Research

Shrimps that pay attention: saccadic eye movements in stomatopod crustaceans

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Discovering that a shrimp can flick its eyes over to a fish and follow up by tracking it or flicking back to observe something else implies a 'primate-like' awareness of the immediate environment that we do not normally associate with crustaceans. For several reasons, stomatopods (mantis shrimp) do not fit the general mould of their subphylum, and here we add saccadic, acquisitional eye movements to their repertoire of unusual visual capabilities. Optically, their apposition compound eyes contain an area of heightened acuity, in some ways similar to the fovea of vertebrate eyes. Using rapid eye movements of up to several hundred degrees per second, objects of interest are placed under the scrutiny of this area. While other arthropod species, including insects and spiders, are known to possess and use acute zones in similar saccadic gaze relocations, stomatopods are the only crustacean known with such abilities. Differences among species exist, generally reflecting both the eye size and lifestyle of the animal, with the larger-eyed more sedentary species producing slower saccades than the smaller-eyed, more active species. Possessing the ability to rapidly look at and assess objects is ecologically important for mantis shrimps, as their lifestyle is, by any standards, fast, furious and deadly.

1. Introduction

The apposition compound eyes of stomatopod crustaceans are unusual in many respects, perhaps reflecting their long and independent evolutionary history of over 400 Myr [1]. Although in many ways basically similar in design to other malacostracan compound eyes, with eight rhabdomeric photoreceptors per ommatidium and orthogonal microvilli, unique specializations also exist. In the species from three of the five existing superfamilies, the gonodactyloids, hemisquilloids and lysiosquilloids, coloured filters and multiple visual pigments are found, along with several adaptations for analysing polarized light not seen in other animals [2–4]. The end result for species with the most developed eye is a visual system with around 20 information channels, including 12 colour sensitivities, six polarization, including left and right circular polarization [5], intensity, form vision and also stereopsis. Stereopsis is, in fact, monocular in many species and this may be associated with their high-speed raptorial strikes, produced by a pair of limbs that either bash or impale prey and competitors [6].

The large number of information channels in these eyes has coevolved with modified optical arrangements within the eye. It is these that, in turn, require the apparently complex eye movements that stomatopods possess [7–9]. Despite their variable eye shapes, the visual axes of ommatidia within the eyes of almost all stomatopods follow a similar plan and have become skewed to point away from normal to the eye's surface (figure 1) [10,11]. The dorsal and ventral peripheral eye regions, or hemispheres, skew towards each other, examining an elongated region in space about 10° wide, into which around 70% of the ommatidia are aimed. Other ommatidia, set even more peripherally, examine the remaining visual space, wrapping around to sample well over 180°. All peripheral ommatidia are essentially identical to those of crabs or other malacostracans, but between the two skewed zones lies a two- or six-row
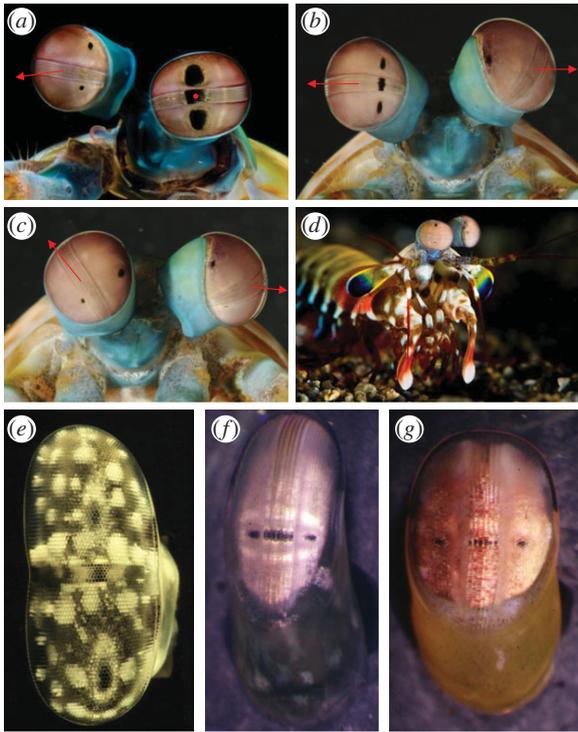
Figure 1. (a–c) Camera-angle view of stomatopod *Odontodactylus scyllarus,* in restraining tube, showing different eye positions. Arrows (red in online colour version) point approximately in the direction that the acute zone is looking in. Black areas on the eyes are pseudo-pupils and show occasional trinocular view of the eye as well as the greatly expanded acute zone pseudo-pupils when this area of the eye is directly facing the camera [10,11]. In this position, the dot (red in online colour version) in the centre of the middle pseudopupil is an end-on view of the direction indicator arrow. (d) *O. scyllarus* walking out of burrow (Photographs, R. L. Caldwell). (e) Eye of *Lysiosquilla maculata*. (f) Eye of *Gonodactylus chiragra*. (g) Eye of *Pseudosquilla ciliata*. (e–g) Show different eye shapes, (f) and (g) are rotated 90° anticlockwise relative to their normal attitude in life. (Online version in colour.)

mid-band. Gonodactyloid, hemisquilloid and lysiosquilloid species possess six rows and it is within these that the colour and some of the polarization detectors lie. The mid-band is also optically aligned with the 10° strip examined by most of the rest of the eye, so within this region, each eye examines an object from three separate points of view [10].

