ATTACK BEHAVIOUR AND DISTANCE PERCEPTION IN THE AUSTRALIAN BULLDOG ANT *MYRMECIA NIGRICEPS*

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SUMMARY

The behaviour of the Australian bulldog ant *Myrmecia nigriceps* (Fr. Smith) has been studied by using moving targets characterized by size-distance equivalence in relation to a stationary zero-point. The attack behaviour of freely moving animals demonstrated that the ants can discriminate between different targets, in the range of 5–80 cm, using movement parallax to extract information about the targets. By studying the antenna response it was possible to demonstrate that the stationary bulldog ant can utilize binocular disparity information and that this mechanism has an effective range of about 90 mm.

INTRODUCTION

A general problem in visual space perception is concerned with how the brain assesses sizes, shapes and distances of objects in the external world, when the physical three-dimensional world is projected onto the two-dimensional retinal mosaic.

Insects are promising experimental animals for both behavioural and physiological studies of these problems. In the present investigation the Australian bulldog ant was chosen for the following reasons. Firstly, it has a large interocular base together with a large binocular overlap (60° in total with a crossover of 30°) thus providing opportunities for good disparity information. Secondly, it is very sensitive to motion and will rapidly turn towards moving objects, preparing for an attack. Thirdly, it is extremely aggressive, rushing towards moving objects, attacking them by biting them with the 4 mm long jaws and even stinging them.

In her study of depth-vision in this insect, Via (1977) drew attention to an important methodological question by stating that a crucial requirement of a test of absolute distance perception is that the animal should be able to respond differentially to different size-distance combinations characterized by the same angular properties in the absence of secondary cues (Ittelson, 1960). On the basis of such a criterion Via concluded that this ant was unable to estimate distances correctly and that instead it exhibited a size-distance ambiguity.

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In view of the fact that several investigations concerned with other species have demonstrated the operation of different cues in space perception, especially binocular disparity and movement parallax (Wallace, 1959; Campan, Goulet & Lambin, 1976; Cartwright & Collett, 1979; Cloarec, 1979; Eriksson, 1980; Rossell, 1980; Goulet, Campan & Lambin, 1981; Burkhardt & de la Motte (1983) it seems probable that the intact bulldog ant should be able to utilize some of these mechanisms.

<div align="center">

METHODS

Experiment 1
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Via's experiments were performed on fixed, isolated heads and the question arises whether the responses of freely moving animals are also characterized by size-distance ambiguity or whether these animals are able to discriminate between different size-distance combinations when the angular properties are initially the same. To find an answer to this question an experiment was conducted in which the attack behaviour of the ants was studied when a moving target, which belonged to a set of equivalent size-distance combinations (Ittelson, 1960), was presented.

Stimulus

Five stimulus patterns were generated by moving black square targets one at a time in such a way that the targets subtended the same visual angle and exhibited the same angular motion properties when viewed from the starting point (see Fig. 1). The properties of the five targets used in the experiment are shown in Table 1. The targets were attached to a needle mounted on an X–Y recorder governed by a Wavetek function generator. The target moved sinusoidally to and fro with a frequency of 1 Hz. The background was composed of untextured white cardboard (width 34 cm, height 50 cm) with a luminance of about 125 cd m^{-2}, and the black targets had a luminance of about 7 cd m^{-2}. The surrounding was an arena made of white cardboard (width
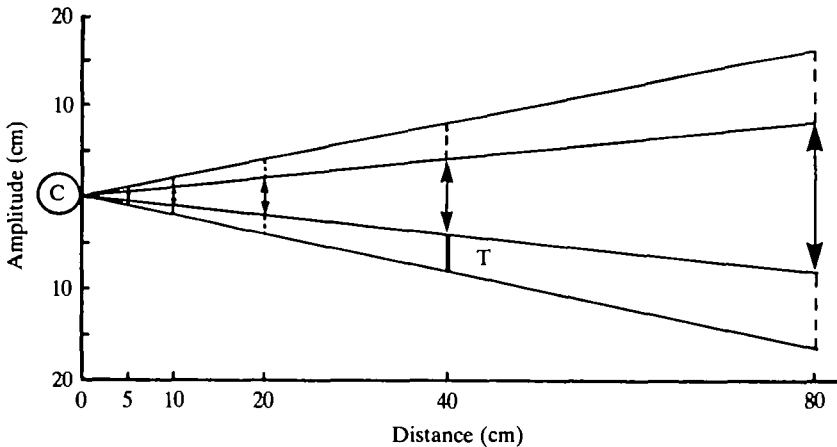

Fig. 1. Design of the experiment. View from above. C, cage with the animal; T, one of the five targets. Motion paths indicated by arrows. The height of the zero-point was 7 mm (mean of eye position).

Table 1. *Description of stimulus targets in relation to the zero-point*

Stimulus	S1	S2	S3	S4	S5
Size(mm)	5 × 5	10 × 10	20 × 20	40 × 40	80 × 80
Distance(mm)	50	100	200	400	800
Amplitude(mm)	7·5	15	30	60	120

Motion frequency was 1 Hz, sinusoidal motion.

34 cm, length 90 cm, height 9 cm) placed over the X–Y recorder according to the design of Via (1977).

