

DIRECT RESPONSE OF THE CRAB *CARCINUS* TO THE MOVEMENT OF THE SUN

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One line of evidence points to the conclusion that eye responses should be measurable in a crab, in air, which sees only the movement of the sun in a clear sky. It has been shown in the previous paper, as an extension of earlier work with slowly moving striped drums, that eyestalk movements follow a single light in a dark room when the light is moved with low angular velocities round the crab in the range $10-20^\circ/\text{hr}$. For horizontal movements which subtend angles of $0.02-1.0^\circ$ at the crab's eye, at a lamp velocity of $0.01^\circ/\text{sec}$., the horizontal eye movement is 20-50% of the light's movement. The light used gave an illumination of 0.05 lux on a surface in the position of the crab's eye. These figures remove any doubt that the crab is able to see the movement of the sun directly. The movement of the full moon, with a maximum illumination of 0.24 lux on the earth's surface, must also be seen by the crab, and possibly some of the brighter stars are also seen directly. Whether the crab responds to these moving lights will depend, not only on whether it sees them, but also on whether there are stationary contrasting objects in the visual field. If the eye begins to follow an isolated moving stimulus, other contrasting objects will move in the opposite direction over the eye, and this will at once diminish the response by an opposite stimulus. Therefore, to make sure of recording a maximum response to celestial movements the animal should see as little as possible besides the object of interest.

That several crustaceans give compass reactions to the sun has been known for some time. The most remarkable results are those of Pardi & Papi (1961) in a series of observations on the littoral amphipods *Talorchestia* and *Talitrus*. They find that in the absence of any landmarks except the sun these animals are able to head correctly towards the sea when too dry or towards the land when submerged, and that the position of the sun at different times of the day is taken into account by reference to an internal rhythm within the animal. More difficult to explain is the finding that the moon can also be used as a reference in the same orientation response. Papi (1960) explains this by supposing the existence of a separate rhythm which is linked to the moon, but the method outlined in the present paper seems equally effective in providing a compass direction by moonlight without requiring a lunar rhythm.

Although fishermen's stories on the subject are common, the only scientific reference to a crab's ability to escape towards the sea when released on land is in an unpublished thesis (van Tets, 1956) quoted by Pardi & Papi (1961), showing that the Pacific shore crab *Hemigrapsus* utilizes some feature of the path of the sun as a basis for directional escape towards the sea. Drzewina (1908) found that *Carcinus* released on a beach goes to the nearest shadow.

METHODS

Movement of the crab's eyestalk was recorded with a light flag (weight 3 mg.) which was arranged to move over the carapace across a horizontally mounted photocell (Texas type L.S. 221). The crab's carapace was clamped with the crab facing due east at an inclination which is typical of normal posture. Methods of recording were exactly as in the previous papers, with the modification that the crab was surrounded by a black card having a horizontal upper edge which obscured all landmarks. This is a further reason for experimenting at noon, for then the stimulus is high in the sky, and the response, being in the horizontal plane, is not modified by the contrasting upper edge of the cardboard. Of necessity, experiments have been carried out behind a large glass window facing south, because outside the slightest breath of wind moves the light paper flag over the photocell, which easily records 10μ of movement.

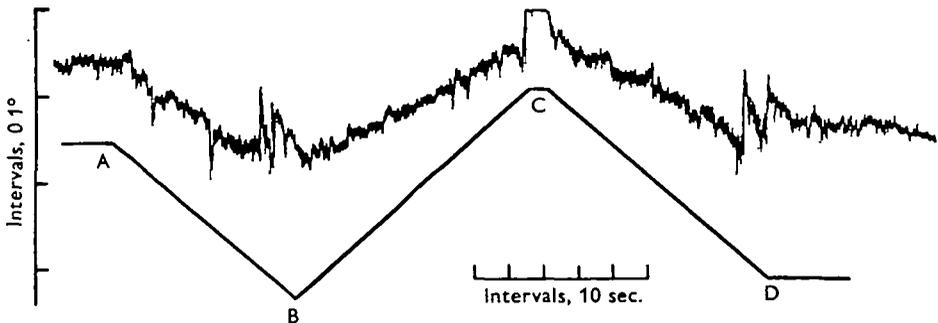


Fig. 1. Horizontal movements of the right eye of a crab, *Carcinus*, facing east, in response to the sun's movement at noon. At A the crab was allowed to see the sun directly, at B the sun was obscured with black paper and was reflected on the left eye with a mirror. At C the normal sun was restored and at D it was obscured again. Disturbances of the trace arise from hand movements at each change. The angular velocity of the sun is twice that shown by the scale.