In common with land-dwelling 'flat-world' crabs [12], more ommatidia from both hemispheres examine one direction (perpendicular to the mid-band and evidenced by the elongated pseudo-pupils in figure 1) than other spatial regions, so there is an anisotropic distribution of resolving power [10,13]. Above and below most of the mid-band, this results in resolution that is twice as acute in the direction perpendicular to the mid-band as along it. As the eyes possess considerable rotational freedom [9], this is rarely parallel to the horizontal. In fact, this optical arrangement of a high-resolution strip containing the mid-band colour and polarization photoreceptors requires the scanning eye movements already described for stomatopods [9]. Slow (average $40°\,s^{-1}$) scans are made, of a relatively uniform speed among species (figure 4), and information is collected during the scan [9].

Embedded within the scanned strip, a further optical modification is found: some ommatidia aimed parallel to those of the mid-band are enlarged and show other modifications consistent with elevated resolution [10,11]. This forms an acute zone, a fovea-like area of heightened (around three to four

times, depending on species) spatial sampling, revealed by an expanded pseudo-pupil (figure 1a, left eye). The acquisitional saccades described in this paper place this acute zone on objects of interest with rapid eye movements of several hundred degrees per second, similar in speed to saccades of other animals and quite different from the slower scanning movements (figure 3; [9]). Stomatopods may also follow objects with smooth or saccadic-tracking movements [8] and show some degree of large-field stabilization or optokinetic eye movements that entail rapid nystagmus movements [7]. Adding to this complexity of eye movement types is the fact that the eyes often move independently of each other, and although sometimes apparently yoked together, may at other times perform tracking with one eye and scanning with the other simultaneously [9].

The combined effect is most uncrustacean-like, suggesting an almost 'primate-like' awareness of their surroundings [14,15]. The best way to describe the apparent eye movement strategy in stomatopods is that the two eyes time-share between different modes; optokinesis, tracking, scanning and saccades. Sometimes these tasks are performed independently, sometimes with both eyes performing the same task.

Acute zones and foveae are found in many animals and almost invariably are associated with the use of saccadic eye movements that position the eye's zone of best resolution on objects of interest, either voluntarily or in response to the sudden appearance or movement of an object. Although many crustaceans show increased resolution in the anterior regions of their eyes [13], none possess discrete acute zones similar to those of the stomatopods, which appear to have coevolved with the use of saccades. Other arthropods, particularly insects, show whole body or head movements associated with placing objects of interest on acute zones. Lacking motile eye stalks, these body or head movements are equivalent to saccades and may entail rapid body turns and/or head movements while stationary or in flight [14,15]. Some spiders, especially the jumping spiders (Salticidae), have eye movements that target moving objects with saccades [14,15].

The presence of stalked eyes in stomatopods allows independent movements of only the eyes, which are not possible in insects or spiders where the eyes are part of the head or body. Similarities therefore exist between stomatopods and vertebrates, including the organization of the eye musculature [16] that controls eye movements. The saccadic eye movements of vertebrates, in particular of primates (including humans), have been intensely studied in recent years, and comparisons between stomatopods, other invertebrates and vertebrates are drawn later in this paper [17,18].

