

reproducing microorganisms such as yeast which, because of their small size, are subject to an extremely patchy and diverse environment that favours local adaptation.

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#### Supplemental data

Supplemental data are available at <http://www.current-biology.com/cgi/content/full/17/3/R81/DC1>

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## Crayfish respond to electrical fields

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Fresh or salt water covers seventy percent of the Earth's surface. Aquatic environments are alive with electrical activity. Electrical signals carry information about the structure of the environment and the activity of other animals, and many aquatic vertebrates have evolved electroreception [1–5]. This sensitivity has been reported only in vertebrates [6], but one might predict it would be phylogenetically widespread, given its potential advantages. Here we present the first evidence that an invertebrate species, a freshwater crayfish, responds with different behaviours to a range of electrical signals.

Electrical fields from decaying organic matter and other physio-chemical sources are common in ponds and rivers [7], such as those where crayfish are found, so we designed an experiment to determine whether *Cherax destructor* could respond to such fields. First we placed two pairs of electrodes in either end of an aquarium and introduced animals singly into the arena in darkness. Following a 10 minute acclimation period we recorded the amount of time they spent in either end of the aquarium (one third) over the next 5 minutes. The animals showed no preference for either end during this control test ( $n = 10$ , paired t-test  $T = 0.357$ ,  $p = 0.729$ ).

We repeated the experiment but, after the acclimation period, a DC field ( $0.4 \mu\text{A}/\text{cm}^2$ ) was created between the electrodes in one end of the arena during the 5 minute observation period. The pair of electrodes activated was chosen randomly for each trial. If *C. destructor* cannot detect electrical fields, their behaviour should be the same as the control group. This was not the case — animals spent more time in the field end than the control end ( $n = 10$ , paired t-test  $T = 2.457$ ,  $p = 0.036$ ; see Figure S1 in the Supplemental data available on-line with this issue). Thus,

*C. destructor* can respond to a constant electric field of a type common in natural environments, and the behaviour described here suggests it may be attracted to such fields.

Because *C. destructor* responds to DC fields, it might also be able to detect dynamic signals generated by the movements of invertebrates and vertebrates [7–10]. To test this, we introduced crayfish singly into an aquarium and, following a 5 minute acclimation period, presented them with a test signal ( $0.4 \mu\text{A}/\text{cm}^2$ ) and a control signal ( $0.004 \mu\text{A}/\text{cm}^2$ ). These were presented three times each in random order and at random time intervals (30–120 seconds between stimuli). The signals were a step function generated by switching the field on for 1 s and then off again. Observations were recorded at the instant the field was turned on, which is when the greatest change in electrical current occurs.

A crayfish would not be expected to change its behaviour if it did not detect the signal. Out of the 60 stimuli presented, a behavioural change occurred 70% of the time upon receipt of the large signal (21/30), but in only 17% upon receipt of the small signal (5/30). Individual crayfish changed their behaviour significantly more in response to the large signal than to the small signal ( $n = 10$ , Wilcoxon sign rank  $Z = -2.873$ ,  $p = 0.004$ ).

To determine a threshold to the response, crayfish were exposed to multiple signals with amplitudes smaller or larger than those in the previous experiment. This time, we played the signals at random intervals after the animals were motionless. We then looked for small and immediate movements of the claws (chelipeds), antennae or legs when the signal was presented (Figure 1 inset). These were often followed by walking and occasionally by defence postures (spreading of the claws). These behavioural changes were most reliably seen in fields of  $0.4$  and  $0.8 \mu\text{A}/\text{cm}^2$ , but occurred down to  $0.2 \mu\text{A}/\text{cm}^2$  (Figure 1).

