

## Spectral sensitivity of four species of fiddler crabs (*Uca pugnax*, *Uca pugilator*, *Uca vomeris* and *Uca tangeri*) measured by *in situ* microspectrophotometry

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### Summary

Fiddler crabs have compound eyes that are structurally fairly well understood. However, there has been much debate regarding their spectral sensitivity and capacity to enable colour discrimination. We examined the visual pigments of two North-American species (*Uca pugnax* and *U. pugilator*), one species from the Indo-West Pacific (*U. vomeris*) and the only Eastern-Atlantic species (*U. tangeri*) of fiddler crabs using *in situ* microspectrophotometry of frozen sections of dark-adapted eyes. Only one spectral class of visual receptor was found in the larger (R1–7) reticular cells of each species, with maximum absorption peaking between 508 nm and 530 nm (depending upon species). The R8 reticular cell, that might contain a short-

wavelength sensitive photopigment and provide a basis for colour vision, was too small to analyze by these methods. Rhabdoms were lined with screening pigment which strongly influenced each species' spectral sensitivity, sharpening the peak and shifting the maximum towards longer wavelengths, on occasion to as far as the 600 nm region. We hypothesize that sensitivity to longer wavelengths enhances contrast between background (blue sky or tall vegetation) and the male major claw during the waving display.

Key words: fiddler crab, spectral sensitivity, microspectrophotometry.

### Introduction

Fiddler crabs are semi-terrestrial crabs that, during low tide, live on a flat and horizontal surface and rely on vision for most of their social interactions and individual activities. During courtship interactions, males use a well known visual display called waving, which consists of a rhythmic and stereotyped elevation of their greatly enlarged claw, to try to attract searching females into their burrows (Crane, 1975) or, less usually, while trying to mate with females at female burrow sites (e.g. *U. vocans*) (Christy and Salmon, 1984). This visual display is also used in a territorial context (Crane, 1975) and, in a few species, females also wave their feeding claws (e.g. von Hagen, 1993). The waving display and the male's major claw are probably the two primary visual cues that fiddlers use to discriminate between male and female conspecifics (von Hagen, 1962; Salmon and Stout, 1962), and are thus crucial in social interactions, but vision plays an important role even at distances where conspecifics cannot be discriminated. Burrow surveillance, for instance, is another situation in which both male and female fiddler crabs need to rely on vision (Zeil and Layne, 2002). The burrow is the centre of most of the crabs' activities, such as foraging and mating, and it also serves as a refuge from predators, a place to hide during high tide, or as a

shelter to prevent desiccation during low tide. Crabs that have been evicted or that have left their burrows wander through the population, sampling the burrows on their way, until they settle for an empty one or evict a resident crab. Although the crabs' homing system seems to rely on path integration and not on visual land marks (Altevogt and von Hagen, 1964; von Hagen, 1967; Zeil, 1998; Cannicci et al., 1999; Zeil and Layne, 2002), burrow owners still rely on vision to monitor the presence of potential burrow seekers near their burrow (Hemmi and Zeil, 2003a; Hemmi and Zeil, 2003b). Predator avoidance is yet another classic situation where crabs depend on their visual systems: not only do they use vision to check for the presence of potential predators, but also to follow conspecifics that are taking cover in their own nearby burrows, in case of imminent danger – particularly if they are wandering individuals that do not possess a burrow at that given moment (Zeil and Lane, 2002).

Given the relevance of vision in all of these activities, fiddler crabs' eyes and their visual systems have long been the subject of research. The major aspects of the eye's optics and the arrangement of ommatidia are common among species throughout the genus *Uca* and are shared with several other ocypodid crabs. To summarize briefly, fiddler crabs have

opposition compound eyes (Cronin, 1986) carried on long vertical stalks; they have a 360° panoramic visual field (Land and Layne, 1995), and their eyes possess an equatorial visual streak, which they keep aligned with the visual horizon by making compensatory movements (Zeil et al., 1986; Layne et al., 1997). The equatorial zone is characterized by larger facet lenses and longer crystalline cones and rhabdoms (Zeil and Al-Mutairi, 1996), and the small inter-ommatidial angles in this region (Zeil et al., 1986; Land and Layne, 1995; Zeil and Al-Mutairi, 1996) enhance vertical anatomical resolution. According to Layne et al. (Layne et al., 1997), this anatomical feature divides the crabs' visual fields into two different zones, allowing them to classify visual stimuli into 'conspecifics' if the stimulus falls below the horizon line or 'predators' if the stimulus is perceived above the horizon line.