RESULTS

Visual responses

The horizontal movements of the right eye with the crab facing east at noon are shown in Fig. 1, with the rate of change of the sun's azimuth drawn at half the vertical scale. As in all records from freely moving eyes the response speed is less than the stimulus speed, being in this case from 10-40% of it when few stationary objects are in the visual field. Actual performance depends very much on the individual crab, but all the variation between animals could be caused by the differing importance of stationary objects in the visual field. For example, some crabs hold their claws in their visual field and in others the carapace edge may have a greater or less effect.

That the movements truly arise from the movement of the sun was demonstrated with a mirror. The sun shines on the right side of the animal, but when it is obscured by a large piece of paper the response falls to zero. When a mirror is arranged on the crab's left side to deflect the sun's rays into the left eye the apparent movement of the sun is now reversed to the crab. The movement of the two eyes are linked in the brain,

so that one drives the other whichever is stimulated. The only condition is that neither eye should have a stationary contrasting object in its visual field. The response to the reversed sun is usually less than that to the real sun on account of the introduction of the black paper and the mirror. Both of these stationary objects add to the stationary contrasting edges which are visible to one eye or the other.

The latency of the response, and therefore the maximum time before the animal gives some sign that it perceives the sun's movement, is about 10 sec., as shown by direct measurements on the records of eye movement. Fig. 2 illustrates a typical case, which also shows how a sudden change in illumination caused by a shadow or

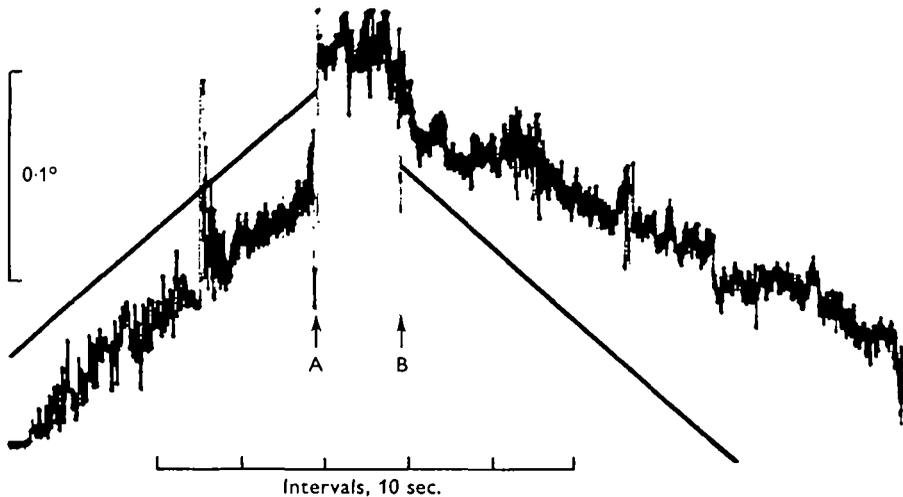


Fig. 2. As in Fig. 1 but showing better the latency to reversal of the sun's apparent movement. At A the sun was obscured and at B the mirror reflected the sun on to the other eye, so causing a second jump in the record. The eye movement is clear after a further 15 sec. The angular velocity of the sun is twice that indicated by the scale.

by the mirror can cause a sudden jump which is superimposed on the eye movement. A latency of 10 sec. implies that a movement of the sun through 2 min. of arc is necessary and adequate before a response is discernible above the noise level. Because vertical eye movements were not recorded, a period for the experiments was chosen when the sun's rate of change of altitude was zero and the rate of change of azimuth (projection to the horizontal) maximal. Therefore experiments were carried out around noon on midsummer day and a few days on either side of 22 June. In fact, at midsummer noon the rate of change of azimuth at St Andrews (latitude $56^{\circ} 20'$) is $25.3^{\circ}/\text{hr.}$ or $0.007^{\circ}/\text{sec.}$, which is well within the known range of response of *Carcinus* to movements of single lights of much lower intensity.

