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SHORT COMMUNICATION

SUBSTRATUM SLOPE AND THE ALIGNMENT OF ACUTE ZONES IN SEMI-TERRESTRIAL CRABS (*OCYPODE CERATOPHTHALMUS*)

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The organisation of the visual system in semi-terrestrial crabs is related to the three-dimensional structure of the environment (Zeil *et al.* 1986; Nalbach and Nalbach, 1987; Nalbach *et al.* 1989*a*,*b*; Zeil *et al.* 1989). In species that live in flat habitats – like sandy ocean beaches or mudflats – we find: (1) long, vertically oriented eye stalks; (2) a small separation between the eyes; (3) an acute zone for vertical resolving power with its maximum along the eye equator; and (4) a specific gradient of vertical resolution towards more dorsal and more ventral directions of view. Species that live in three-dimensionally more complex worlds – like rocky shorelines and within mangrove forests – have short eye stalks far apart at the lateral corners of the carapace and lack prominent acute zones.

We have argued elsewhere (Zeil *et al.* 1986) that these differences have to be interpreted as adaptations to the needs of spatial vision in differently structured environments. We have shown that, in principle, animals that live in a flat world could gain depth and size information from retinal position and retinal size alone. This is a consequence of the peculiar and predictable topography of vision in a flat world: provided animals 'know' their eye height above ground and provided that the world they live in can be assumed to be flat, the distance from an object on the ground can be estimated from the size of its base angle and, through this, its absolute size can be determined from the angular size it subtends at the eye of an animal. The range over which distances and sizes can be determined in this way depends on eye height and vertical resolving power.

For such a 'flat world mechanism' of depth perception to work it is important that the acute zone for vertical resolving power be aligned with the visual horizon of the animal (Zeil *et al.* 1986). A strong prediction from this is that acute zones are not aligned with respect to gravity but that they are aligned with the substratum/sky or substratum/sea boundary (what we called the local visual horizon). We further predicted that this alignment has to be under predominantly visual control and cannot involve the statocyst or leg proprioceptive inputs that are known to contribute to eye stabilisation in crabs (see Neil, 1982; Varjú and

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Sandeman, 1982). A recent survey of the relative contributions of statocyst, leg proprioceptive and visual inputs to the system controlling eye-stalk orientation in different species of crabs has indeed shown that, in crabs from flat worlds, eye stabilisation is predominantly driven by visual input (Nalbach *et al.* 1989*b*).

Here I report on field observations of *Ocypode ceratophthalmus* (Brachyura, Ocypodidae) that live on sections of sandy ocean beaches with a slope of up to 21° relative to the horizontal. The study was carried out at various locations in Goa, India, in 1988. Crabs were photographed on 35 mm film or filmed with video while sitting in their burrow entrances or out on the substratum. Substratum slope (α_s), the direction of gravity or the horizon line, eye-stalk orientation (α_e) and, where possible, the orientation of the body (carapace tilt α_b) were measured from slides or from single video frames using image processing equipment. For definition of variables see Fig. 1A. To gain an estimate of accuracy in the analysis of video films I repeated each measurement 11 times and used average values. As a worst estimate, the maximal standard deviation for α_e was 3.7°, for α_s 2.5° and for α_b 3.0°. Where possible, average measurements for right and left eyes were used.

When animals emerge from the burrow the erection of the eye stalks from their sockets is fast; they reach their final orientation within 20–40 ms. Crabs that live on inclined sections of the beach align their eye stalks perpendicular to the local slope of the substratum (Fig. 1B), irrespective of the tilt of their carapace (Fig. 1C). Tilt of the carapace relative to the substratum (α_b) ranged from +26° to −34° in the 16 cases where it could be measured (Fig. 1C,D). Crabs, therefore, align their equatorial acute zone with the local visual horizon.

The regression line in Fig. 1B is shifted about 3° upwards from the line of equality. This means that most animals have their eye stalks oriented at larger angles relative to gravity than would be required to keep them at right angles to the substratum. A possible reason for this might be that eyes and acute zones are tilted relative to the outline of the eye stalks. However, sorting the data according to pitch, roll orientation and pitch/roll mixtures shows that pure pitch and pure roll orientations tend to lie below the regression line (i.e. closer to the line of equality). Values for animals that were filmed or photographed not directly from the side or from the front tend to lie above the regression line through all points. The shift, therefore, is likely to be an artefact resulting from systematic errors in measuring eye-stalk orientation in animals viewed from 'skew' directions.