2. Material and methods

(a) Animals

Four stomatopod species, three gonodactyloid (*Odontodactylus scyllarus* 11 cm, *Pseudosquilla ciliata* 8 cm, *Gonodactylus chiragra* 9 cm) and one lysiosquilloid (*Lysiosquilla maculata* 18 cm) were used in this study. The animal size and relative eye size, as detailed below, may define eye speed upper limits. All animals were kept in salt water aquaria at 25°C under a 12 h on : 12 off day : night cycle of broad-spectrum illumination. Animals were placed in plastic PVC tubes to inhabit, allowing them the sort of shelter they prefer in their natural habitat.
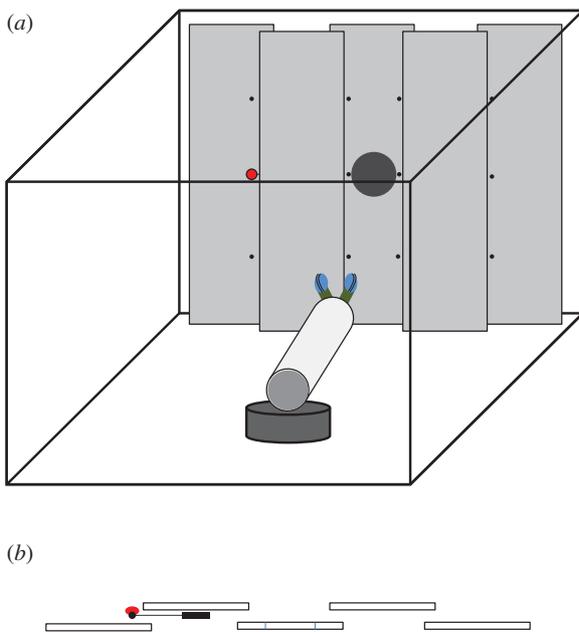
Figure 2. Diagram of experimental set-up. (*a*) Square aquarium with restrained stomatopod looking out of Perspex tube towards stimulus presentation screen. Central black circle is the hole through which camera can videotape from outside the aquarium. Small circle, on the mid-line to the left of the camera hole (red in online version), stimulus presented at 38° from the standardized stomatopod position. Small black dots, not visible to the stomatopod, mark positions of other stimulus presentation points. (*b*) Top-down diagrammatic view of the stimulus presentation screen showing overlapping white Perspex screens and red stimulus sticker on an arm attached to pulley-wheel, allowing stimulus to be suddenly presented at various positions in front of the stomatopod. (Online version in colour.)

(b) Stimulus presentation

A specially constructed glass aquarium was used for stimulus presentation (figure 2). Individual stomatopods were restrained in Perspex tubes of varying sizes to suit the animal's size, using rubber bands that allowed the animals to ventilate and draw water through the tube using their pleopods. Tubes were mounted on a pedestal of Plasticine, so that the head and eyes could be positioned at the proper position and height in the tank relative to the front wall of the aquarium. The whole set-up was enclosed in black cloth with overhead lighting to avoid extraneous stimuli, and any movement of the experimenter being detected. The front wall of the tank was entirely taken up with the stimulus presentation device, a set of slightly over-lapping, rectangular white Perspex screens. The central screen had a 3 cm hole in its centre to allow head-on filming of the stomatopods, a requirement of the computer analysis system.

Using a pulley, arm and disc on the end of the arm, a coloured target attached to the disc could be introduced or removed rapidly from behind the screens in any one of 12 positions (figure 2). Before presentation, the stomatopod would only see white Perspex screens and the dark camera hole in their frontal visual field, so sudden presentation of the stimulus was designed to elicit acquisitional saccades to known positions in the visual field. These were along the edges of the screen overlap positions, at around 10° and 38° laterally displaced left or right from the animal's midline. Three heights of stimulus introduction; 10° above, 40° above and 40° below the head were used, but best results were obtained with stimuli presented in the middle position, level with the camera hole and around 10° above the shrimp's head level, eliciting mainly horizontal saccades (figure 3).

(c) Data collection and analysis

This followed the protocol previously described [9]; a brief account of it follows. Animals were filmed with standard VHS cameras with 50 Hz frame rate before, during and after stimulus presentations. Frame-by-frame analysis of the eye position, and in particular of the angle of gaze of the acute zone, was determined by fitting a computer-generated three-dimensional outline or model to the eye. This was done separately for each eye shape: close to hemispherical for *O. scyllarus*, an elongated oval along the eye stalk in *G. chiragra* and *P. ciliata*, and an elongated oval perpendicular to the eye stalk axis for *L. maculata* (see figure 2 in [10] for further eye shape details). The operator is required to fit the model to the eyes, frame by frame, using a computer tracker ball. The accuracy of this method, as previously calibrated, is better than 3° for the frontal field encompassed by the stimulus screen, which is indicated by the circles around stimulus positions in figure 3. It is notable that in all species, the direction of gaze of the acute zone is around 15° offset from the eyestalk axis, towards the animal's midline, apparently compensating for the natural splaying out of the eye stalks. Saccades were quantified according to their amplitude (angular distance) and angular velocity with positional error in degrees.

3. Results

In general, animals of all species were alert and able to make eye movements, although saccades were not always generated. In a few instances, only one eye was used, while the other appeared to make slower scanning movements or did not move at all. However, usually both eyes were drawn to the target. Four example stimulus presentations and eye-movement responses are graphed semi-diagrammatically in figure 3. The line of stimulus positions level with the shrimp's head was most reliable in generating eye movements, whereas those above and below were attended to less frequently. Several individuals of each species were used, approximately size-matched within species to make data analysis easier. Data are graphed for *P. ciliata* and *O. scyllarus* only, as they generated the most complete datasets.