Conditions

The animals were collected by inserting a thin stick into the entrance hole of the nest. Those which attacked the stick by biting and clinging to it were selected as experimental animals. Since the ants in a pilot experiment seemed to exhibit behavioural adaptation (implying a decline of the responses) it turned out to be important to avoid artefacts due to adaptation. Therefore a 5 × 5 Latin square design (Underwood, 1957) was used with the animals randomly distributed to the five stimulus conditions in order to counterbalance progressive effects. Twenty-five animals were tested in the experiment, each animal giving one response to each target. In this way the first response to each target was obtained for five groups of five animals and the effect of adaptation could be evaluated. The animal was placed in a small white cardboard cage (diameter 50 mm) which was brought to the arena. The target was set in motion and the animal was let out through a small opening in the cage (width 10 mm, height 10 mm). The time interval between the stimulus presentations was 1 min. The motions of the ant and target were recorded with a television camera and a video tape recorder.

Experiment 2

The purpose of this experiment was to make a comparative study of the behaviour of freely moving animals under conditions of monocular and binocular vision. The previous set-up was modified in such a way that the target (10 × 10 mm black square) started its motion (moved to the left, see Fig. 4) when the animal came out of the cage. The distance from the zero-point to the target was 5–20 cm and the target moved with constant velocity (10 cm s^{-1}) perpendicular to that distance. The track as well as the motion of the target were recorded with a television camera and a video tape recorder.

Experiment 3

Since it appears probable that the bulldog ant uses binocular disparity to estimate distances, at least in 'near space', an experiment was conducted to determine the maximum range of the mechanism in question. Therefore all other cues (Ittelson, 1960) except binocular disparity should either be occluded or held constant. Consequently a differential response cannot be ascribed to these cues. However, if the animal uses binocular disparity (either horizontal disparity or vertical disparity, or both) then it should be able to respond differentially to the different targets. The

stimuli which fulfil these requirements to a reasonable degree were generated by black squares moving in depth towards the eye in such a way that the optical changes were the same for different sizes and distances in relation to a zero-point. Thus the stimuli were generated according to the principle of 'equivalent distal configurations' (Ittelson, 1960), and presented to a fixed animal in order to occlude movement parallax information.

Stimuli

The stimulus was one of a set of five different sized squares moved towards the eye with a constant velocity in such a way that, from a zero-point between the eyes, each stimulus appeared to be identical to the others (see Fig. 2). The target sizes, distances, motion amplitudes, target velocities and horizontal disparities are shown in Table 2. The motions were generated by a Wavetek function generator and an X–Y recorder which carried the target. In this way the different targets provided the same optical information when viewed from the zero-point. The angular subtense of the targets was 18·9° at the starting distance, and 28·1° at the stopping distance. Thus the angular change was roughly $30°\,s^{-1}$ (for an exact formula describing the angular velocities and angular accelerations see Eriksson, 1982). The black target had a luminance of about $7\,cd\,m^{-2}$, and the white, untextured background, which subtended a visual angle of 54° in height and 37° in width, had a luminance of about $125\,cd\,m^{-2}$.

Responses

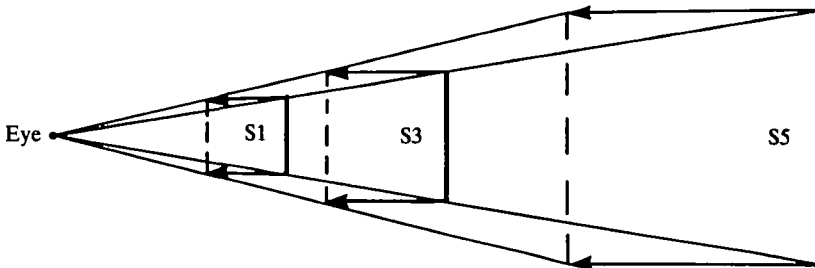The bulldog ant exhibits a very reliable response to an object suddenly moving

Fig. 2. Design of binocular disparity experiment with size-distance equivalent stimuli.

Table 2. *Description of stimulus targets in relation to the zero-point*

Stimulus	S1	S2	S3	S4	S5
Size(mm)	5 × 5	25 × 25	45 × 45	65 × 65	85 × 85
Starting distance (mm)	15	75	135	195	255
Stopping distance (mm)	10	50	90	130	170
Target velocity $(cm\,s^{-1})$	1·67	8·33	15·00	21·67	28·30
Disparity (a_2-a_1) degrees	16·09	3·23	1·80	1·25	0·96

Horizontal disparity is computed for an interocular base of 3·0 mm (mean of measurements on experimental animals).
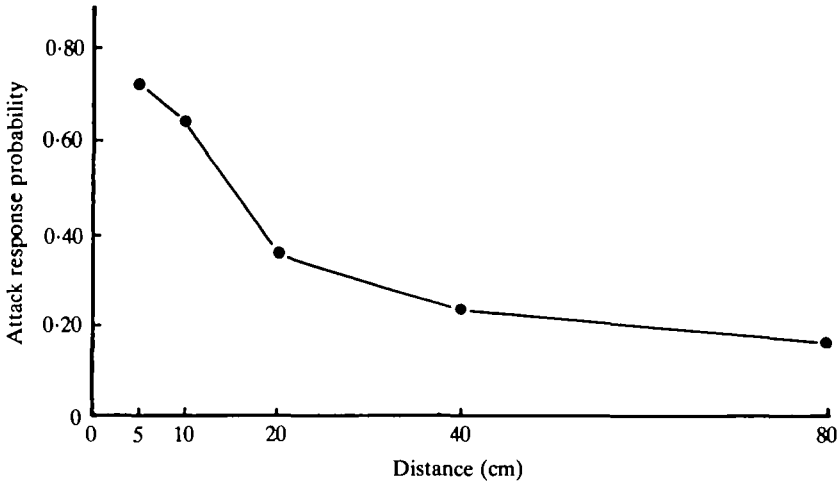
Fig. 3. Attack response probability as a function of target distance.