Although the structural characteristics and ommatidial organization of the eyes are fairly well understood, along with some of their functional specializations (mainly regarding information on size and distance of visual stimuli), there has been much debate about spectral sensitivity and the capacity for colour discrimination in fiddler crabs. Some studies suggest that fiddler crabs possess only one visual photoreceptor class. The electroretinograms (ERG) on *U. pugnax* and *U. pugilator* (Scott and Mote, 1974), for example, suggested the presence of only one receptor type with peak sensitivity around 510 nm. Later, electrophysiological (ERG) and behavioural evidence was presented for the existence of an additional short wavelength receptor class in *U. pugilator* (Hyatt, 1975). Also, using the ERG technique, evidence was found for a two-pigment visual system in the fiddler crab *U. thayeri*: one pigment with peak absorption between 500 nm and 540 nm and another short wavelength pigment with an absorption maximum near 430 nm (Horch et al., 2002). Besides Hyatt's original behavioural work indicating that fiddler crabs could possess true colour vision (Hyatt, 1975), recent work (Detto et al., 2006) indicates that fiddler crabs may use colour cues to recognize individual conspecifics. Cronin and Forward attempted to characterize the visual pigments of *U. pugilator* using microspectrophotometry on isolated rhabdoms (Cronin and Forward, 1988). Unfortunately, this attempt was not successful owing to the presence of photosensitive red screening pigment surrounding the photoreceptors, which masked the changes in the actual visual pigments.

In this study we attempted to investigate the visual pigments of four species of fiddler crabs, covering a wide phylogenetic scope (Rosenberg, 2001), using microspectrophotometry on retinal slices. We examined two North-American species, *U. pugnax* and *U. pugilator*, an Indo-West Pacific species *U. vomeris*, and the only species found in the Eastern Atlantic, *U. tangeri*. Our technique differs from that of Cronin and Forward (Cronin and Forward, 1988) in the experimental preparation of the rhabdoms, and our new approach allows us to avoid many of the earlier problems caused by the presence of the high concentrations of screening pigments immediately adjacent to the rhabdoms. These pigments actually modify and tune spectral sensitivities of fiddler crab photoreceptors, and we

used our results to model spectral sensitivities of the main photoreceptors in *Uca*.

## Materials and methods

### *Animal collection and maintenance*

*U. pugnax* (Smith 1870) and *U. pugilator* (Bosc 1802) were collected on tidal flats near the Duke University Marine Laboratory, in Beaufort, North Carolina, USA in September 2003 and shipped to the University of Maryland Baltimore County, USA for study. *U. vomeris* (McNeill 1920) individuals were collected on tidal flats in southern Queensland, Australia in mid-September, 2003. *U. tangeri* (Eydoux 1835) specimens were collected in Portugal at the Ria Formosa Natural Park, Algarve, near the end of the species breeding season in September 2003. Following collection, animals were transported in containers, in a few millimetres of seawater in order to prevent desiccation, to the University of Maryland Baltimore County Biological Sciences Laboratory. Specimens of all species were kept isolated or in small groups in boxes with access to artificial seawater that was changed whenever it was found necessary and were fed every other day on fish food on moist tissue paper. In most cases, animals were used within 2–3 weeks of collection.

### *Cryosectioning and experimental preparation*

The animals used for analysis were dark-adapted at least for 2 days before use. All subsequent procedures were carried out under dim red light [see Cronin et al. (Cronin et al., 1996) for general procedures]. The eyes were removed from the live animals, placed on cryosection stubs, fast-frozen with cryogenic spray and sectioned at 14 µm on a cryostat at –25°C to –30°C. The eye sections were collected on coverslips and mounted in marine crustacean Ringer's solution, within a ring of silicone grease. After eye removal, the animals were killed by immersing them in a container with ice.

### *Microspectrophotometry*

Microspectrophotometry (MSP) was carried out using a computer-controlled single-beam instrument [for a full description see Cronin (Cronin, 1985)]. The eye section was inspected, and those rhabdoms that were cross-sectioned were selected for measurement. Owing to the small diameter of the rhabdoms all measurements were made with a very small beam (diameter of 1.5 µm), which was also linearly polarized. Special care was taken to measure only within the selected rhabdom and to avoid contamination from other sources. Scans were made from 400 to 700 nm, with measurements taken every 1 nm. For each rhabdom, a baseline scan was made in a clear area of the preparation first; then the dark-adapted rhabdom was scanned twice to check for stability. If the scans had identical shape, the second scan was used as the absorption spectrum for the dark-adapted rhabdom. The rhabdom was then photobleached by exposing it to white light for 2 min and one additional absorption spectrum was obtained. The difference between the two absorption spectra was taken as the absorption

spectrum of the photobleachable visual pigment. Photostable material, such as ommochrome-containing granules and screening pigment granules lining the rhabdoms, was also measured. In this case, the absorption spectrum was obtained directly, after confirming stability, with no need for the photobleaching process.