As well as analysis of responses to stimulus presentations, the eye movements of *P. ciliata* and *O. scyllarus* were monitored for several minutes, while the animal made spontaneous eye movements to objects in their home aquaria, an environment with a more complex background than the deliberately sparse saccade generation set-up (figure 4*a*). In both species, there appears to be a clear demarcation between saccades and scanning eye movements. Scans were made with similar angular velocities, averaging close to $40°\ s^{-1}$ in all four species. The species whose eyes had relatively long stalks, *P. ciliata* and *G. chiragra*, tend to move their eyes more often and thus seem more alert than the other species. This is apparent in a comparison of the number and extent of saccades during the spontaneous long-term observation periods of 5 min (figure 4*a*), where *P. ciliata* makes more saccades over a broader range of angular velocities; 79 at $150–650°\ s^{-1}$, compared with 16 at $230–360°\ s^{-1}$ in *O. scyllarus*. *O. scyllarus* is capable of making very high-speed saccades (exceeding $700°\ s^{-1}$), as is *P. ciliata* (figure 4 middle, right), but *P. ciliata* was more ready to perform saccadic eye movements as can be seen by the larger number of data points gathered compared with *O. scyllarus* in figure 4*b*.

Comparative saccadic speeds between all four species were as follows: *L. maculata*—$470°\ s^{-1}$ top speed and average of $226°\ s^{-1}$, *O. scyllarus*—$780°\ s^{-1}$ top speed and average $363°\ s^{-1}$, *G. chiragra*—$880°\ s^{-1}$ top speed and average $406°\ s^{-1}$
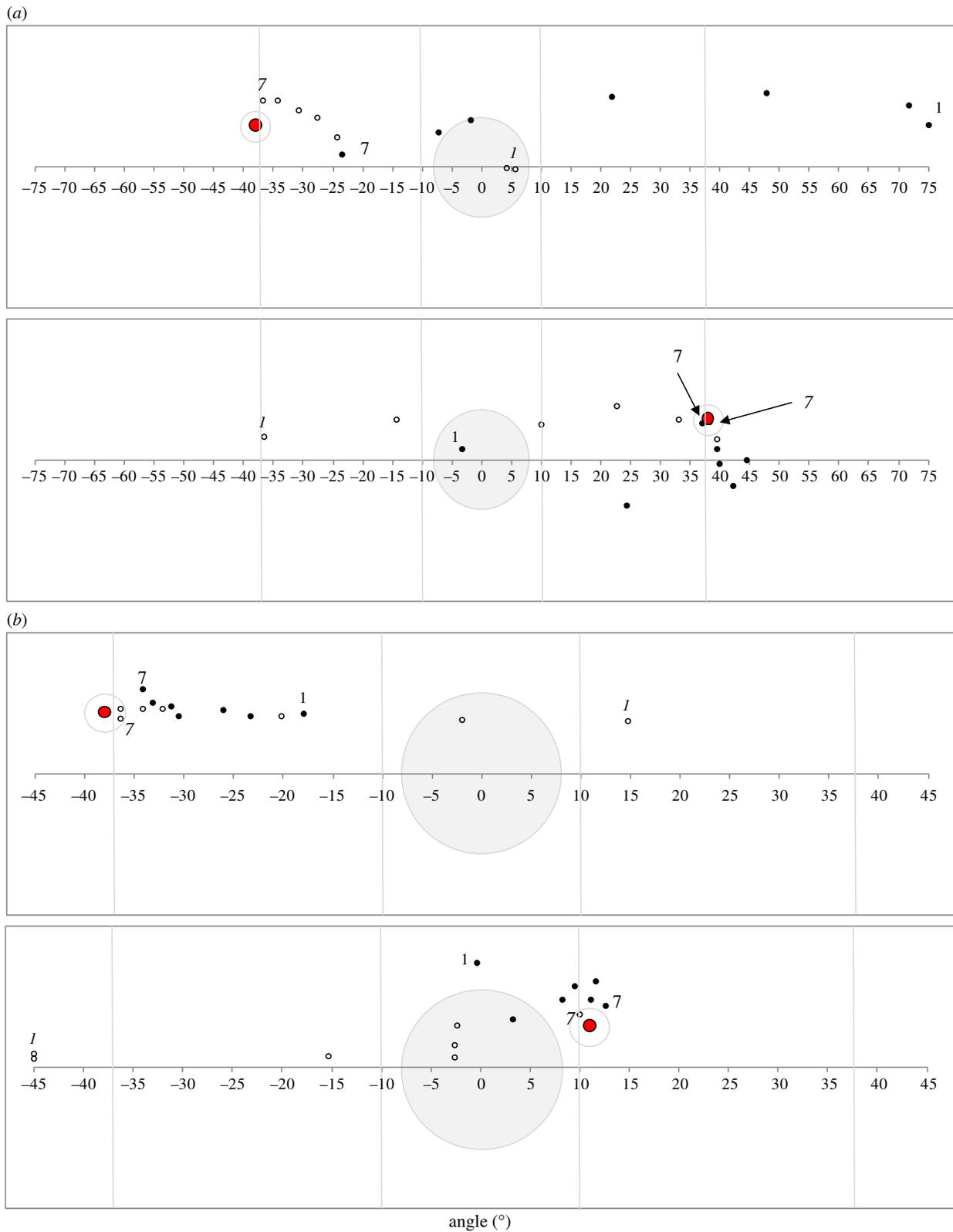
(a)