Since the rate of change of azimuth and the rate of change of altitude of the sun vary regularly during the day it is important to establish the lower limits of the crab's ability to perceive these movements. So far this has not been done because until recently we lacked the ability to record horizontal and vertical eye movements simultaneously. Experiments with a single moving light of 0.05 lux in a darkened room show responses down to a velocity of $6-8^{\circ}/\text{hr.}$, depending on the crab (Horridge,

1966*b*). Experiments with a striped drum which was illuminated by a 60 W. bulb at a distance of about 1 m. show responses down to $5^\circ/\text{hr.}$, at which the eye still gives a reasonable response. This means that the true stimulus, i.e. the relative movement across the eye or slip speed (= drum speed minus eye speed) is even less. The lower limit of movement perception is not determined by the eye's ability to move at these low speeds, for there is no response at stimulus speeds which are equal to the lowest attainable slip speeds (Horridge & Sandeman, 1964). These measurements will be taken into account when the curves of the sun's movement are considered below.

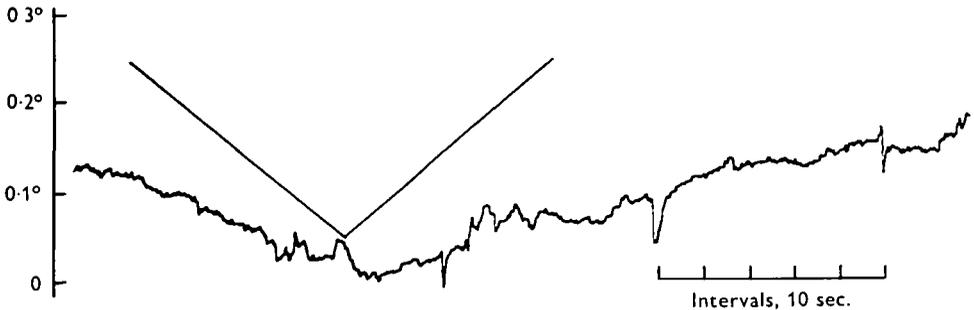


Fig. 3. A, Response to movement of a single small light (0.05 lux at the eye) which moves at a constant velocity of 1° in 240 sec. as shown by the straight lines. Note the eye flicks and the recovery from them.

Gravity response

If an animal is to utilize the direction of the sun's movement or to resolve that motion into horizontal and vertical components it must have an accurate measure of the vertical, either from an artificial horizon or from a gravity sense. In fact it has long been known (Bethe, 1897) that crabs move their eyes and compensate for tilting of the body axis. Although a measure of the extent of compensation is relevant, no accurate figures are available for *Carcinus*, or any crab. Results for forward and backward tilting are summarized in Fig. 4. The most informative presentation (filled circles) shows the change in eye angle per degree change in carapace inclination. This quantity never falls to zero, i.e. eye movements never completely compensate for body movements. However, over a central range of about 20° the change in eye angle is less than a tenth of the change in body angle. This conclusion relates to average values and ignores four important factors: the hysteresis effect, the fact that natural deflexions will not be purely in one plane, the influence of vision, and variability on repetition.

The two curves in Fig. 4 each bear an arrow showing the direction of movement in which the measurements were taken. Since the eye follows the stimulus without ever completely compensating there is an effect resembling the hysteresis in magnetization. For a crab this will introduce a corresponding error unless it has information to compensate for the directional effect or unless it oscillates about a mean value at which it is able to arrive by a process of averaging.