#### Mathematical analysis

Once the spectral features of the photopigment in the rhabdom and the screening/filtering pigment around the rhabdom were known, we used these to model the spectral sensitivity functions of main rhabdoms of the four *Uca* species, assuming that the red screening pigments act as lateral filters. In carrying out this analysis, we used the theory of lateral filtering originally developed by Snyder et al. (Snyder et al., 1973) to account for the function of fused insect rhabdoms. That treatment showed that the absorbance per unit length,  $\xi(\lambda)$ , of a composite rhabdom (or a rhabdom plus the surrounding filter border) is simply the sum of the contributions of the absorbing components, each multiplied by its respective fraction of the total area of the structure. Thus:

$$\xi(\lambda) = \alpha_F(\lambda)C_F \frac{A_F}{A} + \alpha_R(\lambda)C_R \frac{A_R}{A}, \quad (1)$$

where  $\alpha(\lambda)$  is the absorbance coefficient at wavelength  $\lambda$ ,  $C$  is the concentration, and  $A$  is area; the subscripts F and R represent the rhodopsin and the lateral filter, respectively. The products of absorbance coefficient and concentration can be replaced with the absorbance per  $\mu\text{m}$ , measured using MSP. We used a rhodopsin absorbance of  $0.006 \mu\text{m}^{-1}$  at the peak (see

Cronin and Forward, 1988); for the filters we used the value of  $0.1 \mu\text{m}^{-1}$  (similar to that measured directly in the frozen sections). This leaves as the only unknowns the relative areas,  $A_R$  and  $A_F$ , occupied by the visual pigment and the lateral filtering pigment, respectively (the total area  $A$  equals  $A_R + A_F$ ):

$$\xi(\lambda) = \alpha_F(\lambda) \frac{A_F}{A} + \alpha_R(\lambda) \frac{A_R}{A}. \quad (2)$$

We computed sensitivity spectra, modelling curves based on the appropriate rhodopsin for each species, using templates (Stavenga et al., 1993) and the typical lateral filtering pigment found in each species. Because the density of the filter per unit length of receptor is so much greater than the density of the visual pigment, the calculation is very insensitive to values of either  $\alpha_F$  or  $A_F$  within realistic ranges of values. As described earlier, we used 0.1 for the axial density of lateral filter pigment ( $\mu\text{m}^{-1}$ ), which was typical for values we measured in all species, and assumed that the lateral filter pigment occupied 20% (0.2) of the cross-sectional area of the photoreceptor's absorption profile.

## Results

### Visual pigments

Owing to the small diameter of most rhabdoms and the fact that they were all lined with coloured material and screening pigment granules (Fig. 1), it was difficult to obtain 'clean' absorption spectra. Bleaching changes were also minimal, causing numerous scan pairs to be rejected. Our final sample consists of the absorption difference spectra of 11 rhabdoms

