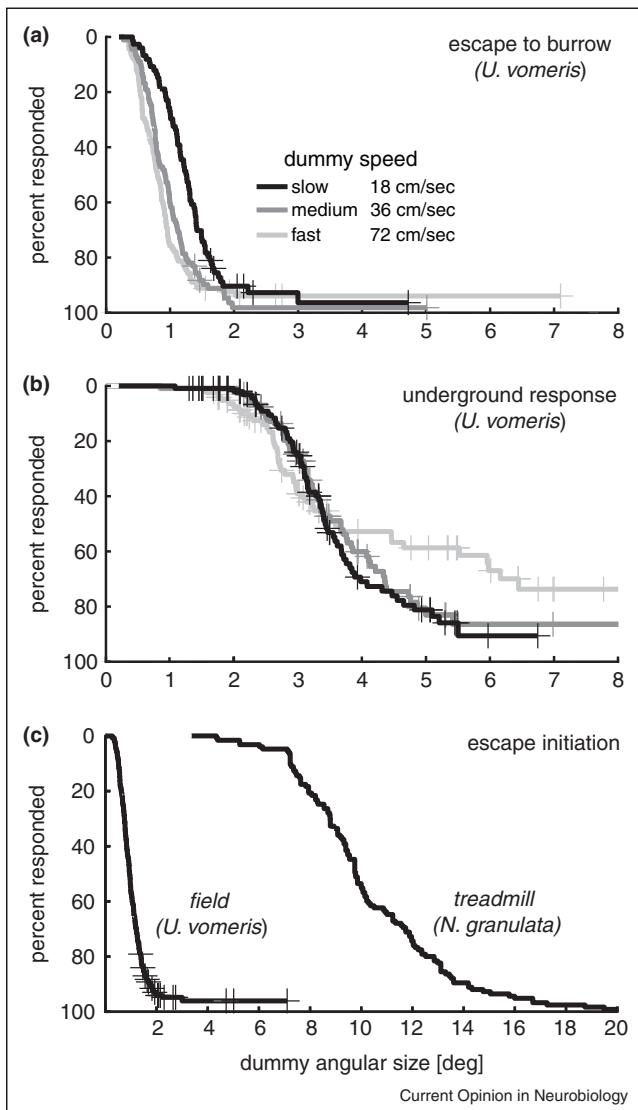
Field experiments have shown that *Uca vomeris* responds to approaching predators in multiple stages. They first freeze, then run back to the burrow before finally disappearing underground into the safety of the burrow [23,24] (Figure 2a,b). The initial freeze response makes it harder for predators to detect the crabs and brings the crabs' own visual system to rest, reducing motion blur. Only when a bird comes closer, do the crabs run towards their burrow. Escape responses occur very early, at the limits of the crabs' low sampling resolution, when the angular size of a bird is mostly less than 2 degrees [12,17,23]. The part of the eye used to detect predators, has a low sampling resolution of about 0.5 cycles/degree at 10 degrees above the horizon (1 degree interommatidial angle) [18*]. When crabs first run to the burrow, a predator is thus seen by only one or two ommatidia. Despite this low resolution, the early decision to escape

Figure 1



The escape response of crabs can be investigated both in the field and the laboratory making it an excellent model system for understanding the neural control of behaviour. (a) A tethered grapsid crab *Neohelice (Chasmagnathus) granulata*, mounted above a freely rotating styrofoam ball, attempts to run away from an expanding black square. This relatively simple stimulus can be used for both behavioural and electrophysiological experiments. Two optic flow sensors are used to measure the ball's rotations and estimate the trajectory and speed of the crab's escape run. (b) The natural environment of the fiddler crab *Uca vomeris* together with three video cameras used to record crab behaviour during field experiments. The fiddler crabs' size, simple environment and their burrow-oriented behaviour allow us to reconstruct the sensory input crabs have available during natural and dummy predator attacks (see text for more detail). Insets show a male fiddler crab with its massively enlarged claw emerging from the security of its burrow (left) and the typical dummy predator used to trigger escape responses (right).