When the carapace is tilted sideways in roll about its antero-posterior axis the compensation by the eye movements is not nearly so complete, or over such a wide range (Fig. 5). The change in eye angle now only falls to about 0.4 of the change of

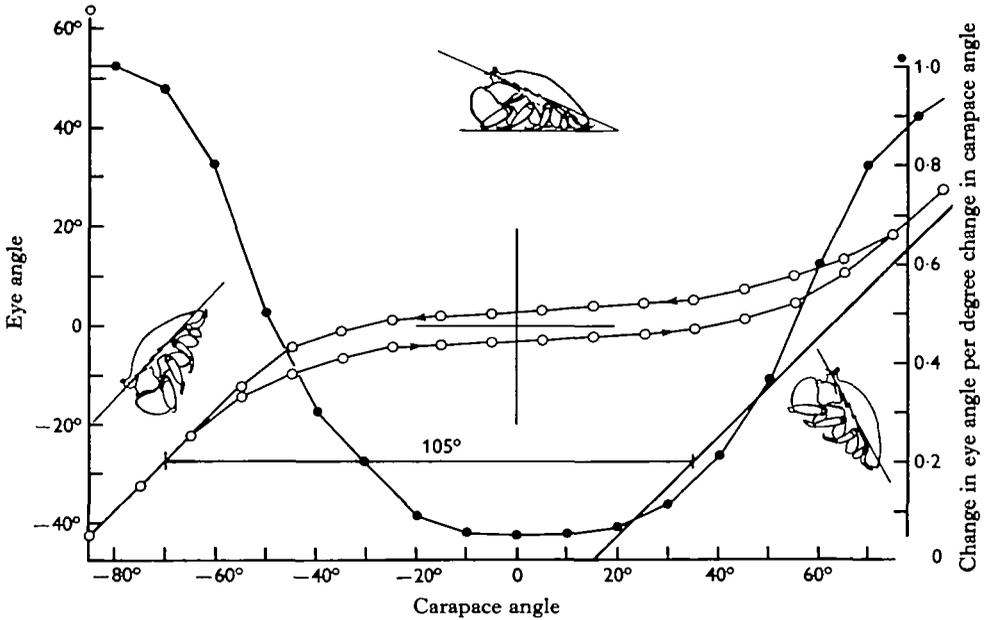


Fig. 4. The partial maintenance of eye position during forward tilting. Open circles show average eye deflexions from normal when the crab is tilted, head down or head up, as indicated by the inset. The normal position of the carapace for a resting crab is taken as zero. The arrows show the direction of movement. Filled circles (ordinate on right) show the average change in eye angle per degree of change in carapace angle, with a minimum below 0.1° for the central range of about 20° . Straight lines at 45° mark the limit of eye movements over a range of 105° .

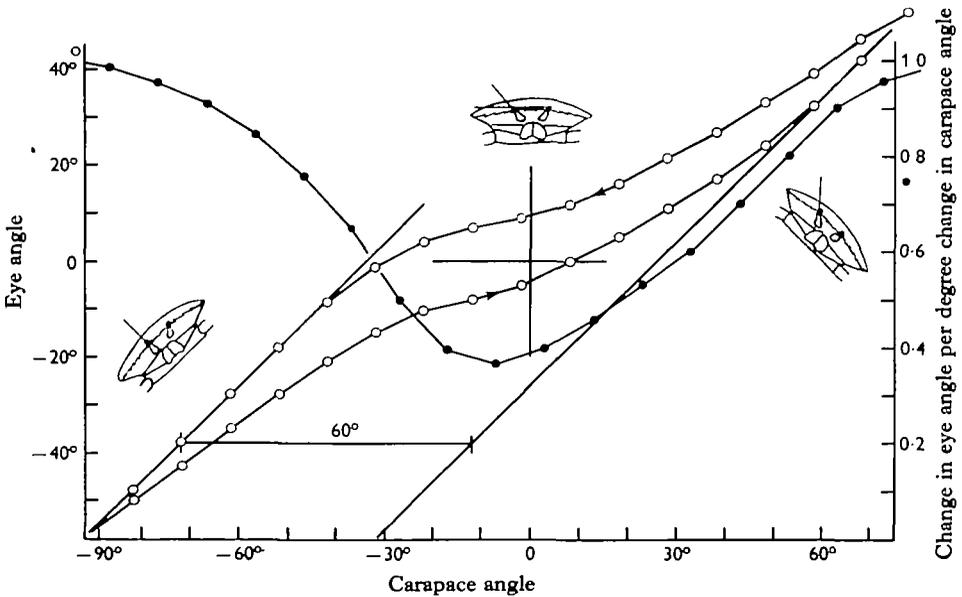


Fig. 5. The partial maintenance of eye position during sideways tilting. Open circles show average eye deflexions, in the two directions of movement. Filled circles show change of eye angle per degree of rolling angle with minimum only at 0.4° . The maximum eye movement of 60° is less than in Fig. 4.

carapace angle, and then only over a small range. There is the same hysteresis effect as before. Because any natural tilt would almost always involve some degree of roll, it is difficult to see how so-called compensatory eye movements could provide a means of maintaining the sun at an angle to the retina with an accuracy better than about two interommatidial angles (each of 2°).