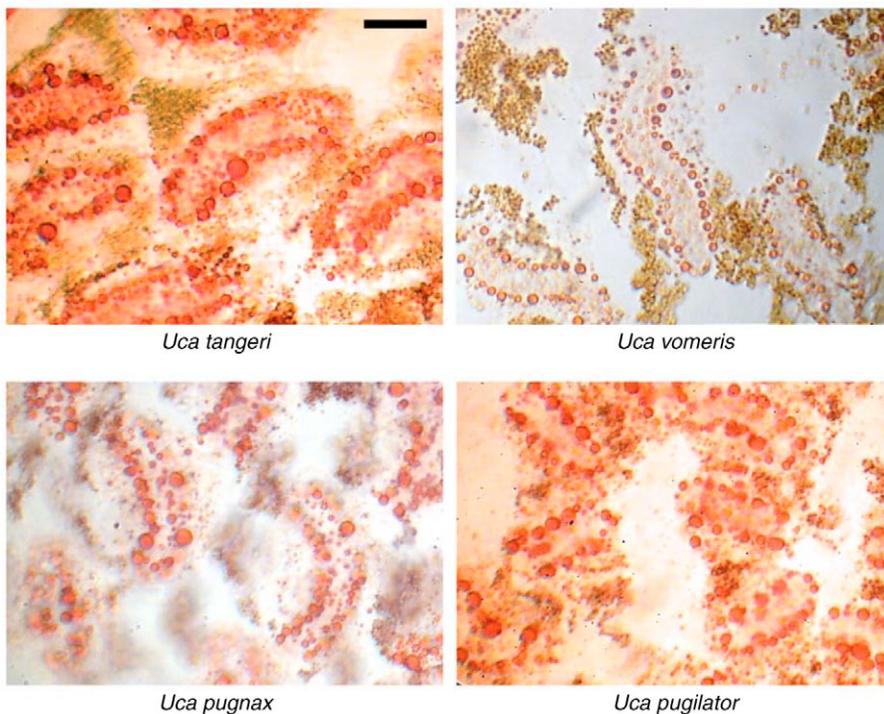


Fig. 1. Photographs of sectioned photoreceptors and lateral screening pigments from four species of fiddler crabs, of genus *Uca*, as viewed in the microspectrophotometer. In each panel, the elongated rectangular or oval-shaped structures are rhabdoms, sectioned obliquely and viewed laterally, surrounded by droplets or granules of screening pigments. Absorption spectra of these screening pigments are plotted in Fig. 4B. Scale bar,  $10 \mu\text{m}$  (applies to all panels).

Table 1. Statistical summary of microspectrophotometric results obtained from all study species

Species	Number of individual crabs sampled	Number of rhabdoms sampled	$\lambda_{\max}$ (nm)	$\lambda_{\max}$ of fit to average curve
<i>Uca pugnax</i>	3	11	513.1±2.8	521
<i>Uca pugilator</i>	3	7	520.3±2.1	525
<i>Uca vomeris</i>	1	8	502.2±4.3	508
<i>Uca tangeri</i>	4	13	528.0±4.8	530

Data are taken from difference spectra for photobleaching of individual photoreceptors, fitted to templates (Stavenga et al., 1993) as described in the text.  $\lambda_{\max}$  is given as the mean  $\pm$  s.e.m.

from three different *U. pugnax*, seven rhabdoms from three *U. pugilator*, eight rhabdoms from one *U. vomeris*, and 13 rhabdoms from four different *U. tangeri*. Except for *U. vomeris* for which only one animal was used, there was no indication of sex differences in the other three species, so our data set includes absorption difference spectra from both males and females (Table 1). We believe it is parsimonious to assume that the absence of sex differences is also true for *U. vomeris*. The quality of the data is limited by the very small absorption changes generated by photobleaching (see Fig. 2 for a typical absorption spectrum for *U. tangeri* as an example), but by averaging across numerous individual bleaches we were able to obtain good estimates of the absorption spectra of visual pigments in all species (Fig. 3). Our sections for MSP covered most of the retina and there was no suggestion of regional variation in the results. We found no evidence for the existence of more than one class of photoreceptors in any of the four species examined and we believe that the reasonably tight standard errors suggest that a second visual pigment class with a very different maximum absorption wavelength ( $\lambda_{\max}$ ) is unlikely to be present in the main rhabdoms of these crustaceans. Average results are described in Table 1 and plotted in Fig. 3, along with the best-fit template curves.

#### Photostable pigments

We observed several types of photostable pigments, typical of crustacean eyes, in the ommatidia of all four species. They varied in appearance from gold to red, depending on the retinal region. Most of these pigments do not lie in the optical path and thus play no direct role in affecting the spectral sensitivities of retinal photoreceptors. Fig. 4A shows their typical absorption spectra. The screening pigments lining the photoreceptors themselves appeared to be orange or red to the human eye. Typical normalized absorption spectra are plotted in Fig. 4B. These pigments strongly modify the spectrum of light travelling down the rhabdom.

#### Spectral sensitivity

Knowing the absorption spectra of the visual and screening pigments, it becomes possible to model the spectral sensitivities of the four *Uca* species, following the methods developed by Snyder et al. (Snyder et al., 1973) and described above. The computed spectral sensitivities were normalized to their maxima, and the resulting curves are plotted in Fig. 5. The

