

SHORT COMMUNICATION
DISCONTINUOUS TURNING REACTION DURING ESCAPE IN
SOLDIER CRABS

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Accepted 21 August 1989

In many animals, the approach of an object is perceived visually and elicits an escape reaction (Dill, 1974). The escape is often aimed directly away from the threat. In some cases, however, the animal heads towards a nearby refuge, or another preferred place. Blue crabs, for instance, escape from the shore into deeper water (Woodbury, 1986). When ghost crabs are threatened while foraging far away from their burrow, they may change their heading erratically during escape in response to the visually perceived movement of the approaching object (Vannini, 1980). Soldier crabs (*Mictyris longicarpus* Latreille) face a similar problem because they live on estuarine mud flats and have no permanent burrows. They may react to an approaching person at a distance of 29–33 m, i.e. when the person has a vertical angular size of 2.2–3.2° at the eye of the crab. This illustrates the high vertical visual acuity across the acute zone of the ‘flat-world type crab’ *Mictyris* (Zeil *et al.* 1986). Usually, they can avoid being caught by ‘screwing’ themselves into the substratum with astonishing speed (Cameron, 1966). On hard substrata, however, they have to escape. Unlike ghost crabs (Burrows and Hoyle, 1973), soldier crabs are slow, with a maximum velocity of about 10 cm s⁻¹. This may be a consequence of their habit – atypical of brachyurans – of walking exclusively forwards (Sleinis and Silvey, 1980). During escape, soldier crabs walk on a straight path away from the approaching object and usually change their direction only in response to changes of the approach direction of the threatening object. I observed that when one walks around a soldier crab on a circular path at some distance, it still walks along straight paths and changes direction by making abrupt turns from time to time.

Here I suggest a mechanism that could be involved in eliciting this ‘discontinuous turning reaction’ of an escaping soldier crab. The observations I present demonstrate that *Mictyris* evaluates the angular displacement of a moving object in external coordinates and not – as might be expected – relative to its body. Since crabs carry their eyes on mobile stalks I speculate that, during walking,

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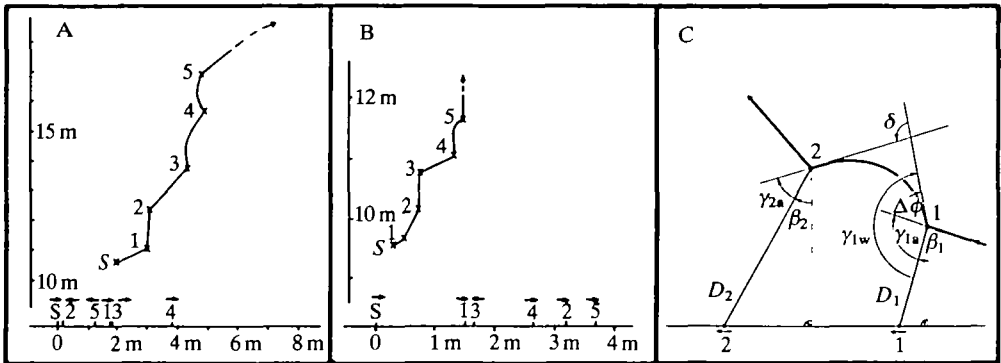


Fig. 1. (A, B) Paths of two individuals of *Mictyris* while a person walked along a straight line (abscissa). Numbers indicate the crab's turning points and the associated positions of the person with arrows showing his walking direction before the crab's reaction. *S* marks the starting positions of crab and person. (C) Different angles between crab and stimulus $\Delta\beta = \beta_2 - \beta_1$; $\Delta\phi = \phi_{1w} - \phi_{1a}$; $\Delta\gamma = \gamma_{2a} - \gamma_{1w}$; *D*, distance between crab and stimulus. Subscript a denotes arrival at the turning point, w denotes departure.

compensatory eye movements automatically provide the world-centred reference system.