If the above measurements are made in a dim red light, or with no contrasting objects in view, the ability to compensate falls, in so far as the change in eye angle is now generally less per degree change of body angle. Results are illustrated in Fig. 6, which also shows the considerable variability of measurements of the eye position. The small additional element of eye stabilization is apparently attributable to the

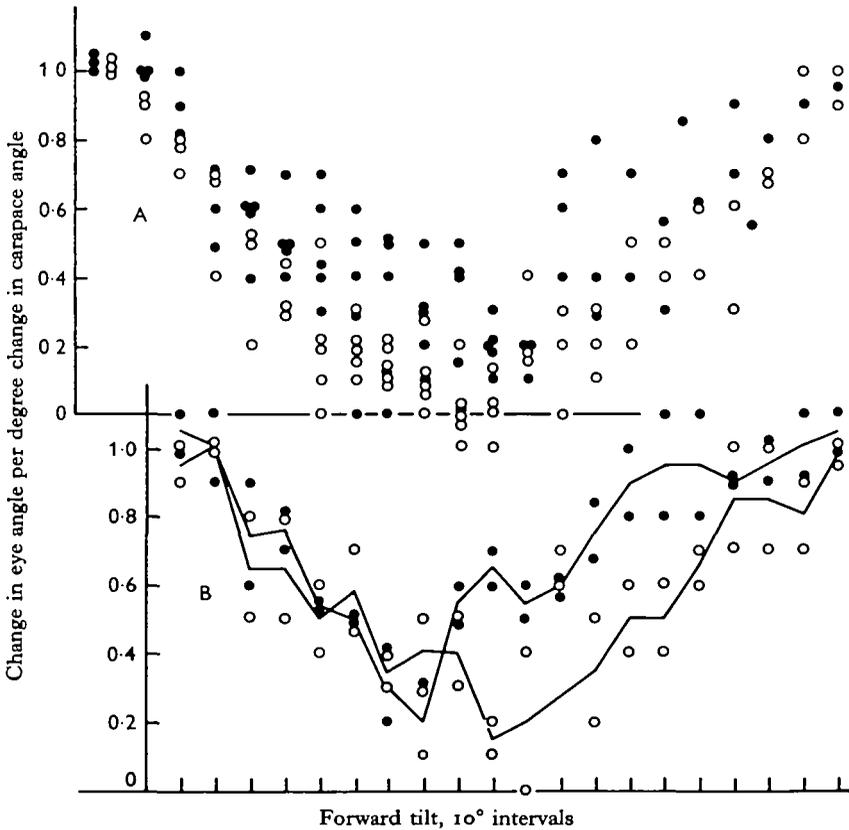


Fig. 6. Inconsistency of eye movements in the light (O) and in the dark (●). Each point is a measurement of change in eye per degree change in carapace position in the forward (diving) plane shown in Fig. 4. Measurements made in the light show better stabilization than those in the dark, but even so there is considerable scatter. A and B are results from two crabs.

optokinetic memory, which is only able to act in the light, or when contrasting objects are in view. If a series of highly contrasting objects, such as stripes, were in the visual field one might be able to obtain better eyestalk compensation to tilt of the body in the appropriate direction in the light. This, however, would be an abnormal situation which is hardly relevant to the problem of orientation by the sun or moon.