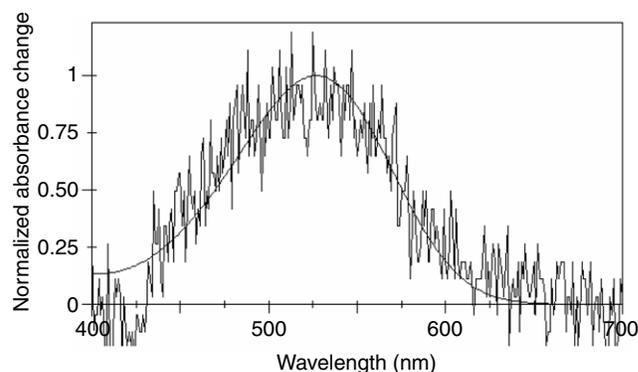


Fig. 2. Difference spectrum for photobleaching obtained from a single rhabdom from *U. tangeri* (jagged curve). The smooth curve represents the best-fit template (Stavenga et al., 1993), with  $\lambda_{\max}$  of 527 nm. In this example, the data are normalized to 0.011 optical density units (the average maximum difference at  $527 \pm 2$  nm).

modelled functions commonly have two peaks, one near the visual pigment  $\lambda_{\max}$  and another sharper, higher one, shifted to longer wavelengths in the orange-red region of the visible spectrum.

## Discussion

### Overview

The structure and organization of the photoreceptors in the four species of *Uca* that we have studied were practically identical. They are also similar to those of other intertidal and semi-terrestrial species (Cronin and Forward, 1988): the rhabdoms are very small and have a heavy coating of strongly coloured pigment granules around them. This is a well known adaptation to bright light environments; the pigment granules around the rhabdoms act as screens or 'sun-shades' and reduce the photoreceptors' exposure to light. This organization had already been described for *U. pugilator* in a previous study (Cronin and Forward, 1988).

### Visual pigments

The MSP measurements only revealed the presence of a single spectral class in main rhabdoms of all four species of *Uca*, with the maximum absorption peak ranging from 508 nm to 530 nm, depending on the species (Table 1 and Fig. 3). This

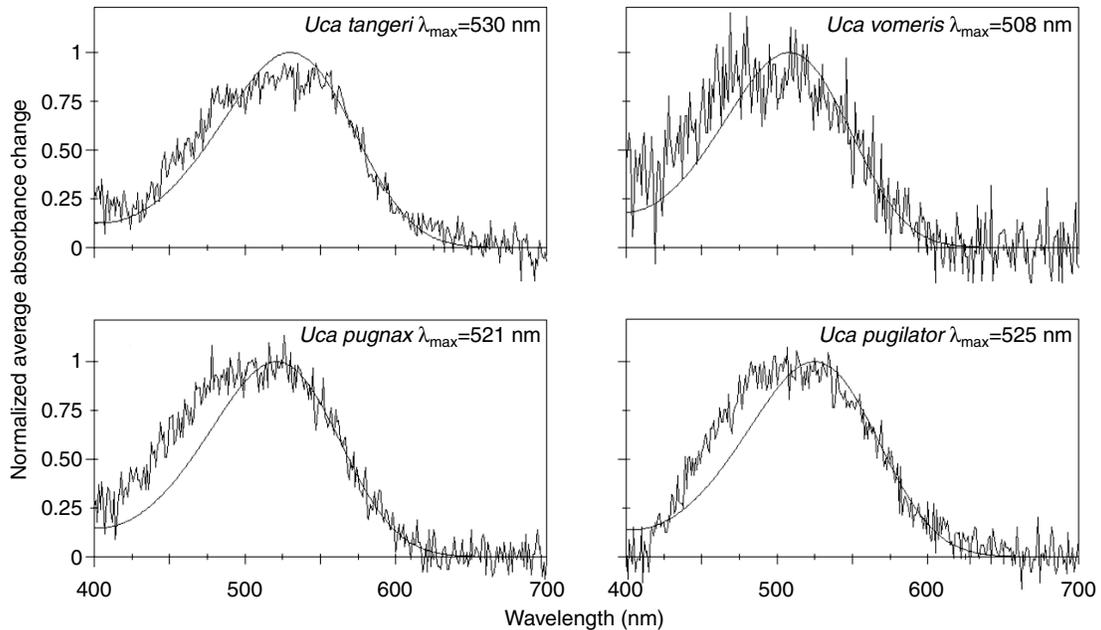


Fig. 3. Normalized average absorbance change in main rhabdoms of all four study species. In each panel, the smooth curve is the template (Stavenga et al., 1993) that is fitted to the data.

range of values is in accordance with those of previous studies on the spectral sensitivity of the genus *Uca*, independently of the technique used. As reviewed in the Introduction, Scott and Mote (Scott and Mote, 1974) suggested the peak sensitivity of *U. pugnax* and *U. pugilator* to be 510 nm, whereas Horch et al. (Horch et al., 2002) suggested that one of the visual pigments in *U. thayeri* would have a peak sensitivity between 500 nm

and 540 nm. Hyatt (Hyatt, 1975) identified one photoreceptor type maximally sensitive at longer wavelength, in the yellow region of the spectrum, which is consistent with our results (after accounting for the effects of screening pigments). Together, these findings (both across studies and across species) support the idea that there is only one visual pigment class in the main rhabdom (cells 1–7) of the genus *Uca*, with slight differences in absorption maximum between species.