towards the animal, especially if the object is approaching obliquely from above. The animal rapidly lifts the antenna towards the object. The response is visually guided since it is equally well elicited when a sheet of glass is placed between the animal and the object. In the present experiment the animal was fixed in wax *via* a cardboard bridge from head to thorax and was tilted down about 20°. The antenna response as well as a meter needle showing the target motion were recorded with a television camera equipped with a micro-lens. The responses (motion of the antenna tip from the downward, hanging position to the upward, maximum position) were analysed by single-frame analysis. A small mirror was placed below the animal in such a way as to produce an image of the jaw movements. This image was displayed on the television screen together with the above mentioned information.

Procedure

Since a preliminary experiment using very short pauses between trials had demonstrated behavioural adaptation with regard to both the antenna responses and the jaw responses, the following procedure was used in order to obtain data which were not biased by adaptation effects or other habituation effects. In order to fulfil these requirements the experiment was conducted using a randomized 5 × 5 Latin square design (Underwood, 1957). Five ants were used, each receiving five trials in each of the five blocks (stimulus distances). The time interval was 10 min between blocks and 60 s between trials within blocks. A later check of the data revealed no systematic changes due to presentation order.

RESULTS

Experiment 1

No significant adaptation effects could be established when the data in the Latin square were analysed. Of 125 stimulus presentations the animals exhibited an attack response (moving towards the target and biting it) in 53 cases. On the basis of the

hypothesis that the bulldog ant cannot discriminate different size-distance combinations it is expected that the attack responses should be randomly distributed among the five stimulus conditions. This, however, is not the case. A Cochran Q-test for related samples (Siegel, 1956) reveals that the overall differences between the conditions are statistically significant ($P < 0.001$). When the attack response probability is plotted against target distance it is evident that the responses are related to target distance (Fig. 3).

On average the animals attacked the smallest target in 79 % of the presentations and the largest target in only 16 % of the presentations. This is supported by an analysis of the movements of the animals. Typically, with the target at shorter distances (5 and 10 cm) the animal comes out of the cage and without delay rushes directly towards the target, biting it and sometimes even stinging it. In the group of five ants given the smallest target first, all the animals attacked it.

In contrast, the animals reacted differently to the largest target. Here the typical behaviour was characterized by hesitation and even what might be termed an avoidance reaction. After being released from the cage the animals usually moved rather slowly towards the target. But after a short while they hesitated and started to move sideways (like the target) and finally even turned back, moving away from the target. A few animals started rushing towards the target, then slowed down and turned back. In fact, one of the animals only moved 10 cm, then started to reverse while still watching the target and making small lateral movements! This animal, as well as the ones showing the avoidance reaction to the largest target, usually demonstrated no such responses to the smallest target. More exactly, the largest target elicited only 4 attacks out of 25 presentations, while the smallest target elicited 18 attacks. The avoidance reaction was present in 16 cases out of 25 when the largest target was used but only in one case out of 25 when the smallest target was used. These two differences are statistically significant when tested with the Cochran Q-test for related samples ($P < 0.001$). The mean turning point was 47.5 cm from the zero-point, i.e. approximately half-way to the largest target.

From the results above it is clear that the reactions of the experimental animals are not confused by size-distance ambiguity. Instead the animals, in one way or another, were able to extract differential information for the different conditions. The results strongly support the conclusion that the ants accurately perceived the different targets, that the nearest target was experienced as small (or close or moving with low velocity) and thus could safely be attacked, but that the largest targets were experienced as large and/or fast moving and should be avoided. The experiment, however, does not allow any conclusions to be drawn as to whether the ants were using binocular disparity, motion parallax or both of these mechanisms. To answer these questions, the following two experiments were conducted.

Experiment 2

Intact animals

When released from the cage, the intact animal usually started moving towards the moving target in a characteristic path ending with an attack (biting and sometimes stinging the target). A typical track showing an attack by an intact, binocular animal is presented in Fig. 4.
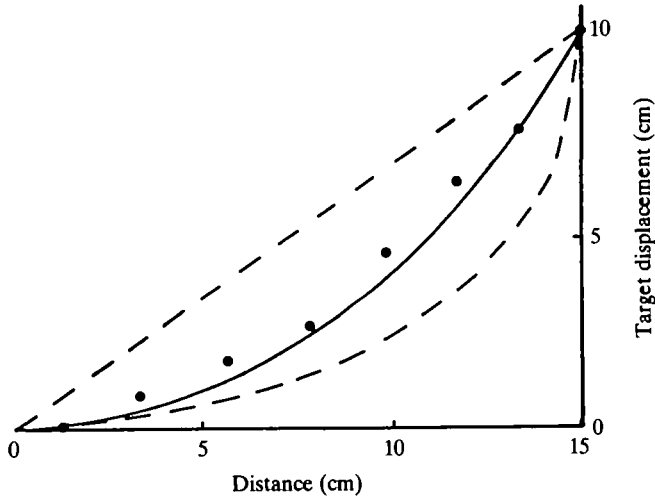
Fig. 4. Attack trajectory for an intact, binocular animal. Solid line, position vector curve. Dashed curved line, velocity vector curve; dashed straight line illustrates the interception strategy. Dots show animal positions sampled during the locomotion; see text.