Inconsistencies in the eye movements on repetition and between crabs are also brought out in Fig. 6. Careful repetition of the observations shows that the eye does not come back to the original resting position after being disturbed. Near the normal postural position the eye position is usually held accurately to about 2° . Quantitative figures are valueless until we know whether the horizontal and vertical resolution of the sun's movement is really of importance to the crab. At St Andrews an error of 1.5° in estimation of the vertical at noon in summer would give the impression of a motion which would normally occur when the sun is about half an hour away from noon, and therefore cause an error of about 12° in the estimation of compass direction from the sun's rate of change of altitude combined with azimuth position. During the middle 4 hr. of the day the rate of change of altitude is reasonably proportional to time away from noon, so that a directional error of approximately 8° would be found throughout this period for each degree per hour of error in estimation of the vertical movement of the sun.

DISCUSSION

In this field the traditional course of inquiry has been to discover a behavioural ability to orientate by the sun and then seek an explanation in terms of sensory abilities. Here the position is reversed; there is no doubt about the sensory ability but the question is whether the crab utilizes it. If so, we are in a strong position to analyse the nervous basis of the mechanism, which is not so accessible when the sensory abilities are inferred from the behaviour.

One problem which can no longer be shelved is the extent to which the crab averages out the irregularities in its eye movements. The eye movements in response to sun movements and the partial compensation for tilting are revealed as full of small irregularities when recorded in detail. An increase in accuracy can be achieved if the changes can be stored and smoothed. Apart from the optokinetic memory, outlined in an earlier paper (Horridge, 1966*a*), there is no indication that a crab can do this. The same question can be asked about a pigeon which circles before setting out for home—whether there is in fact an averaging process at work, or whether this is no more than a human concept which explains an otherwise enigmatic accuracy.

Although the crab responds to the sun's movement, the aspects of that movement which are relevant to the crab are as yet unknown. Solar movements as seen from St Andrews (latitude $56^\circ 20'$) have been resolved in Figs. 7 and 8 into vertical and horizontal rates of movement; dashed lines show actual altitude and azimuth positions. From these figures it is clear that one reasonable method of orientation which is independent of the clock and therefore applicable to sun or moon on the same day is to estimate the rate of change of altitude. This immediately identifies the position in the orbit without ambiguity, with reasonable linearity, with a latency of a few seconds and without independent information. To determine the direction of escape to the sea the animal must then have a memory of the position of the sea on its local shore in relation to the sun's azimuth, for each value of the rate of change of altitude.

As in the classical example of the electric fish, it is sometimes difficult to envisage the beginnings of an attribute which is of value to the animal only when developed to a sophisticated degree. When we know that a lower animal can appreciate the direction

and velocity of the sun's movement and also that it has a sufficient knowledge of the direction of the vertical to resolve the motion into horizontal and vertical components, we can see that a progressive perfection of these abilities could lead, in a higher

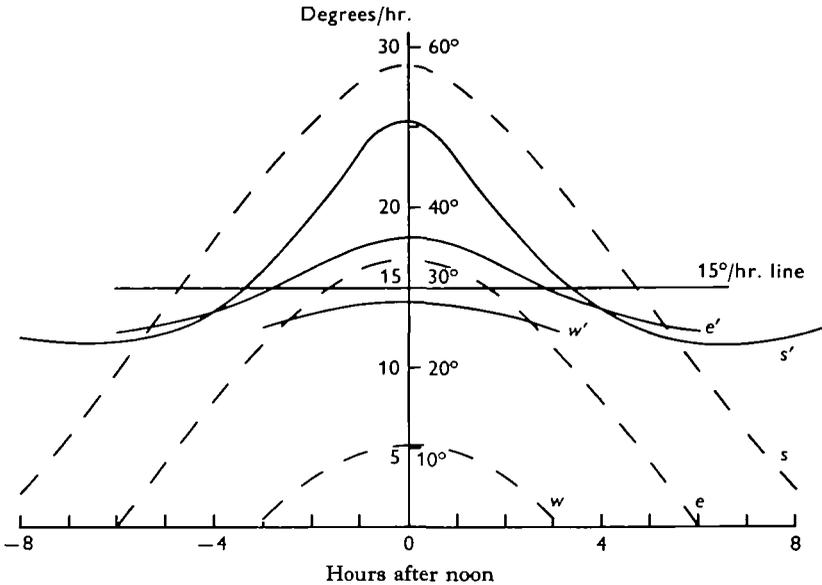


Fig. 7. Movements of the sun as seen at St Andrews. Solid lines show rate of change of azimuth on the scale of degrees per hour; dashed lines show actual altitude on the scale of degrees. s, Midsummer; e, equinox; w, midwinter.

