MOVEMENT PARALLAX AND DISTANCE PERCEPTION IN THE GRASSHOPPER (*PHAULACRIDIUM VITTATUM* (Sjöstedt))

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It has sometimes been argued that insects use binocular vision to obtain correct perception of sizes and distances in their visual world (cf. Wigglesworth, 1972). In the praying mantids it has also been claimed that monocular animals essentially lack depth perception (Maldonado, Benko & Isern, 1970).

Recently, however, the importance of binocular cues in insect vision has been questioned (Beersma, Stavenga & Kuiper, 1977; Via, 1977) and it has been suggested that insects may use movement parallax as a mechanism for generating veridical space perception (Horridge, 1977). As emphasised by Horridge there is too little evidence at present to allow us to evaluate the idea that movement parallax constitutes an effective mechanism in space perception. Some support in favour of the idea derives from Wallace (1959) who proposed that peering movements of locusts are conducted to obtain parallax information. He also showed that monocular locusts can distinguish different distances, and in a recent study (Collett, 1978) further indications of the role of movement parallax in *Schistocerca gregaria* are presented. In the present paper this work is extended by an account of a study of jumping behaviour in adult grasshoppers (*Phaulacridium vittatum* (Sjöstedt)).

The purpose of the first experiment was to compare the jumping behaviour of binocular animals with that of monocular animals under as normal conditions as possible. Monocular vision was obtained by applying three coats of enamel to one compound eye and the three ocelli. The animals were placed in a small wooden-framed cage (30 × 30 × 30 cm), the sides of which were made of wire mesh (diam. 0·3 mm). The observations were conducted on a meadow outside the Neurobiology Department, Canberra between 10.00 and 14.00 hours on sunny February days with temperatures varying between 27 and 32 °C.

The results show that the animals generally were very active (in contrast to their behaviour when the cage was placed inside the laboratory where the temperature was about 20 °C). When placed in the sunshine they usually jumped away after a while and then moved into the shadow of the corners of the cage. As a rule the jumps were preceded by the peering behaviour described by Wallace (1959) and seemed to be carefully prepared. The force of the jumps also corresponded to the distance to the surface. When the animals were placed close to the surface (3–4 cm) they made a

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Table 1. *Percentage hits in landing during monocular and binocular conditions*

		Self initiated jumps			Escape jumps		
		No.	% hit	Distance (cm)	No.	% hit	Distance (cm)
Binocular animals	1	10	90	3–20	19	89	5–25
	2	5	100	8–15	10	100	3–30
	3	6	100	4–23	10	100	4–22
	4	3	100	3–28	20	90	5–32
Monocular animals	1	23	91	3–25	10	90	8–22
	2	10	100	2–14	10	100	8–18
	3	6	83	4–22	10	90	2–25
	4	10	100	3–23	10	100	3–12
	5	10	90	6–26	10	70	4–28

(A hit was recorded when the animal jumped away and landed on the surface. A miss was recorded when the animal bounced against the surface and fell down to the floor or bounced to a second surface where it succeeded in landing.)

smooth response and landed softly on the wall. When they were placed at a distance from the surface they exerted a much greater force and the landing was accompanied by a distinct sound when the animals landed on the wire mesh. No apparent differences between monocular and binocular animals were observed.

From Table 1 it is seen that the binocular animals seldom missed a jump and were equally efficient when the jump was of a short range as when they jumped across the whole cage.

The binocular animals exhibited a hit probability of 96% for self-initiated jumps (from a platform placed at different distances from the wall) and a hit-probability of 93% for the escape jumps (in response to stimulation of the back by means of a piece of cardboard). The monocular animals were almost equally successful although there was a tendency to make more misses for some of them. The hit probability was 93% for self-initiated jumps and 90% for escape jumps. When judged by a test for in-dependent proportions (McNemar, 1962, p. 56) the differences in hit probability are not significant (1% level) for monocular versus binocular jumps (the data pooled for escape jumps vs self-initiated jumps, since also this difference is nonsignificant).

Control experiments established that the three coats of paint (which still were present after the experiment) abolished visual information because of total inhibition of peering and jumping behaviour when all the eyes were painted. When placed on an electric bulb these animals jumped away, collided with the roof and fell down to the floor when the bulb was lit. Monocular and binocular animals succeeded in a correct landing during these conditions. A second control showed that successful landing does not depend on the animal's ability to detect the surface with the antennae during flight (or alternatively to jump in such a way that the legs are in correct landing position). Thus when a clear pane of glass was substituted for the wire mesh the animals forcefully bounced against the pane during the jump towards a plant 20 cm on the other side of the pane. When the mesh was placed immediately behind the pane the animals often succeeded in landing on the pane.