(b)

angle (°)

Figure 3. Example acquisitional saccades in (a) *Pseudosquilla ciliata* and (b) *Odontodactylus scyllarus*. In each graph, the *y*-axis has been removed but is the same as the *x*-axis, and each includes a representation of the positions of the stimulus screen (vertical lines at the edge of each panel and large grey circle showing position of hole for filming through) and stimulus presentation position (grey circle (red in online version) within circle) drawn in (see also figure 1). Individual data points are angular positions of the acute-zone direction, frame by frame (frame intervals 20 ms), for the right eye (filled circles) and left eye (empty circles) for seven frames during the saccade. First and last frame only are numbered on the graph for clarity and left eye numbers are italicized. Grey circles around stimulus positions show known experimental error in eye position recording using computer models [9]. (Online version in colour.)

and *P. ciliata*—750° s⁻¹ top speed and average 408° s⁻¹. End-on, eye corneal area dimensions, not including the eyestalk, were around 5 × 3 mm (*L. maculata*), 3 × 3 mm (*O. scyllarus*), 2 × 3 mm (*G. chiragra*) and 2 × 3 mm (*P. ciliata*), although this varied slightly with individual animal size. The eyestalk is relatively long compared with the end corneal section in *P. ciliata*
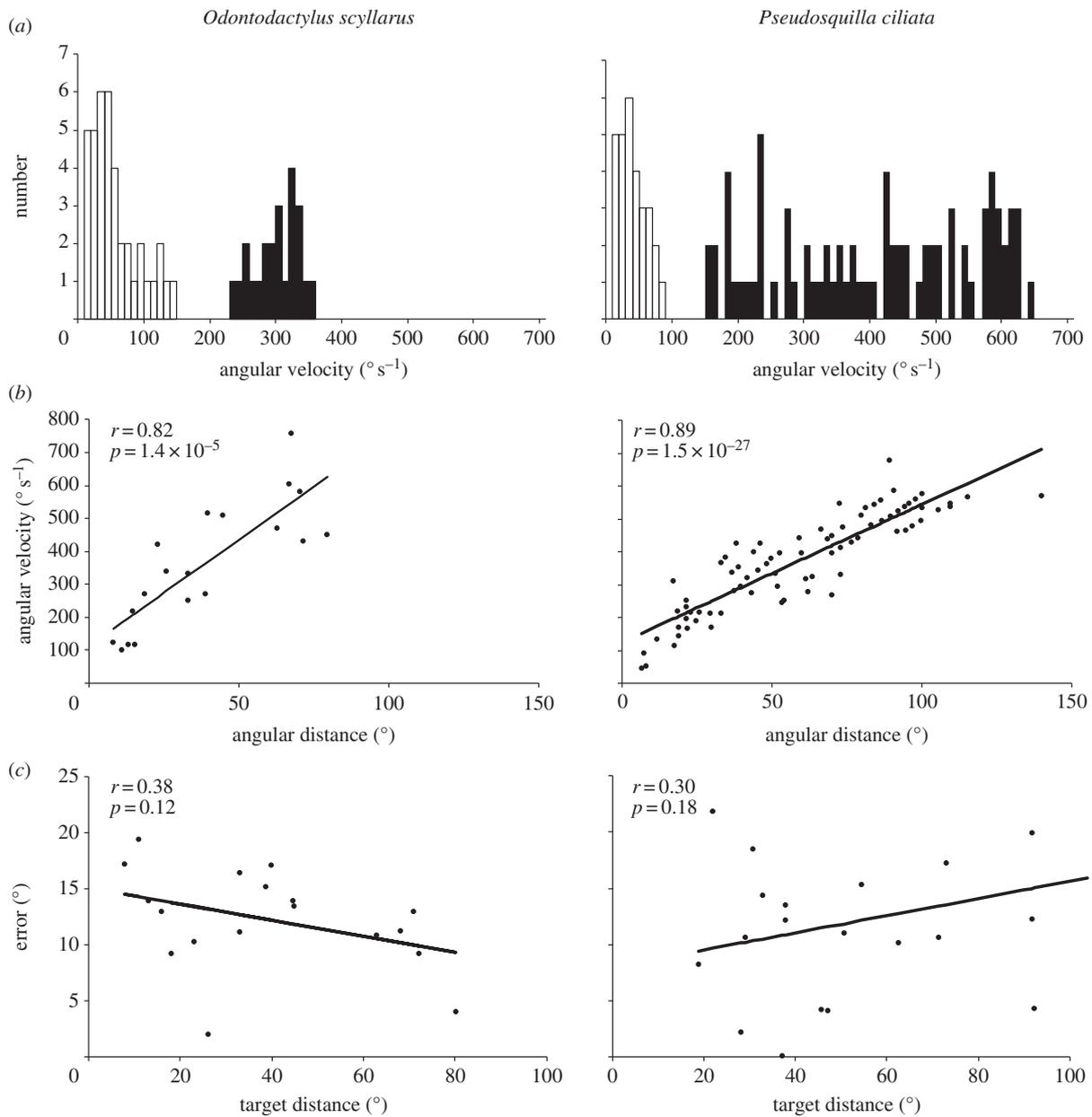
Figure 4. Analyses of eye movements in *Pseudosquilla ciliata* (right) and *Odontodactylus scyllarus* (left). (*a*) Several seconds of continuous eye movement showing both rapid saccadic movements (black bars) and scanning eye movements of around $100°\,s^{-1}$ or less (white bars) [9]. *P. ciliata* exhibits a wider saccade speed range than *O. scyllarus*. (*b*) Data from individually induced saccades using sudden stimulus introduction apparatus (figure 1) showing correlation between angular distance of eye movement and angular velocity. (*c*) Saccadic accuracy plotted as error angle taken at the final frame of the rapid movement (e.g. as in figure 3) relative to actual stimulus position. Both species show high degree of error, averaging around $10°$, not correlated with distance to target from previous direction of acute-zone gaze.