Figure 2



Escape thresholds vary substantially depending whether crabs are away from their burrow (a), at the burrow's entrance (b) or in the laboratory on a treadmill (c). All lines depict inverted cumulative distribution functions, also known as a survival curves. The curves show the percentage of crabs that responded before the dummy reached a certain angular size. Crosses indicate censored data points, where the dummy had reached its largest possible angular size before a response was triggered. (a) In their natural environment, fiddler crabs (*Uca vomeris*) escape towards their burrow very early (when predator distances are large), when the dummy's angular size is still below 2 degrees. Data have been separated into the three groups according to the speed of the approaching dummy. Crabs escape towards their burrow earlier when the dummy moves faster. (b) When crabs are at the entrance of their burrow, they respond later, after the dummy's angular size has increased to about 3–4 degrees. For experimental details see [17]. (c) When tethered to a treadmill, responses to a 5 cm black square approaching the crab directly at 20 cm/s from a 75 cm distance are initiated much later in *N. granulata* (black lines and bars) than in fiddler crabs in the field. On average, *N. granulata* run away when the angular size of the stimulus has increased by about 6 degrees from its initial starting size of 4 degrees. For experimental details see [13]. Fiddler crab response

towards the burrow is affected by numerous stimulus attributes. Fiddler crabs run home earlier in response to larger, higher and in particular faster dummy predators [12,17], indicating that they use retinal speed as part of their decision criteria [17,23].

One clear difference between dummy predators and real birds is that the beating wings produce flickering changes of light intensity. Depending on the direction of sunlight, wings can appear very bright or almost black. In recent experiments where natural predation events were filmed simultaneously with crab responses, flicker (calculated as the temporal variation of light intensity reaching a photo-receptor) was the strongest predictor of response onset [25]. This might indicate that the decision to escape to the burrow is not triggered by retinal speed *per se*, but rather by flicker to which retinal speed contributes – faster movements produce stronger flicker.

In laboratory experiments, where grapsid crabs (*N. granulata*) are restricted to a treadmill [13], escape responses show a similarly staged organization to those of fiddler crabs. In response to a looming stimulus, *N. granulata* often first freezes and then runs away. Only when the stimulus approaches very close and expands quickly do animals raise their claws in defence. Like fiddler crabs, *N. granulata* react to tangentially moving objects as well as to directly approaching stimuli [13] and changes in the direction of an approaching object induce immediate changes in the crabs' escape direction. This indicates that escape is continuously adjusted using visual information [26,27]. There are a number of interesting differences, however, in the way crabs in the laboratory respond to computer-generated stimuli, compared to crabs confronted with bird dummies in the field. The absence of a refuge in the laboratory is probably a main factor contributing to these differences. Firstly, response thresholds for escape are significantly higher in the laboratory, regardless of whether the stimuli are looming or not [17,22,28] (Figure 2c). Secondly, on the treadmill crabs always run away from the stimulus, while under natural conditions they may run towards an approaching bird to reach their burrow. When there is no burrow available, however, they similarly run away from the stimulus [27,28].

Context dependence of the escape response

The experiments described above demonstrate that the 'simple' escape response is surprisingly flexible and is continuously adjusted according to the animal's immediate behavioural and environmental circumstances. The following three examples further highlight the diversity of contextual influences on the escape response.