In the second experiment the animal was placed on a jumping platform (Wallace, 1959) where it was presented with a target at varying distances (4–12 cm). The target

Table 2. *Jumping accuracy during monocular and binocular conditions*

		Distance (cm)								
		4			8			12		
		M	s.d.	N	M	s.d.	N	M	s.d.	N
Binocular animals	1	0	0·79	5	−0·20	0·84	5	−0·70	2·17	5
	2	−0·50	1·32	5	0·50	1·58	5	0	2·55	5
	3	−0·60	0·42	5	0·70	1·44	5			
	M	−0·37	0·84		0·33	1·29		−0·35	2·36	
Monocular animals	1	0·36	0·61	5	0·10	0·14	2	0·68	3·53	2
	2	0·75	0·35	2	0·50	1·47	2	−4·0	—	1
	3	1·14	0·76	5	−1·17	2·36	3	—	—	—
	4	0·50	0·41	4	—			—	—	—
	M	0·69	0·68		−0·33	1·94		—	—	—

(The means (M) and standard deviates (s.d.), expressed in cm, of the vertical landing positions (zero being the centre of the target, positive position upwards, the insect's head being used as the reference point) and the number of jumps (N) for different target distances.)

consisted of a black cardboard square (10 × 10 cm). tilted 45° from the frontal plane. In the centre a flower (diam. 2 cm) and a grassblade (2 × 10 cm) was fastened in a horizontal position. The target centre was at the same height as the head of the animal.

The results showed that both monocular and binocular animals were rather unwilling to jump under the present conditions, especially at larger distances. The animals often tried to climb down from the platform. When forced back to the jumping position they frequently made an escape jump which was preceded by peering, a lifted head and the antennae directed upwards in a divergent position. These escape jumps, often up to 1 m in range, were not recorded. When the animals jumped at the target the behaviour was quite different and it was possible to predict when the animal was going to jump, since the jump was preceded by a rather fixed behavioural sequence: (*a*) the animal first peered (one or several times), (*b*) then it usually corrected the leg posture, (*c*) finally it turned down the head and moved the antenna down to a parallel position aiming at the target. After that the jump occurred within a few seconds. Only one miss (out of 40 jumps) was recorded on the binocular animals, and one miss (out of 26 jumps) on the monocular animals.

As shown in Table 2 the binocular animals exhibit a considerable accuracy in their jumping. The general feature is that the animals land on the middle of the target. The mean of means show that after landing the head of the animal is positioned almost exactly on the centre of the target (only 1·3 mm undershoot). The monocular animals exhibited a similar accuracy and the mean vertical position showed only a small overshoot (6 mm). Thus, when the monocular animals jump (they hesitate much more than binocular animals) they nevertheless seem to behave almost as accurately as binocular animals.

It is concluded from the two experiments that binocular vision is not a necessary condition for accurate jumping onto a target at different distances. On the contrary the results show that monocular animals exhibit a jumping behaviour which is essentially similar to the behaviour of binocular animals. It is not possible to account for correct distance perception on the basis of accommodation and convergence (since these cues are not available to the fixed-eye system of the insects) neither can it be

accounted for by optical stimulus factors since cues such as linear perspective and relative size are ambiguous (Ittelson, 1960)). Thus a certain proximal size (retinal image size) may correspond to a small object situated close to the animal as well as to a larger object situated at a larger distance. Similarly it has been shown (Eriksson, 1973; O'Keefe & Nadel, 1978) that even 'higher order variables of stimulation' (Gibson, 1967) in reality only provide the organism with ambiguous, relative distance, information.

On the basis of the experiments and above considerations it is concluded that correct distance perception in the monocular grasshoppers depend essentially on movement parallax (i.e. on an integration of ambiguous optical information and information from the body-state system). This conclusion is consistent with that proposed for human space perception in which monocular observers obtained correct space perception during locomotion when presented with unfamiliar, artificial, stimuli (Eriksson, 1974a). Thus movement parallax seems to constitute a rather general principle in space perception and its theoretical formulation (Eriksson, 1974b) may be of some value in the attempts to achieve a neurophysiological elucidation of this mechanism.

REFERENCES

BEERSMA, D. G. M., STAVENGA, D. G. & KUIPER, J. W. (1977). Retinal lattice, visual field and binocularities in flies. *J. comp. Physiol.* **119**, 207–220.

COLLETT, T. S. (1978). Peering-a locust behaviour pattern for obtaining motion parallax information. *J. exp. Biol.* **76**, 237–241.

ERIKSSON, E. S. (1973). Distance perception and the ambiguity of visual stimulation: A theoretical note. *Percept. & Psychophys.* **13**, 379–381.

ERIKSSON, E. S. (1974a). Movement parallax during locomotion. *Percept. & Psychophys.* **16**, 197–200

ERIKSSON, E. S. (1974b). A theory of veridical space perception. *Scand. J. Psychol.* **15**, 225–235.

GIBSON, J. J. (1967). *The Senses Considered as Perceptual Systems.* Boston: Houghton Mifflin.

HORRIDGE, G. A. (1977). Insects which turn and look. *Endeavour* **1**, 7–17.

ITTELSON, W. H. (1969). *Visual space perception.* New York: Springer.

MALDONADO, H., BENKO, M. & ISERN, M. (1970). Study of the role of binocular vision in mantids to estimate long distances, using the deimatic reaction as experimental situation. *Z. vergl. Physiol.* **68**, 72–83.

McNEMAR, Q. (1962). *Psychological statistics.* New York: Wiley.

O'KEEFE, J. & NADEL, L. (1978). *The Hippocampus as a Cognitive Map.* Oxford: Clarendon Press.

VIA, S. E. (1977). Visually mediated snapping in the bulldog ant: A perceptual ambiguity between size and distance. *J. comp. physiol. Psychol.* **121**, 33–51.

WALLACE, G. K. (1959). Visual scanning in the desert locust (Schistocerca gregaria Forskål). *J. exp. Biol.* **36**, 512–525.

WIGGLESWORTH, V. B. (1972). *The Principles of Insect Physiology.* London: Methuen.