To prevent the crabs from digging into the substratum, they were transferred to a concrete surface. Small pots of ink were fastened to their carapaces so that the animals traced their own path on the substratum. A crab was released and chased by one person who then withdrew and observed the crab from a distance of about 5 m. A second person walked up and down approximately perpendicular to the mean course direction of the crab with a constant speed of about 60 cm s^{-1} at distances of 9–33 m from the crab. When the animal changed its course this was marked on the path of the walking person and was later compared with the path of the crab. Examples that illustrate the discontinuous pattern of the crab's turning reaction are presented in Fig. 1, along with an explanation of the geometrical situation. It should be noted that the person only reversed his direction *after* the crab had changed its course. Abrupt turns of the crab, therefore, cannot be attributed to sudden changes in the stimulus situation.

When the person is walking to the right (filled circles in Fig. 2; remember the stimulus constellation shown in Fig. 1) the crab at some stage turns to the left ($\Delta\phi < 0^\circ$ in Fig. 2); when the person walks to the left (unfilled circles in Fig. 2) the crab turns to the right ($\Delta\phi > 0^\circ$ in Fig. 2). This does not depend on whether the person walks on the right or the left side of the crab. In 31 cases, only one deviation from this rule was observed. I tested two alternative hypotheses about the turning angle of the crab. (i) $\Delta\phi$ is adjusted to lead the animal 180° away from the momentary angular position of the person (see dotted line in Fig. 2) or (ii) $\Delta\phi$ has a particular size, independent of the angle γ_a at which the crab sees the person. The variances of $\Delta\phi$ calculated for these hypotheses differ significantly (one-tailed

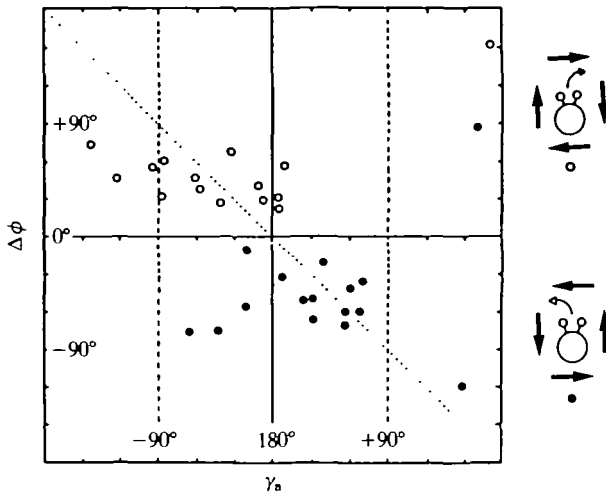


Fig. 2. Change $\Delta\phi$ of walking direction after a turning reaction (positive to the right) versus the angle γ_a at which the crab sees the stimulus before reacting (positive on the right). The dotted line indicates the change $\Delta\phi$ in walking direction necessary for the crab to run in a direction opposite to the momentary angular position of the stimulus. Unfilled circles, stimulus to the left; filled circles, stimulus to the right. Experiments with four crabs. The pictograms illustrate the relationship between the walking direction of the person and the turning direction of the crab observed in the vast majority of cases.

F -test, $0.05 > P > 0.025$), and the variance is smaller for the second alternative. From this it follows that the crab usually turns by a stimulus-independent angle of $20\text{--}80^\circ$ (mean \pm s.e. $|\Delta\phi| = 56.8 \pm 5.3^\circ$, $n = 29$ measurements, $N = 4$ crabs) and in the same direction as the line of sight towards the person as he moves around the crab's eyes (see pictograms in Fig. 2). It is only when *Mictyris* walks more or less towards the person ($|\gamma_a| < 90^\circ$) in Fig. 2; note that the graph is symmetrical around $\gamma_a = 180^\circ$) that it may turn through a larger angle, but this situation rarely occurred.