Motion parallax animals

Two different ways of investigating the role of motion parallax were tested.

(a) The left eye of each of a group of six ants was entirely covered with paint, thus effectively destroying disparity information. These animals were tested as above using different target distances (5–30 cm), different target sizes (5–40 mm squares), as well as several other objects (including a grasshopper and a living ant tied to the moving target holder). Out of a total of 24 trials only one attack (at 5 cm distance) was recorded. The dominant behaviour was that of the ant disregarding the target and slowly moving along different tracks unrelated to the target. This behaviour may be due to the fact that by painting the whole left eye we may have destroyed not only the binocular disparity mechanism but also motion parallax which reasonably should require an interaction between the two optical flow fields in the two eyes.

(b) In order to test the idea that motion parallax requires an interaction between the two eyes (but with binocular disparity occluded) we painted the left eye of two animals in such a way that disparity was destroyed but the animal could still use the lateral part of the eye (paint covering about 37 columns of facettes or about 30° off the median plane; see Via, 1977, Fig. 9) as well as the corresponding areas below, above and behind the lateral centre of the eye. In this way the left eye had an intact, roughly circular area, the centre of which looked out to the left. Since the right eye of these animals was intact they should be able to use movement parallax despite the lack of disparity information.

When these animals were tested they both moved around quite normally and also attacked the moving target in the same way as normal animals. Fig. 5 shows the track of a successful attack ending with the ant biting the target.

From the outcomes of these two tests we conclude that binocular disparity is not necessary in order to release attack behaviour. The data suggest that the proper attack behaviour is possible on the basis of movement parallax information and that this mechanism requires an interaction between the two eyes.
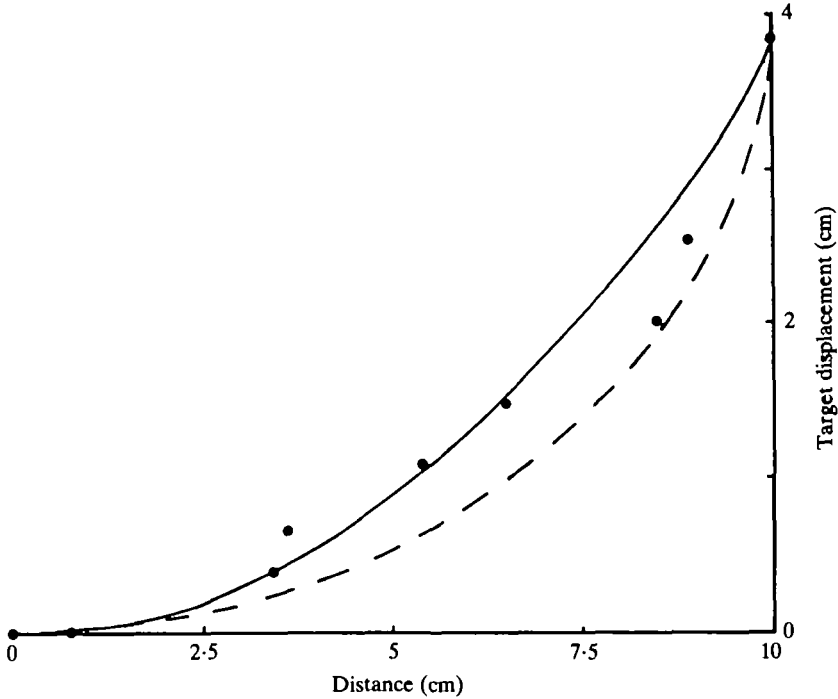
Fig. 5. Attack trajectory for a binocular movement parallax animal. Solid line, position vector curve; dashed line, velocity vector curve; see text.

Animals with frontal retinas

Some new ants were used in a study in which both eyes were painted symmetrically in such a way that motion information from the lateral parts was occluded and only information from the frontal (disparity) parts of the eyes was provided (see Via, 1977, Fig. 9). Thus the animals should be able to perceive the target properly using these frontal areas even if motion information from the lateral parts is missing.

The results showed that the attack behaviour could be elicited in these animals even if they sometimes did not appear to see the target. The result from an attack of one animal is shown in Fig. 6.

In summary, experiment 2 has demonstrated that normal attack behaviour is found in animals when binocular disparity, but not bilateral motion information, is occluded as well as in animals which only had the frontal retinal areas intact. From this outcome we conclude that binocular disparity is not a necessary condition for attack behaviour in the bulldog ant and that the data suggest the operation of a motion parallax mechanism which requires interaction between the two eyes.

Analysis of attack strategies

In order to describe the attack behaviour in the present situation, i.e. the trajectory over time in relation to target motion, three different attack strategies will be discussed.