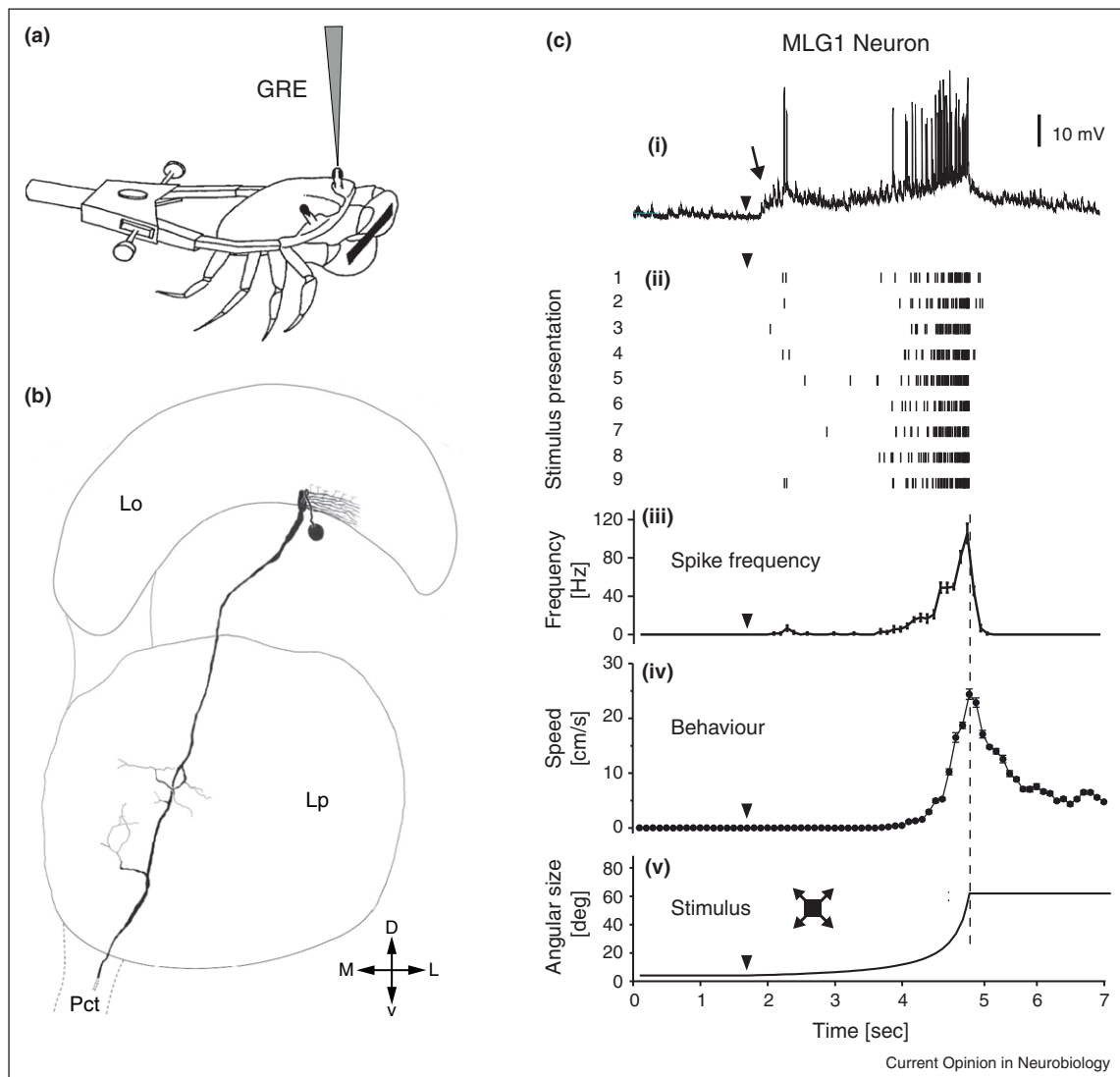
averages have been replotted from panel (a) for comparison. Note the change in x-axis scale for panel (c). The absence of a refuge in the laboratory is probably one of the main factors contributing to these differences.

First, fiddler crabs respond earlier to a threat when they are further away from the safety of their burrow [12,25^{*}]. Crabs can only see their burrow when they are within 10–15 cm of its entrance [29,30] and must rely on path integration when further away [31,32]. Path integration uses proprioceptive information to continuously update the crabs' position relative to the burrow [31,33,34]. The

neural escape circuits thus need to integrate visual and proprioceptive information to appropriately adjust their response timing.

Second, crabs in their natural environment use different response criteria at different stages of their escape sequence. While the decision to escape towards the

Figure 3



Morphological and physiological characteristics of MLG1 neurons. **(a)** A schematic of the electrophysiological preparation. *N. granulata* is held firmly by its carapace without restraining the legs. A rubber band glued to the claws restricts their movement. The eyestalks are cemented to the carapace and a glass recording electrode (GRE) gains access to the optical neuropils through a small opening in the medial-dorsal surface of the eye's cuticle. **(b)** Illustration of one of the 14 units that compose the MLG1 class of neurons [26], constructed from whole mount confocal images of an intracellularly stained cell. *Abbreviations:* Lo, lobula; Lp, lateral protocerebrum; Pct, protocerebral tract. **(c)** **(i)** The spike frequency of MLG1 cells reflects the timing and speed of escape runs. The trace shows a typical response of a MLG1 neuron [13] to the same directly approaching stimulus (Figure 1a) as used for the experiments in Figure 2c. A thin arrow indicates when synaptic activity of the neuron clearly increases above resting level. Arrowheads mark the start of the stimulus expansion in all panels. **(ii)** The timing of spikes from nine consecutive stimulus presentations illustrate the consistency of the response. **(iii)** Spike frequency: Peristimulus time histogram illustrating mean spike rate for the nine presentations for 100-ms time bins (mean \pm s.e.). **(iv)** Behaviour: The escape response of animals on a treadmill exposed to the same stimulus correlates well with the peristimulus time histogram. **(v)** Stimulus: The angular size of the looming stimulus as a function of time.

burrow is highly dependent on retinal speed, the criterion used to decide when to retreat underground does not depend on speed but rather on angular size or elevation [23].