As a consequence, the crab increases the angle between its own heading and the heading of the stimulus by a turn in the appropriate direction. Its tactics fail, however, whenever it is walking towards the aggressor ($\gamma_a < 90^\circ$), a situation which hardly ever occurs under natural conditions, since an approaching object usually induces escape and overrides the turning reaction.

The discontinuous pattern of the turning response, in addition to the unique forward locomotion in *Mictyris*, allows one to analyse the visual information the crab uses to initiate a turn directly from the paths of animal and experimenter. The data presented in Fig. 2 show that the turning reaction cannot be understood as an antifixation: (i) the turn is not initiated when the crab sees the stimulus at a particular angular position γ_a ; (ii) the turn does not bring the object to a particular angular position γ_w (e.g. 180°); (iii) the direction of turn does not depend on the angular position of the stimulus γ_a but on its *direction of movement*. Further

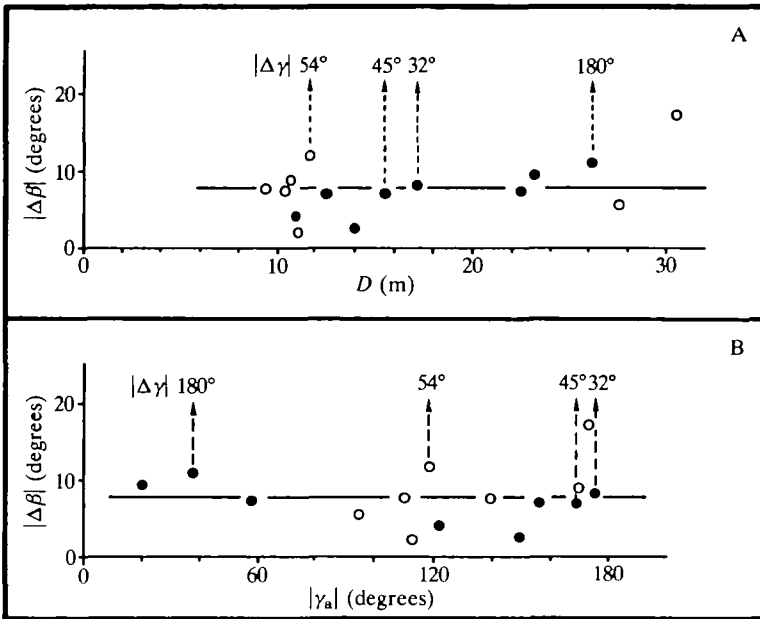


Fig. 3. Absolute values of angular change between position of stimulus and position of crab ($\Delta\beta$) between two turning reactions versus (A) distance D and (B) angular position γ_a of the stimulus relative to the crab. Since the angular change between stimulus position and the heading of the crab is $\Delta\gamma = -\Delta\beta + \delta$ (Fig. 1C), with δ being the change of body orientation between two turning reactions, $|\Delta\gamma| = |\Delta\beta|$ when the crab walks along straight paths and $|\Delta\gamma| > |\Delta\beta|$ when it walks along strongly curved paths (indicated by dashed arrows). Experiments with two crabs (filled and unfilled circles).

analysis of the data revealed that *Mictyris* initiates a turn when the person has changed his position relative to the crab by a fixed value: $|\Delta\beta| = 7.7 \pm 1^\circ$ ($n=15$, $N=2$; Fig. 3). This change ($\Delta\beta$) is independent of the angular position (γ_a) of the person relative to the crab and the distance (D). Furthermore, the sign of $\Delta\beta$ reflects the person's direction of movement relative to the crab and thus is the proper cue to induce a turning reaction in the appropriate direction.