Can natural signals from moving animals also elicit a response? We presented crayfish with analogues of electrical activity from moving animals. Crayfish emit an electrical

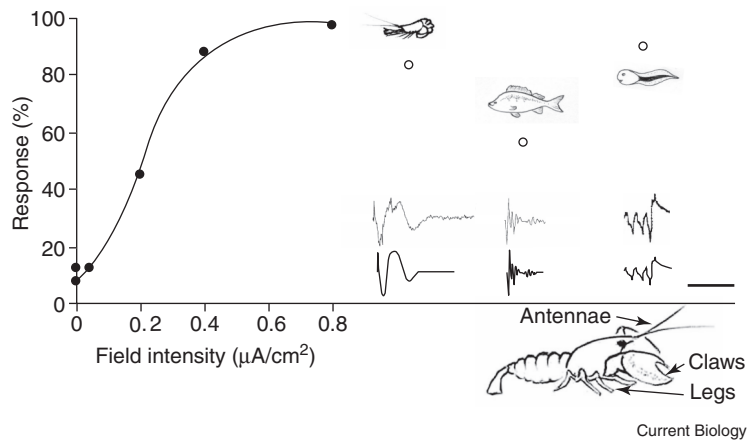


Figure 1. Responses to dynamic electrical fields.

The curve represents the response of *C. destructor* to different voltages of a step function. Points are the total number of responses for all animals in each test (out of 40, 30, 40, 50 stimuli presentations for the curve, crayfish, tadpole and fish signals, respectively). Responses to electrical signals from swimming animals are indicated by the animal icons. Waveforms shown beneath for *C. destructor* (left), *C. carpio* (middle) and *Rana* sp. (right): the top signal of each is the recorded swimming signal [9,14,15], the lower signal is our analogue. Time scale bar lower right is 1.5 seconds for the tadpole and 100 ms for the other two signals. Inset lower right is *C. destructor*. The body and labelled appendages were monitored for movement changes.

signal when executing an escape tailflip [11], which might usefully warn other crayfish in the vicinity so we presented test animals with this signal. They responded to 83% of the tailflip signals (25/30,  $0.4 \mu\text{A}/\text{cm}^2$ , Figure 1) and only 10% to the control stimulus (3/30), a statistically significant response ( $n = 10$ , Wilcoxon sign rank  $Z = -2.850$ ,  $p = 0.004$ ).

Crayfish hunt swimming prey [12,13]. If *C. destructor* detects electrical activity while searching for food it could improve its chance of a meal. We tested for a response to tadpoles, a potential food source [13] that generates an electrical field when they start to swim [9]. *C. destructor* responded more often to the tadpole electrical stimulus than to a control signal (Figure 1;  $n = 10$ , 90% response to signal, 36/40, 35% to control, 14/40; Wilcoxon sign rank  $Z = -2.827$ ,  $p = 0.005$ ).

Swimming fish also emit electrical signals [8], particularly when moving rapidly. Such signals could potentially alert crayfish to approaching danger. We found a significant, but weaker, response to a fish signal (Figure 1;  $n = 10$ ; 56% response to signal, 28/50, 10% to control, 5/50; Wilcoxon sign rank  $Z = -2.680$ ,  $p = 0.007$ ). This suggests *C. destructor* gives a higher priority

to signals from conspecifics and prey than to those from predators.

In natural situations, signals from aquatic animals could emanate from small sources in the water. We therefore played the tadpole signal through a dipole (two carbon electrodes 25 mm apart, ~5 cm from the crayfish) and found that behaviour changed ( $n = 15$ , paired  $t$  test  $T = -12.150$ ,  $p < 0.001$ ; see Figure S2 in the Supplemental data). This established that *C. destructor* responds to electrical fields from point sources as well as fields that cover larger areas of water.

Our data show crayfish respond to low-level electrical signals of the type previously shown to be biologically significant to vertebrates. The animals could be employing an undescribed sensory system or one shared with another modality. This has implications for the interpretation of the biology of all aquatic invertebrates and the vertebrates that interact with them.

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#### Supplemental data

Supplemental data including experimental procedures, additional references and figures are available at <http://www.current-biology.com/cgi/content/full/17/3/R83/DC1>

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