and *G. chiragra* and short in *O. scyllarus* and *L. maculata* (figure 2 and see figure 2 in [10]). It is possible that the different sizes and relative inertia or water resistance of the eyes in different species influences saccadic speed. All eyes are articulated with a joint made from suspending muscles [16] at the end of the eyestalk, so both the smaller size and longer moment (relative to body size) of the eyes of *P. ciliata* and *G. chiragra* may allow their more rapid movement.

In all species, the angular velocity of saccades increases approximately linearly with angular distance to the target (figure 4*b*). This latter measure was quantified as the angular distance between the eye position just before stimulus presentation to the position after the eyes had stabilized post-saccade for at least 1 s in time.

Saccadic accuracy by either eye was often poor (figure 3*a*, lower panel shows an exception) and errors from 5° to 20°

were typical (figure 4*c*). Often, one eye was more accurate, the other eye apparently 'giving up' having made it most of the way (figure 3*a* top). There was no discernible correlation between the saccadic distance and error in any species. After the initial ballistic saccade, eyes often remained still for several seconds, so adjustment saccades seen in other animals to correct such errors were apparently not made. However, the post-saccadic period was not analysed in detail here.

4. Discussion

(a) Stomatopods

It is worth recapping previous work on stomatopod eye movement. As noted in §1, anyone observing a stomatopod viewing its immediate surroundings might have the impression that the

two eyes move in an apparently random way, although the movements are in some way loosely connected to some things in the environment. Contributing to this apparent confusion is the fact that, similar to chameleons [19,20] and the sand lance (a small reef fish) [20,21], mantis shrimp eyes move independently, although when following a single target both eyes may become yoked to the same task. Stomatopods are capable of performing several different types of eye movement with each eye and often switch from one mode to another [9,14]. Such modes may include both smooth and saccadic tracking [8,22], scanning (a type of eye movement almost unique to stomatopods [9,14,15]), large-field optokinetic stabilization [7] and now, as confirmed in this study, acquisitional saccades [8,9]. Perhaps the most unusual aspect of stomatopod eye-movement repertoire is that they frequently switch from any one mode to another. It is this apparently 'conscious decision' to time-share between modalities that makes their eye movements so confusing. We still do not understand the factors that govern the allocation of this time [9].

As detailed in §1, the optical sampling directions of the eyes have coevolved with eye movement. It is the high-resolution band of receptors in both mid-band and peripheral eye regions that demands scanning eye movements, whereas the secondary increase in resolution near the centre of the mid-band results in the need for saccades. It is often mistakenly assumed that scanning is designed around the mid-band photoreceptors only, with their array of colour and polarization channels. Recall that 70% of the hemisphere ommatidia also examine the same strip of space and that they also contain likely linear polarization receptor channels set at four angles, approximately $0°$, $\pm 45°$ and $90°$, relative to each other. The triangulation in space of upper and lower hemispheres may allow monocular stereopsis, possibly important in the rapid ballistic strike of the mantis shrimp [23]. As a result, at least six channels of information come through these eye regions, four linear polarizations, stereopsis and potentially an intensity channel, to add to the mid-band sampling capability. While it is unlikely that this high-density strip plays a role in the generation of saccades, relocating the majority of the eye's photoreceptors to be able to line up with an object and then scan it may be part of the visual strategy. It is not clear from the observations made here how the acute zone is used by stomatopods. However, we assume that, as in other animals, it allows examination of the object of interest with higher resolution. Owing to the high degree of rotational freedom of the eyes [9], the mid-band is rarely horizontal. Scanning eye movements are generally made along trajectories orthogonal to the mid-band [9], and saccades can apparently be generated with the eye at any rotational position.