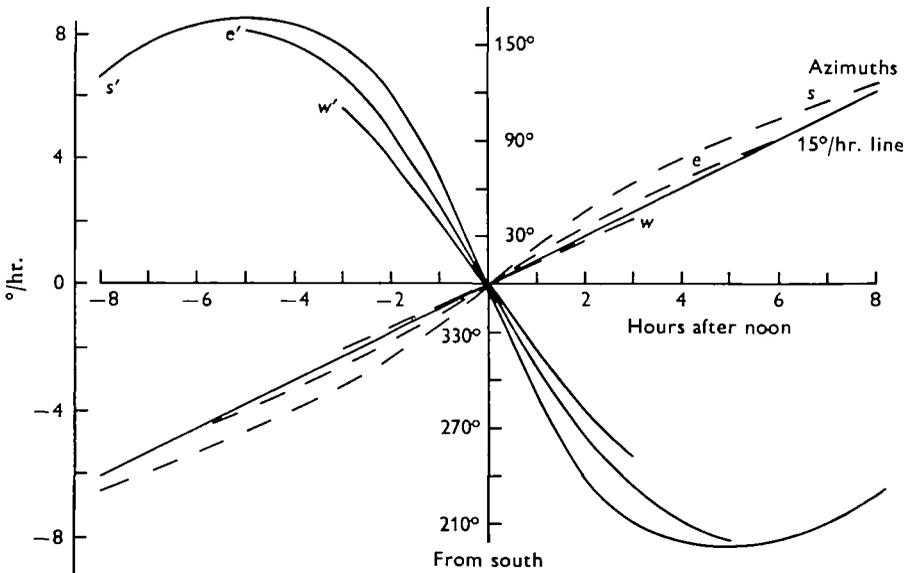


Fig. 8. Movements of the sun as seen at St Andrews. Solid lines show rate of change of altitude on the scale of degrees per hour; dashed lines show actual azimuth on the scale of degrees. The straight line shows the azimuth for a sun moving at constant rate of change of azimuth of 15°/hr.

animal, to directional homing by a method such as that outlined by Pennycuick (1960). We start with an animal (amphipod) which heads towards the sea by moving in a direction relative to the sun's azimuth as dictated by its internal clock. To do the same by moonlight it can avoid having a second clock, linked to the moon's cycle, by using the rate of climb of the moon. This is directly related to the azimuth, i.e. to the direction, almost as for the sun, since the two orbits differ by 5.18° . So far we have been concerned only with the use of the sun or moon as a compass, but as Pennycuick (1960) has shown, improvement of the estimate of variables which we know can be measured, i.e. rate of rise, together with azimuth and time of day, provides rules which would enable a bird to fly towards home when released in an unknown direction from it.

In conclusion, the demonstration that a shore crab when dropped without landmarks requires only 10 sec. before it begins to show a demonstrable response to the movement of the sun raises more problems than it solves, although, based on this fact, an investigation of the orientation behaviour is likely to prove rewarding. The retina, lamina, and more posterior neuropiles are all arranged with strict reference to the horizontal and vertical axes of the animal in its normal posture. Therefore, if the vertical and horizontal components of the sun's movement turn out to be of importance, these long known but hitherto unexplained nerve-fibre orientations acquire a new significance.

I would like to thank Mr T. B. Slebarski, of the Observatory, St Andrews, for information on the movements of the sun, but any errors of interpretation are my own.

SUMMARY

1. The eyes of the crab follow the movement of the sun if stationary landmarks, which would arrest the eye movement, are obscured.
2. Therefore, even if the eyes do not move when the crab is in a normal environment, the sun's movement is certainly seen by the crab.
3. The eye movements in response to tilting the whole animal only partially compensate for the body tilt. Therefore an obvious contrasting object such as the sun is not absolutely stabilized on the retina in tilting.
4. This sensory ability of the crab could form the basis of a compass response with a minimum latency of 10 sec.

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