The debate still remains concerning whether there is an additional short wavelength-sensitive pigment in the eyes of fiddler crabs. Short wavelength sensitivity has been described for other brachyuran crabs such as *Carcinus maenas* (Martin and Mote, 1982), where it is associated with a second class of photoreceptors in the very small eighth reticular cell (R8) of rhabdoms. Although *in situ* MSP generally provides an

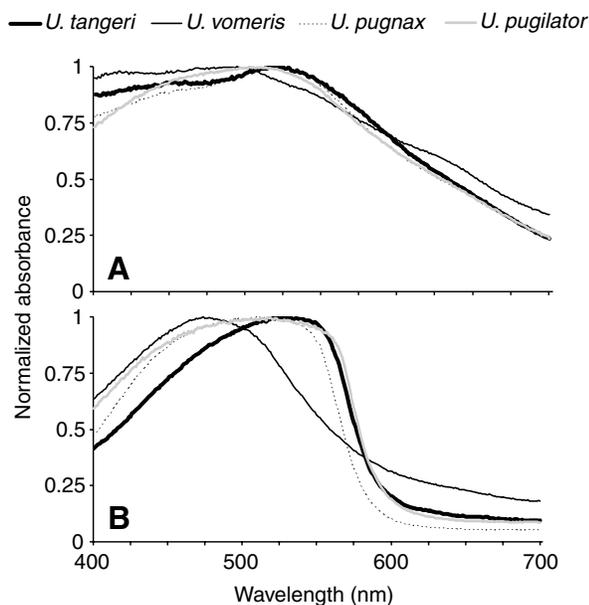


Fig. 4. Absorption spectra of photostable pigments in the eyes of the four *Uca* species. Each curve is a single normalized scan. (A) Representative spectra from ommochrome granules. (B) Representative spectra from rhabdomal lateral screening pigments.

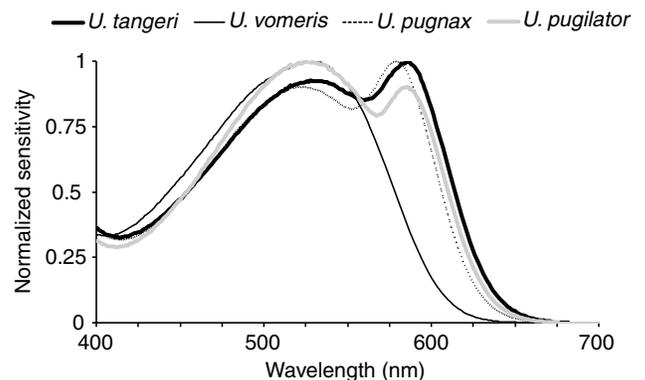


Fig. 5. Normalized spectral sensitivities in all four study species of *Uca*, computed as described in the text.

accurate description of the spectral absorption characteristics of photoreceptors, this technique is difficult to apply to cells in the size range of the R8 cells in crabs. Electrophysiological techniques such as the ERG have the advantage of measuring the electrical response of the whole eye to specific wavelengths. Although they are limited in their ability to identify the actual visual pigments, they give us direct information on how the eye reacts to a particular wavelength (that can either coincide with a visual pigment absorption maximum or be modified by any optical filtering). Considering this difference in techniques, along with good evidence that a two-visual-pigment system is somewhat common in decapod crustaceans (Johnson et al., 2002), we doubt that the *Uca* visual system contains only the single photoreceptor type measured in this study. Other evidence for a multiple-receptor system is provided by the selective chromatic adaptation experiments done by both Hyatt (Hyatt, 1975) and Horch et al. (Horch et al., 2002), both providing results consistent with the existence of a putative short wavelength visual pigment. Additionally, Hyatt (Hyatt, 1975) also performed behavioural experiments, presenting pairs of different wavelength lights at intensities that were perceptually equal. *U. pugilator* clearly discriminated between those choices. Also, recent work (Detto et al., 2006) suggests that some fiddler crab species can discriminate among stimuli varying in colour: *U. mjoebergi* individuals clearly discriminate between unmanipulated males and males with the major claw painted over with yellow pigment that looks very similar to the human visual system. The existence of an additional short wavelength visual pigment, like that suggested by Horch et al. (Horch et al., 2002) for *U. thayeri*, would enable this ability, and such a pigment probably resides in the eighth reticular cells of rhabdoms, just as Horch et al. (Horch et al., 2002) suggested for *U. thayeri* and perhaps other species of *Uca*.