Third, crabs quickly learn to ignore repeated presentations of a stimulus that has proven harmless [35,36[•]] (see Section ‘Learning under the threat of predation’).

The neurobiology of escape

The robustness of semi-terrestrial crabs makes them highly amenable for neurophysiological investigations. Stable intracellular recordings can be made from restrained but otherwise intact healthy animals [36[•],37]. In *N. granulata*, this preparation has allowed the morphological [38–40] and physiological [26,40,41] identification of four distinct classes of motion sensitive lobula giant (LG) neurons. These neurons probably play a central role in the organization of visually guided behaviours. They all respond to visual motion, but vary in morphology, the number of elements that are present in each cell class, their receptive field properties [26,40] and the amount of binocular input they receive [42].

In the laboratory, the response strength of LG neurons correlates closely with the intensity of the escape response of unrestrained crabs across a range of conditions. Response strength varies seasonally and reflects different stimulus characteristics and whether or not stimuli are seen monocularly or binocularly [43]. The time course of LG responses also correlates well with the temporal dynamics of the escape response [13,36[•]], suggesting that these neurons process most of the relevant information that drives the escape behaviour (Figure 3). Three classes of LG neurons respond not only to visual information, but also to proprioceptive input from the legs [26,41]. This may allow them to process some of the contextual information during predator escape, such as path integration information, which has been shown to influence the escape and burrow defence behaviour in the field [16,44].

Interestingly, when exposed to looming stimuli, LG neurons show an early response component that substantially precedes the initiation of the escape run on the treadmill [13] (Figure 3c). Since the intensity of behavioural and neuronal responses strongly co-vary across a range of contextual situations [43] we predict that this early component will strengthen, if crabs are tested under natural conditions, where the animals respond to moving objects at smaller angular sizes than in the laboratory.

Learning under the threat of predation

Crabs quickly learn to suppress the escape response following repeated presentations of a threatening stimulus that provides no adverse consequences, both in the laboratory [45,46] and under natural conditions

[35,47–49]. The acquired memory reflects a strong stimulus–context association [36[•],49–51]. Most of the learning-induced modifications of the escape behaviour can be accounted for by changes that occur in the LG neurons and persist for at least 24 h [36[•],52]. The response of LG neurons, however, shows no evidence for stimulus–context associations [53[•]].

Habituation in *U. vomeris* in the field [35,49] is slower and weaker than in *N. granulata* in the laboratory [35,49]. It is also highly stimulus specific and not all threatening stimuli elicit habituation [52]. It will be interesting to test whether this reflects stimulus or species differences, or the fact that only the crabs in the field are able to appropriately respond to a threatening stimulus. Being able to escape gives crabs not only more options but also makes deciding whether a stimulus is harmless or dangerous more difficult.

Conclusions and outlook

With their lives at stake, the escape behaviour of crustaceans, and most other animals, needs to be fast and reliable. For this reason alone, it has often been considered a reflex action. The research reviewed here highlights that escape behaviour is far from a simple reflex, but rather a finely tuned, complex behavioural sequence that is modulated at all levels of organization. The escape behaviour reflects seasonal adjustments, environmental and behavioural contexts – such as position relative to the refuge – and is modified by learning.

It is imperative that future experiments take electrophysiology outdoors to accurately test how environmental and behavioural contexts and stimulus complexity are represented and integrated in neural systems. In crabs, the individually identifiable LG neurons are located in the optic lobe within the eyestalk, and their axons project to the midbrain along the protocerebral tract [26,41], providing access for stable extracellularly recordings from single fibres [54]. The crabs’ size and robustness makes it technically feasible to use miniature data logger amplifiers to record from identified LG neurons [55]. Such recordings from freely moving locusts helped clarify which aspects of the neuronal activity are relevant for the control of the escape behaviour [56^{••}]. Recordings from neurons in crabs during natural and simulated predator attacks will help us understand how context and stimulus complexity affect the neural responses of LG neurons and in turn the crabs’ behaviour.

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References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- of outstanding interest

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.conb.2011.11.012](https://doi.org/10.1016/j.conb.2011.11.012).

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