The interception strategy

This strategy, which is used by some species, e.g. bats and hoverflies (Collet &

Land, 1978), implies that the animal correctly perceives the situation and from values of distance to the target (D), target velocity (V_T), velocity of the organism (V_O) and time (t) computes the predicted point of collision (P_c) (see Fig. 7).

In this case the animal moves with, say, constant velocity ($V_O = k$) towards the predicted point of collision. Thus the mathematical criterion for this strategy is given by:

$$dP_o/dt = V_O. \tag{1}$$

The position vector ($P_{o,t}$) of the animal at time (t) can be obtained by integrating the velocity vector (V_O). Hence we obtain:

$$P_o = \int V_O dt = \int (V_O \cos \theta)dt + \int (V_O \sin \theta)\ dt. \tag{2}$$
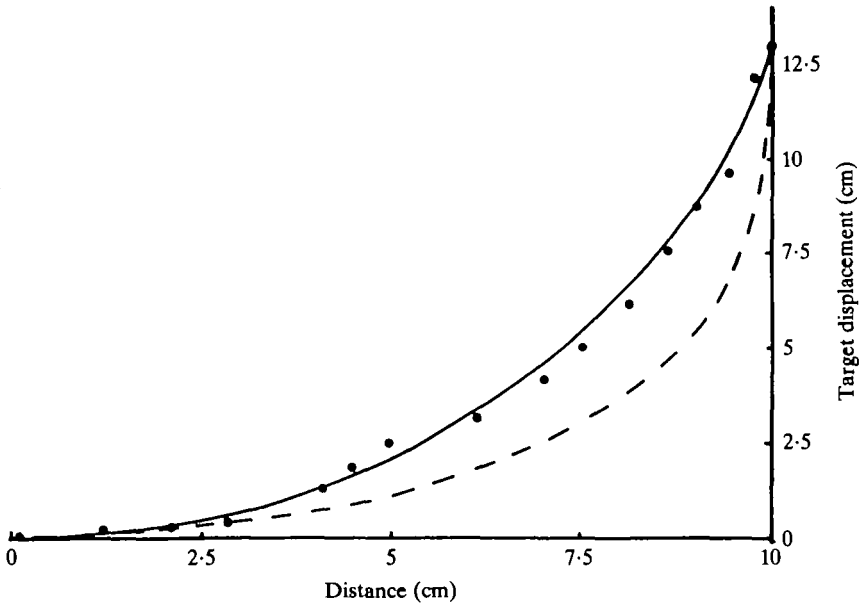

Fig. 6. Attack trajectory for a binocular (frontal retinae) animal. Solid line, position vector curve; dashed line, velocity vector curve.
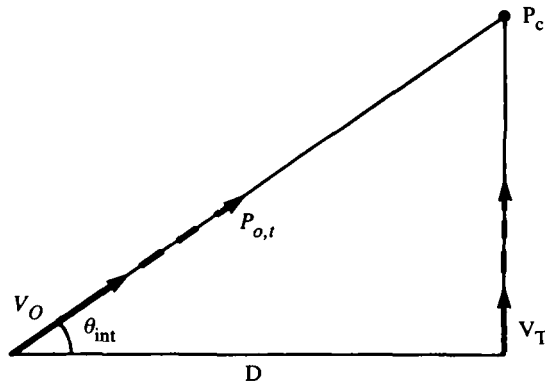

Fig. 7. The interception strategy. V_O, velocity vector of the animal; P_o, position vector over time; P_c, point of collision; V_T, target velocity; D, distance; θ_{int}, interception angle.

Consequently the position vector of the organism is given by:

$$P_{o,t} = (V_O t \cos\theta)i + (V_O t \sin\theta)j. \tag{3}$$

Using the Pythagorean theorem, it can be shown that the time to collision is given by:

$$t_c = D^2/(V_O{}^2 - V_T{}^2). \tag{4}$$

The predicted point of collision can be computed from target velocity (V_T) and time (t). Hence we find

$$P_c = V_T t_c. \tag{5}$$

Finally the interception angle (θ_{int}) is given by:

$$\theta_{int} = \arctan V_T/D \cdot [D^2/(V_O{}^2 - V_t{}^2)]^{0.5}. \tag{6}$$

The target-locking strategy

According to this strategy the animal moves straight towards the target during the attack. However, this strategy can be implemented by applying at least two different mathematical criteria.

The position vector strategy. If we regard the position vector of the animal over time, the criterion implies that the position vector from the starting point should be directed towards the target all the time. This criterion (see Fig. 8) is then expressed by:
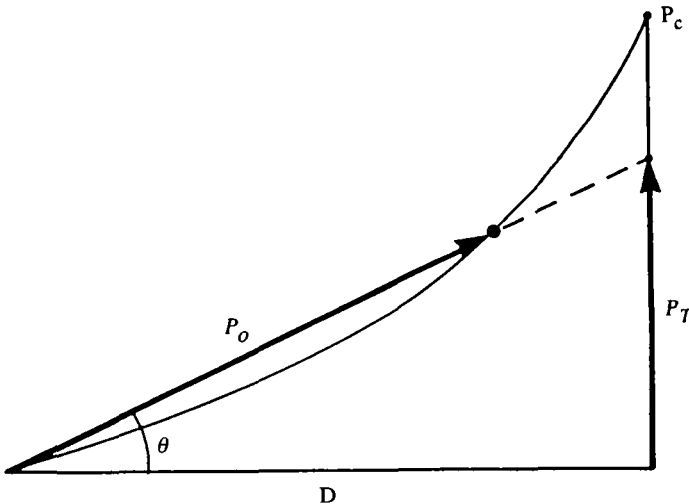
$$\theta = \arctan V_T t/D. \tag{7}$$

Fig. 8. Position vector strategy. Position vector of the animal *(P_o)* as a function of distance (D) and target position vector *(P_T)*.