#### Spectral sensitivity

Although the spectral absorption of the visual pigments that we found peaks in the 508 nm to 530 nm range, the actual spectral sensitivity of fiddler crabs' eyes is modified by the coloured screening pigment granules or vesicles that line the photoreceptor cells (Snyder et al., 1973). The resulting spectral sensitivity in many species within this genus is thus sharpened and shifted towards longer wavelengths, producing a clear sensitivity peak in the orange–red region of the spectrum, together with a peak near the spectral maximum region of visual pigment (Fig. 5). According to Zeil and Hemmi, the colour of the screening pigment varies across the dorsal and ventral parts of the eye, at least in *U. vomeris* (Zeil and Hemmi, 2006). This way, spectral sensitivity may also vary across the visual field. However, in the presence of such a gradient, colour vision cannot be achieved unless ommatidia with different spectral sensitivity view the same object, or at least have the same visual field, which seems unlikely given the ommatidial arrangements of fiddler crab compound eyes.

Clearly, the screening pigments function to reduce the amount of light reaching the photoreceptors in species inhabiting bright light habitats. However, evolution has

favoured pigments that also modify these crabs' spectral sensitivity, making the visual system in this genus relatively more sensitive to long wavelengths. One explanation of this finding relates to social signalling, which is typical of all species of fiddler crabs. Specifically, waving is one of the most important signals in the fiddler crabs' social system. Because of the flat topography of their mudflat habitat, during the waving movement, when the claw is completely extended, it is usually viewed against the sky. We suggest that a visual system maximally sensitive to long wavelengths enhances the contrast between the white coloration of the claw and the blue sky background. Even in the absence of colour vision, enhancing the achromatic contrast between the white or yellowish claw would make it stand out clearly against the blue sky (M. E. Cummings, J. M. Jordão, T. W. Cronin and R. F. Oliveira, manuscript submitted). Of course, there are species that inhabit salt marshes and mangroves containing a background of tall, and often dense, vegetation which, in these cases, would be the displaying background instead of the sky. Only a study including reflectance measurements of both the crabs and habitat would enable us to evaluate if a species spectral sensitivity has evolved to enhance the contrast between the claw and these alternative backgrounds. However, if we assume that a vegetation background will mainly be green, the sensitivity to long wavelengths that we have found in this study will also adequately heighten the contrast between the claw and the vegetation (M. E. Cummings, J. M. Jordão, T. W. Cronin and R. F. Oliveira, manuscript submitted). If it turns out that fiddler crabs are capable of recognizing colour, having a waving signal that is enhanced in visibility by a particular receptor class makes good evolutionary sense as well.

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#### References

- Altevogt, R. and von Hagen, H.-O. (1964). Über die orientierung von *Uca tangeri* Eyndoux im Freiland. *Z. Morphol. Ökol. Tiere* **53**, 636-656.
- Cannicci, S., Fratini, S. and Vannini, M. (1999). Short-range homing in fiddler crabs (Ocypodidae, genus *Uca*): a homing mechanism not based on local visual landmarks. *Ethology* **105**, 867-880.
- Crane, J. (1975). *Fiddler Crabs of the World: Ocypodidae: Genus Uca*. Princeton, NJ: Princeton University Press.
- Christy, J. H. and Salmon, M. (1984). Ecology and evolution of mating systems of fiddler crabs (genus *Uca*). *Biol. Rev.* **59**, 483-509.
- Cronin, T. W. (1985). The visual pigment of a stomatopod crustacean, *Squilla empusa*. *J. Comp. Physiol. A* **156**, 679-687.
- Cronin, T. W. (1986). Optical design and evolutionary adaptation in crustacean compound eyes. *J. Crust. Biol.* **6**, 1-23.
- Cronin, T. W. and Forward, R. B. (1988). The visual pigments of crabs. I. Spectral characteristics. *J. Comp. Physiol. A* **162**, 463-478.
- Cronin, T. W., Marshall, N. J. and Caldwell, R. L. (1996). Visual pigment diversity in two genera of mantis shrimps implies rapid evolution (Crustacea; Stomatopoda). *J. Comp. Physiol. A* **179**, 371-384.
- Detto, T., Backwell, P. R. Y., Hemmi, J. M. and Zeil, J. (2006). Visually