Cronin et al. [8] demonstrated both smooth and 'saccadic tracking' of rapidly moving targets by Neogonodactylus oerstedii, the fastest of these movements reaching $300° \, s^{-1}$ and therefore towards the middle of the range of saccade velocities generated here. The animals use the acute zone, or at least the frontally directed peripheral ommatidia in this process [22]. As these eye movements are part of a tracking behaviour, and possibly governed by a predictive process based on the movement of an object, they may not be best classified as acquisitional saccades. Similarly, if an eye loses track of an object, owing to background clutter, and then suddenly regains the position and initiates a saccade to the object, is this any different to the static presentations detailed here [8]? The speed of the eye movements of $300° \, s^{-1}$ or less is most likely governed by the

relatively short distances of these rapid eye movements. Notably, during tracking, large error angles between eye direction and target were also present.

Land et al. [9] also measured both scanning and saccadic eye movements in O. scyllarus. Scans averaged around $40° \, s^{-1}$, whereas faster movements (between 230 and $360° \, s^{-1}$) were noted as likely saccades to relocate towards objects of interest. These are similar to the data presented in figure 4a, generated by observing 'natural' eye movements of an animal for several minutes as it surveyed its environment. It is not known what the animal was observing. The deliberately induced saccades to known target locations presented here indicate that O. scyllarus is capable of very rapid eye movements when large angles require it (figure 4). The optokinetic eye movements of O. scyllarus, P. ciliata and N. oerstedii to large-field striped-drum stimuli have also been quantified [7]. These include rapid eye movements or nystagmus flicks to reposition the eye either after reaching a positional limit or apparently spontaneously. As with other animals, the purpose of this rapid nystagmus flick is quite different from the saccades described here, and the velocities of such flicks are well below saccade speed, lying between 30 and $40° \, s^{-1}$ [7].

In a comparison between species studied here, L. maculata saccades were notably slower than other species and, although capable of very rapid movements, O. scyllarus was on average slower than P. ciliata and G. chiragra. L. maculata has a markedly different lifestyle to the other three gonodactyloid species, living for its entire life in a sand or mud burrow in mangrove areas or other coastal or shallow tidal habitats. It hunts by looking upwards out of its burrow and lunging forward with lightning speed, simultaneously striking with its spearing raptorial appendages [6]. L. maculata may grow up to 40 cm in body length and its eyes are proportionally larger and elongated away from the mid-band to be rugby-football shaped. Possibly because of the eye size and shape, it possesses the highest resolution, both along and orthogonal to the mid-band, of any stomatopod [10,11]. As this species is clearly capable of rapid saccades, the comparatively slow speed of the saccades seen in this study may be due to a number of factors. First, the eyes are larger and harder to move through inertia or water resistance than those of other species. This may also explain the slower and less frequent movements of O. scyllarus. Second, the ecology of this species, where they track and kill relatively slow-moving fish cruising the mud-flats, may not be as fast and furious as is required on the reef (the habitat of the other species). Finally, the horizontal retaining tube used in all species clearly made this species the most uncomfortable and reluctant to perform. Future observations might best be performed with the animal vertical, its preferred hunting position.

(b) Comparison with arthropods and other invertebrates

Stomatopods are the only crustaceans known with saccadic eye movements or with acute zones of sufficient resolution difference from the rest of the eye to demand such movements. Other crustaceans are more 'bovine' in that their eyes rarely or never turn to look at objects, but instead let them pass over the retina, keeping track of their position through internal neural mechanisms. As well as the ubiquitous 'saccadic nystagmus' during optokinesis [24,25], crabs that live in flat-worlds show one kind of rapid eye movement, that is in a way the matching of an acute zone to object [26,27]. Ghost crabs, fiddler crabs

and a few other semi-terrestrial species inhabiting flat habitats possess vertically elongated eyes and a horizontal streak of higher resolution, in a way similar to the high resolving power of stomatopods congruent with the mid-band [12]. Unlike stomatopods, however, crabs are careful to keep this streak aligned to the local horizon in order to match resolution to distance over the substrate to aid in object classification and distance estimations [12]. Crabs emerging from burrows or changing position will 'snap' their eyes to align their internal optical arrangement to the substrate direction at saccade-like speeds.

Acquisitional saccadic eye movements are known in several insect species as well as some in spiders and in the cephalopods [14,28]. Rapid and presumably saccadic eye and/or body repositioning towards objects of interest are noted in octopus, squid and cuttlefish [28,29]. This would be expected from such voracious predators that also show a visually guided ballistic tentacular strike similar to, although orders of magnitude slower than, that of stomatopods. Both the optics and eye movements involved are poorly known in this group. Among spiders, the jumping spiders (salticids) show equivalent eye relocations. Of the four pairs of eyes in the cephalothorax, the antero-median eyes have become enlarged and developed in salticids and, necessarily using rapid body repositioning, many jumping spiders can turn and look at objects of interest [15,30]. These movements place the antero-median eyes on the object and interestingly, similar to stomatopods, scanning eye movements are then used to analyse the object closely [14,15]. Resolution within these eyes varies across their vertically extended visual fields, with the highest resolution in the centre.