By inserting this value of θ in vector equation (3) we obtain the following formula for the position vector of the animal over time:

$$P_{o,t} = [V_O \cdot \cos(\arctan V_t \cdot t/D) \cdot t] \, i + [V_O \cdot \sin(\arctan V_t \cdot t/D) \cdot t] j. \qquad (8)$$

Thus, if we know the velocity with which the animal moves as well as target velocity, time and distance from animal to target, then we can compute the theoretical trajectory. This theoretical curve (the position vector curve) has been computed by first roughly estimating the animal's velocity from data and then adjusting the values of V_O requiring that the curve should predict the empirical collision point. The obtained curves are shown in Fig. 4 ($V_T = 10 \, \text{cm s}^{-1}$, $V_O = 17 \cdot 6 \, \text{cm s}^{-1}$), Fig. 5 ($V_T = 10 \, \text{cm s}^{-1}$, $V_O = 28 \, \text{cm s}^{-1}$) and Fig. 6 ($V_T = 10 \, \text{cm s}^{-1}$, $V_O = 14 \cdot 5 \, \text{cm s}^{-1}$).

The velocity vector strategy. A different, and apparently more meaningful criterion, implies that the velocity vector should be directed towards the target all the time. Mathematically this criterion is defined by:

$$\theta = \arctan[(V_T t - y_t)/(D - x_t)], \qquad (9)$$

where $V_T t$ gives the target position over time and x_t and y_t are the coordinates of the animal over time, see Fig. 9.

By using a computer and an iterative method, successive values for optional time intervals (Δt) could be defined for θ and hence the coordinates x_t and y_t could be computed according to the following formulae:

$$\theta_n = \arctan[(n\Delta t V_t - y_n - 1)/(D - x_{n-1})], \qquad (10)$$

$$x_n = x_{n-1} + V_O \Delta t \cos\theta_n, \qquad (11)$$

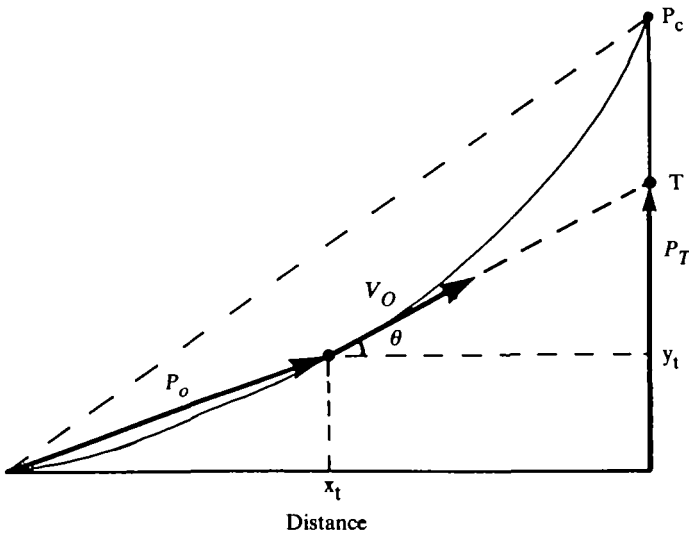$$y_n = y_{n-1} + V_O \Delta t \sin\theta_n. \qquad (12)$$

Fig. 9. Velocity-vector strategy. Illustration of the animal position vector (P_o) generated by the velocity vector (V_o) fixated at the target (T). P_T position vector of target; x_t, y_t, coordinates of the animal. The theoretical trajectory is shown by the solid line. The dashed line through the point of collision (P_c) shows the trajectory according to the interception strategy.
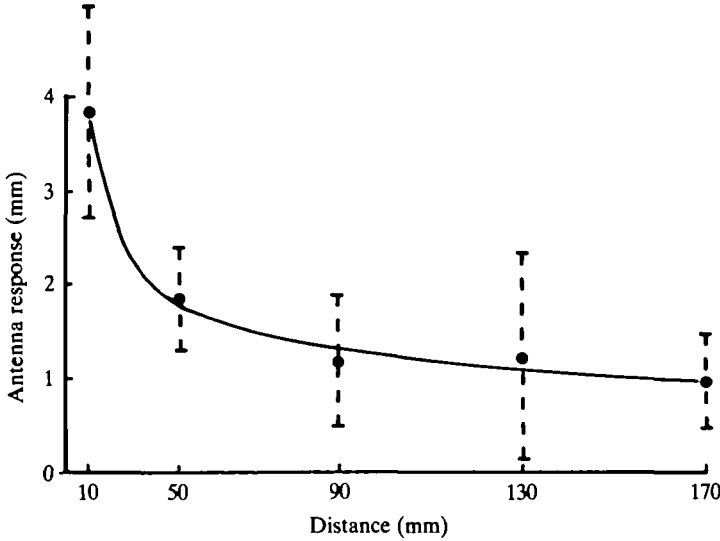
Fig. 10. The antenna response as a function of target distance. Vertical bars show standard deviations.