- mediated species and neighbour recognition in fiddler crabs (*Uca mjoebergi* and *Uca capricornis*). *Proc. R. Soc. Lond. B Biol. Sci.* **273**, 1661-1666.
- Hemmi, J. M. and Zeil, J.** (2003a). Burrow surveillance in fiddler crabs I. Description of behaviour. *J. Exp. Biol.* **206**, 3935-3950.
- Hemmi, J. M. and Zeil, J.** (2003b). Robust judgement of inter-object distance by an arthropod. *Nature* **421**, 160-163.
- Horch, K., Salmon, M. and Forward, R.** (2002). Evidence for a two pigment visual system in the fiddler crab, *Uca thayeri*. *J. Comp. Physiol. A* **188**, 493-499.
- Hyatt, G.** (1975). Physiological and behavioral evidence for colour discrimination by fiddler crabs (Brachyura, Ocypodidae, genus *Uca*). In *Physiological Ecology of Estuarine Organisms* (ed. V. Vernberg), pp. 333-365. Columbia, SC: South Carolina University Press.
- Johnson, M. L., Gatens, E. and Shelton, M. J.** (2002). Spectral sensitivities of five marine decapod crustaceans and a review of spectral sensitivity variation in relation to habitat. *J. Mar. Biolog. Assoc. UK* **82**, 835-842.
- Land, M. and Layne, J.** (1995). The visual control of behavior in fiddler crabs. I. Resolution, thresholds and the role of the horizon. *J. Comp. Physiol. A* **177**, 81-90.
- Layne, J., Land, M. and Zeil, J.** (1997). Fiddler crabs use the visual horizon to distinguish predators from conspecifics: a review of the evidence. *J. Mar. Biolog. Assoc. UK* **77**, 43-54.
- Martin, F. G. and Mote, M. I.** (1982). Colour receptors in marine crustaceans: a second class of retinular cell in the compound eyes of *Callinectes* and *Carcinus*. *J. Comp. Physiol. A* **145**, 549-554.
- Rosenberg, M. S.** (2001). The systematics and taxonomy of fiddler crabs: a phylogeny of the genus *Uca*. *J. Crust. Biol.* **21**, 839-869.
- Salmon, M. and Stout, J. F.** (1962). Sexual discrimination and sound production in *Uca pugilator* Bosc. *Zoologica* **47**, 15-20.
- Scott, S. and Mote, M. I.** (1974). Spectral sensitivities in some marine Crustacea. *Vision Res.* **14**, 659-663.
- Snyder, A. W., Menzel, R. and Laughlin, S. B.** (1973). Structure and function of the fused rhabdom. *J. Comp. Physiol. A* **87**, 99-135.
- Stavenga, D. G., Smits, R. P. and Hoenders, B. J.** (1993). Simple exponential functions describing the absorbance bands of visual pigment spectra. *Vision Res.* **33**, 1011-1017.
- von Hagen, H.-O.** (1962). Experimentelle studien zum Winken von *Uca tangeri* in Südsanien. *Verh. Dtsch. Zool. Ges.* **25**, 424-432.
- von Hagen, H.-O.** (1967). Nachweis einer kinästhetischen Orientierung bei *Uca rapax*. *Z. Morphol. Ökol. Tiere* **58**, 301-320.
- von Hagen, H.-O.** (1993). Waving display in females of *Uca polita* and of other Australian fiddler crabs. *Ethology* **93**, 3-20.
- Zeil, J.** (1998). Homing in fiddler crabs (*Uca lactea annulipes* and *Uca vomeris*: Ocypodidae). *J. Comp. Physiol. A* **183**, 367-377.
- Zeil, J. and Al-Mutairi, M. M.** (1996). Variation of resolution and of ommatidial dimensions in the compound eyes of the fiddler crab *Uca lactea annulipes* (Ocypodidae, Brachyura, Decapoda). *J. Exp. Biol.* **199**, 1569-1577.
- Zeil, J. and Hemmi, J. M.** (2006). The visual ecology of fiddler crabs. *J. Comp. Physiol. A* **192**, 1-25.
- Zeil, J. and Layne, J.** (2002). Path integration in fiddler crabs and its relation to habitat and social life. In *Crustacean Experimental Systems in Neurobiology* (ed. K. Wiese), pp. 227-247. Heidelberg, Berlin, New York: Springer Verlag.
- Zeil, J., Nalbach, G. and Nalbach, H.-O.** (1986). Eyes, eye stalks and the visual world of semi-terrestrial crabs. *J. Comp. Physiol. A* **159**, 801-811.