Insects also lack eyestalks and possess compound eyes embedded in their heads. Stalk-eyed flies do exist, including certain *Drosophila* and other species [14]; however, these stalks remain part of the head and are not independently mobile. Using both head and/or body movement, several species that possess acute zones generate saccades [15]. In flying species, such as flies, other dipterans and orthopterans, rapid body and head movements have been extensively analysed, since the pioneering work of Land & Collett [31,32]. Many such flying insects are exquisitely adapted for locating and following small objects, mates or prey while in flight, and both saccadic and tracking movements requiring body–head coordination to keep the acute zone locked to the object are described [33,34]. This is sometimes for prey location, but there are several examples where male eyes contain optical adaptations that are designed for finding, following and accosting females [33,34].

More akin to stomatopods, insects with their feet on the ground may also perform saccadic head or body movements, or combinations of these, to look at objects [14,15]. Species of bull ant and some of the digger wasps, for example cicada killers (*Sphecius speciosus*), will turn their heads to look at curious photographers or biologists, even more unnerving than a glance from a busy stomatopod. Because of their convergent prey-capture technique, praying mantids (the insects after which mantis shrimps were named) show a number of parallels to stomatopods. These raptorial insects will look at and align their bodies with rapidly moving prey before strikes [35]. They also show tracking eye movements, both smooth and saccadic, using rotational head movements. Peak saccadic velocities on the order of $470–560° \, s^{-1}$ are similar to or slower than those of stomatopods and are also correlated with saccadic amplitude [36]. Interestingly, during tracking,

as the speed of the object or the clutter of the background increases, more frequent saccades are made to keep track of the object, as also noted in stomatopods [8]. This may, in part, be a requirement to break free of the optokinetic reflex that stabilizes the eyes on the world [15].

(c) Comparison with vertebrates

Several factors make some of the stomatopod repertoire of eye movements, including saccades, more similar to those of vertebrates than most invertebrates. As noted earlier, their eye movements give them a 'primate-like' appearance, although when they start to scan they become more similar to an earth-imaging satellite [4]. Interestingly, even the musculature that achieves eye movements has converged on a design much similar to that of vertebrates, with pairs of muscles for each degree of freedom of movement. In the stalk-eyed crabs, which from the outside might seem much as stomatopods, 13 muscles are found to be arranged quite differently from those of stomatopods [16]. Almost all vertebrate groups (with the exception of the amphibians) contain some species that display saccades associated with acute zones (or true foveae). As in stomatopods, this hand-in-hand relationship of optics and eye movement is often associated with a predatory lifestyle. For obvious reasons, particularly in primates, saccadic eye movements have been studied extensively and are classified according to type. There are those that target new objects in the periphery (most as the situation in the experimental set-up here for stomatopods), fast phases of nystagmus that, in fact, should not be termed saccades [17], and also 'voluntary' gaze-relocating saccades (perhaps similar to those seen in figure 4*a*).

Primates may sometimes be predatory, but it is hand–eye coordination that has driven the use of saccadic relocation of the eyes, specifically associated with object manipulation [18] or at least placing objects of interest in the mind's eye [37]. They show similar saccadic speeds to stomatopods, and as stomatopods (figure 4) speed increases with amplitude. Human saccades, however, have an upper saturation limit of around $500° \, s^{-1}$, at least $200° \, s^{-1}$ slower than the fastest saccades measured here [17]. Occasional saccades up to $700° \, s^{-1}$ are made but these are exceptions. It is possible that the raptorial strikes that stomatopods use in conspecific competition as well as prey-capture demand increased eye speed. Unpublished data (Chiou & Marshall 2013) indicate that flicker fusion rates in stomatopods are higher than that in humans, also indicating a faster living speed, however they are not as high as those of flies and other airborne insects.

Measures of saccadic accuracy in primates also indicate that they also often over or undershoot on the first attempt. Unlike stomatopods, post-saccadic repositioning after this primary saccade usually corrects this [17]. In addition, unlike stomatopods, in primates there is a linearly increasing error of the primary saccade with distance. Why stomatopods appear not to readjust this inaccuracy and make equally poor first attempts independent of distance (figure 4) is not clear. It may be more important to position the eye for a post-saccadic scan of the object than for precise acute zone alignment. Not enough post-saccadic analysis was done here to allow more comment, although the overall impression is that stomatopods keep their eyes relatively stationary after saccades. In field conditions, again rather subjective observations suggest that there are more post-saccadic movements, possibly including either corrections or scans, and indicative that the

featureless arena we used here does not generate fully natural eye movements. Little red dots do not usually appear from behind curtains in nature, so while this may be a useful protocol for initial observation of this unique eye movement in crustaceans, more work on the post-saccadic period in more natural conditions is worthwhile.

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