It is important to note that the only information available to the crabs for the alignment of eye stalks perpendicular to the substratum is visual. The fact that they do not align their eye stalks parallel with gravity shows that input from the statocysts and from leg proprioceptors does not play a significant role. It is not clear, however, whether the fast alignment of eye stalks during emergence from the burrow is a position-dependent reaction with the local visual horizon line as input. Nalbach *et al.* (1989*a*) have shown that semaphore crabs (*Heloecius cordiformis*) and soldier crabs (*Mictyris longicarpus*) in fact fixate a horizontal contrast line. Initial alignment – at least of the leading eye – could also be based on a dorsal light reflex, since the upper section of the burrow tube intersects the

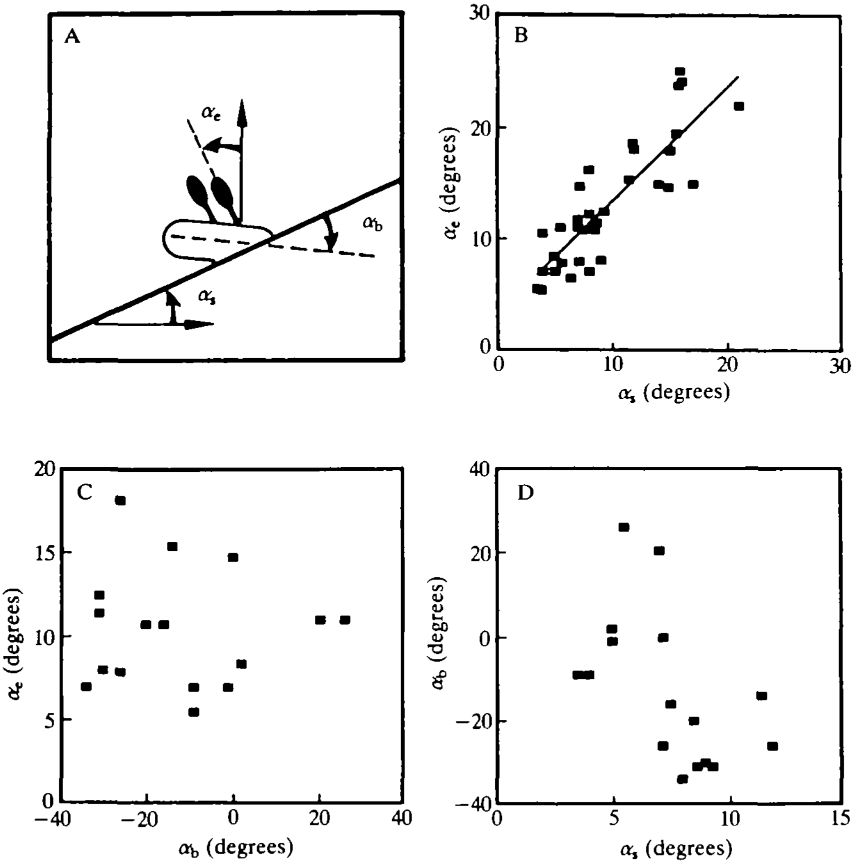

Fig. 1. (A) Diagram of a crab on an inclined substratum. α_s, angle between substratum and the horizontal; α_b, angle between carapace and substratum; α_e, angle between eye stalks and the vertical plane. (B) Eye-stalk orientation (α_e) *versus* substratum slope (α_s) for 21 crabs (*Ocypode ceratophthalmus*), some at different carapace tilts relative to the substratum. Points include pure pitch, pure roll orientations and various pitch/roll mixtures. The line is a regression line through all points (N=34; b=1.02; r=0.85). If eye stalks were oriented parallel to gravity they would all have a 0° orientation. (C) Eye-stalk orientation (α_e) *versus* carapace tilt (α_b) for 16 cases where α_b could be measured. (D) Carapace tilt (α_b) *versus* substratum slope (α_s) for the same 16 cases. There is no obvious correlation between α_e and α_b or α_b and α_s.

substratum at the surface more or less at right angles. Crabs emerge sideways from their burrows and, seen from inside, the exit hole is a very bright beacon. Finally, it is not inconceivable that the crabs memorise the slope of the substratum.

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