By using different time intervals (Δt) it was found that no significant increase in precision could be obtained with time intervals shorter than 0·03 s. The theoretical velocity vector curves are shown in Figs 4, 5 and 6 ($V_T = 10\,\mathrm{cm\,s}^{-1}$, and $V_O = 19·6$, 29·4 and 12·75 cm s^{-1}, respectively).

A comparison between the different theoretical attack strategies indicates that the bulldog ant utilizes a position vector strategy (Figs 4–6).

Experiment 3

The bulldog ant demonstrates a three-fold behavioural reaction to the approaching targets under the present conditions. It starts moving its legs rapidly, especially if the target is close to the animal. It opens its jaws and sometimes shows snapping behaviour (Via, 1977). The snapping reaction never appeared when the three most distant targets were presented but in some cases the reaction was elicited by the nearer targets. However, the jaw reactions were too infrequent to provide reliable data. The animal finally exhibits an antenna reaction which turned out to be a very good indicator of target distance. The animals reacted every time the target was presented at the shortest distance and the amplitude of the response was related to target distance. (Fig. 10).

Obviously the antenna response is graded with regard to target distances up to about 90 mm. Thereafter the animals cannot discriminate between the different target distances (or disparities) but give the same, small response to the three larger distances. A statistical analysis (Friedman's two-way analysis of variance, see Siegel, 1956) demonstrated an overall significant difference between distances ($P < 0·02$). The difference between stimuli S3 and S5 (see Table 2) is not significant, while the difference between stimuli S1 and S3 is significant ($P < 0·025$) as are the differences between stimuli S1 and S2 ($P < 0·025$), and between stimuli S2 and S3 ($P < 0·05$) according to the randomization test for matched pairs (Siegel, 1956). The bulldog ant can therefore discriminate between different, short target distances (0–90 mm).

In order to check whether the antenna responses were due to binocular vision or to monocular optical changes, a new ant was tested using the same stimuli but with larger motion amplitudes (the motion path distances in Table 2 were doubled, maintaining the same stopping distances). Under binocular conditions the animal reacted every time to the shorter·distances but no response at all was evoked for the larger distances. However, when the entire left eye was covered with a non-toxic water-soluble paint no responses could be elicited under any condition despite several trials. The animal was hanging as dead, exhibiting no antenna responses, no leg movements and no jaw movements. In the final test a thin, sharp needle was used to remove the paint from the eye. When the animal was tested again it now quite clearly demonstrated the normal behaviour with antenna, legs and jaws. For about 10 stimulations with the smallest target it responded every time in the normal way with the antenna. It is concluded that the antenna reaction is due to binocular vision and not to monocular factors or possible artefacts, either mechanical, thermal or chemical.

Theoretical analysis

In order to arrive at an exact estimation of disparity information present in the experimental targets we computed the binocular disparities (a_1-a_2) for the different targets (Fig. 11).

The values for a_1 were computed according to the formula:

$$a_1 = \arctan(S/2 - B/2)/D \tag{13}$$

and for a_2 according to:

$$a_2 = \arctan(S/2 + B/2)/D. \tag{14}$$

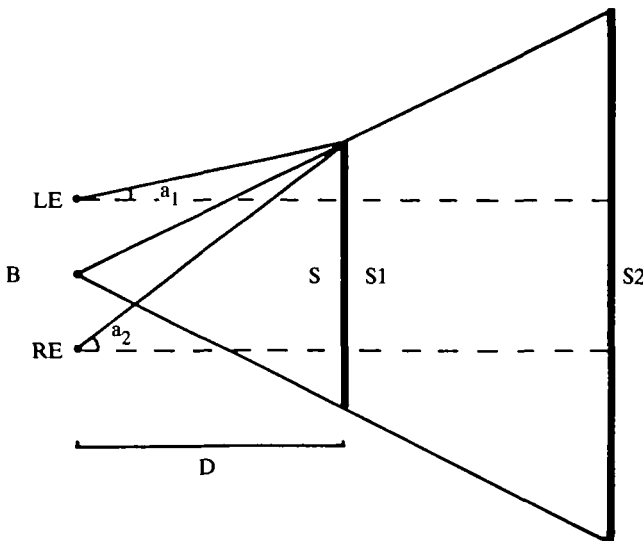The disparity information then can be defined as a_2-a_1 (Table 2).

Fig. 11. Computation of binocular disparity. LE, left eye; RE, right eye; B, interocular basis (3 mm); D, distance from eye to target; S, target size; a_1, a_2, binocular disparities.

If binocular disparity constitutes an effective stimulus, the reaction (the antenna response) should be a function of the stimulus. A well established principle from psychophysics states that the response is a power function of the stimulus, i.e.

$$R = aS^n. \tag{15}$$

Consequently, we can find out whether the response (R) is a power function of the stimulus (S) by plotting the logarithm of the antenna response against the logarithm of the stimulus (disparity). This implies that

$$\log R = \log a + n \log S. \tag{16}$$

A plot of the data revealed that the log R-log S relationship was linear with an intercept approximately equal to zero (log a) and a slope (n) equal to 0·48. Thus:

$$R = S^{0.48}, \tag{17}$$

which implies that the antenna reaction is approximately equal to the square root of disparity. This theoretical curve (the solid line in Fig. 10) is drawn through the data points and the correspondence is fairly good.