These data allow one to decide whether *Mictyris* relies on a world-centred or a body-centred reference system when initiating the turning reaction. There were a few instances when the crabs walked along a curved rather than a straight path between two turns. During these sequences, the angular change ($\Delta\beta$), which is defined in a world-fixed reference system, is different from the change ($\Delta\gamma$) of the angle (γ) relative to the crab's body axis at which it sees the walking person. The angular change ($\Delta\gamma$) is modified by the turning angle (δ) of the crab's path: $\Delta\gamma = -\Delta\beta + \delta$ (Fig. 1C). While both angular changes are equal along straight paths, $|\Delta\gamma|$ is much larger than $|\Delta\beta|$ when the crab walks along a curved path (indicated by dashed arrows in Fig. 3). In these instances the values of $|\Delta\beta|$ are not significantly different from the values obtained along straight paths (two-tailed

t -test, $0.4 > P > 0.3$). As it is $\Delta\beta$, and not $\Delta\gamma$, which determines the initiation of a turning reaction, it follows that the crab compensates for its continuous body turn (δ).

There is no need, however, to assume that *Mictyris* has to separate both components in its retinal image [object displacement that is caused by object movement ($\Delta\beta$) and by the crab itself (δ)]. *Mictyris* probably compensates for its own body turns by appropriate visually (Nalbach and Nalbach, 1987) and statocyst-mediated eye-stalk movements (H.-O. Nalbach, unpublished observations). It keeps the direction of sight constant, except for short nystagmic resetting saccades during large angular movements (Dijkgraaf, 1956; Barnes, 1985; Paul, 1988). The angle β then represents the angle at which the crab sees the stimulus relative to its eye so it could easily evaluate the critical change $\Delta\beta$ independently of its own changes in orientation.

Supported by the Studienstiftung des Deutschen Volkes, an ARGS grant to D. C. Sandeman and by a DFG grant to D. Varjú (SFB 307). I thank G. Nalbach for help throughout the experiments and critical discussion. J. Zeil greatly improved the manuscript.

References

- BARNES, W. J. P. (1985). Introduction to the control of equilibrium. In *Feedback and Motor Control in Invertebrates and Vertebrates* (ed. W. J. P. Barnes and M. Gladden), pp. 253–258. London: Croom Helm.
- BURROWS, M. AND HOYLE, G. (1973). The mechanism of rapid running in the ghost crab, *Ocypode ceratophthalma*. *J. exp. Biol.* **58**, 327–349.
- CAMERON, A. M. (1966). Some aspects of the behaviour of the soldier crab, *Mictyris longicarpus*. *Pac. Sci.* **20**, 224–234.
- DIJKGRAAF, S. (1956). Kompensatorische Augenstieldrehungen und ihre Auslösung bei der Languste (*Palinurus vulgaris*). *Z. vergl. Physiol.* **38**, 491–520.
- DILL, L. M. (1974). The escape response of the zebra danio (*Brachydanio rerio*). I. The stimulus for escape. *Anim. Behav.* **22**, 723–730.
- NALBACH, H.-O. AND NALBACH, G. (1987). Distribution of optokinetic sensitivity over the eye of crabs: its relation to habitat and possible role in flow-field analysis. *J. comp. Physiol.* **160**, 127–135.
- PAUL, H. (1988). Augen- und Körperbewegungen der Felsenkrabbe *Pachygrapsus marmoratus*. Diploma thesis, University of Tübingen.
- SLEINIS, S. AND SILVEY, G. E. (1980). Locomotion in a forward walking crab. *J. comp. Physiol.* **136**, 301–312.
- VANNINI, M. (1980). Notes on the behaviour of *Ocypode ryderi* Kingsley (Crustacea, Brachyura). *Mar. Behav. Physiol.* **7**, 171–183.
- WOODBURY, P. B. (1986). The geometry of predator avoidance by the blue crab, *Callinectes sapidus* Rathbun. *Anim. Behav.* **34**, 28–37.
- ZEIL, J., NALBACH, G. AND NALBACH, H.-O. (1986). Eyes, eye stalks and the visual world of semi-terrestrial crabs. *J. comp. Physiol.* **159**, 801–811.