In order to find the maximum range of binocular disparity we need some measure of threshold sensitivity. Using the fact that the interommatidial angle ($\Delta\phi$) is $2°$ (Via, 1977), a calculation on the basis of the formulae above shows that a disparity threshold of $2°$ corresponds to a maximum distance of 80 mm. A theoretical calculation for maximum distance discrimination according to the formula $b = 2a/n$ (Ogle, 1959), or according to the formula by Burkhardt et al. (1973), yields estimates of 86 mm (85·7 and 85·9 mm respectively) for maximum distance discrimination. The formula of Burkhardt et al. (1973) assumes that the optical axes are parallel. This may be a correct approximation in several cases (Chmurzynski, 1963; Horridge, 1977; Cloarec, 1979) and the correspondences between the different formulae are acceptable.

DISCUSSION

The present study provides evidence for depth perception in the Australian bulldog ant *Myrmecia nigriceps*. Because insects have a fixed-focus system with a large depth of focus and have immovable eyes, they cannot utilize the cues of accommodation and convergence. Of several possible variables or cues influencing the perception (Gibson, 1950; Ittelson, 1960), there are two which now seem to play a dominant role in space perception, namely binocular disparity and motion information (movement parallax).

Disparity theory

As pointed out by Via (1977), binocular vision does not necessarily imply depth perception, i.e. stereopsis. However, certain species do use disparity information to govern their behaviour (Maldonado & Levin, 1967; Maldonado, Benko & Isern,

1970; Maldonado & Rodriguez, 1972; Rossell, 1980; Burkhardt & de la Motte (1983). The present study provides further support for a disparity mechanism in insects since the data show that the Australian bulldog ant can utilize disparity information in near space (0 to about 90 mm).

Theoretical calculations by Burkhardt *et al.* (1973) and Horridge (1977), as well as in the present study, demonstrate a good correspondence between theory and data but also that binocular vision in insects has a restricted range. Hence, outside this range other factors must be responsible for their visually guided behaviour, a conclusion which has also been drawn by Goulet *et al.* (1981).

Movement parallax

Since insects exhibit behaviour which clearly implies that they perceive the size of objects far beyond the range of binocular disparity, they must possess a far-range visual mechanism which gives them correct information about the gross spatial relationship in their environment (Horridge, 1977). A recent investigation, (Goulet *et al.* 1981) demonstrated that crickets can discriminate distances up to about 1 m. Motion parallax has also been shown to be effective in the grasshoppers (Wallace, 1959; Collett, 1978; Eriksson, 1980). The present study provides corresponding data for the bulldog ant (experiment 1 *vs* experiment 3). Of special interest here are the differential reactions (attack *vs* avoidance) to the smallest and largest targets. The avoidance reaction was on average elicited 33 cm from the larger targets and in some animals as far as 70 cm from the target. Obviously these distances are outside the range of binocular disparity.

The mechanism which is probably responsible for far-range visual information is movement parallax, a mechanism which implies that optical size-distance ambiguity is resolved *via* body-state information in the moving animal (Eriksson, 1973, 1974).

Attack strategies

This study has demonstrated that bulldog ants do not utilize an interception strategy during attack. Nor do they seem to utilize a velocity-vector strategy, which may appear to be a very simple method (cf. Lanchaster & Mark, 1975). However, the velocity-vector strategy implies a longer locomotion path than the other two strategies and therefore it is not as economical as, for example, the interception strategy. On the other hand, the interception strategy means that the predator has to start its motion at a large interception angle, which in turn presupposes that the prey will continue to move in a predictable manner. If the prey avoids the collision by a course change, then the predator has to execute gross corrections and the interception strategy may be rather inefficient, especially if the prey completely reverses its course.

A compromise between an interception strategy and a velocity-vector strategy would be to use a reduced interception angle in order to avoid extreme course changes. This is essentially what the position-vector strategy means and hence it may be an optimal method for attack when the prey is able to change its course rapidly. The present data (Figs 4, 5, 6) indicate that the bulldog ant utilizes an attack strategy which can roughly be described as the position-vector strategy. However, since some data indicate a goal gradient (animal velocity increases the nearer it is to the goal), it may be possible that a velocity-vector strategy with variable locomotion velocity will

approach a position-vector strategy with constant velocity. This question needs clarification in future studies.

With regard to the neural mechanisms underlying attack behaviour, this study has shown that the bulldog ant may utilize both binocular disparity and movement parallax to gain information about the moving object. However, since in both cases motion information is involved it is possible that there is one single neural principle operating in these seemingly different cases. Such a principle would require synchronous changes of optical stimulation over time in a way which is reminiscent of *common motion extraction* according to the rules of neural vector analysis that appear to govern the functioning of certain neurones in the optic lobe of the blowfly *Phormia terraenovae* (Eriksson, 1984).

The next step, therefore, is to conduct neurophysiological studies on the bulldog ant in order to discover if such neural mechanisms exist.

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