

## THE LANDING RESPONSE AND VISUAL PROCESSING IN THE MILKWEED BUG, *ONCOPELTUS FASCIATUS*

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A crucial function of the visual system of a flying insect is the detection and recognition of the visual correlates of imminent collision so that an appropriate motor output may be generated to enable landing or avoidance of collision. This reaction, which indeed appears to be part of the behavioural repertoire of most flying insects, is known as the *landing response* (Goodman, 1960). The response is essentially identical whether a free-flying insect approaches a surface or whether a tethered insect is approached by a surface (Goodman, 1960).

Simple dimming of the surround illumination, which is one feature of the visual stimulus experienced by a flying insect approaching a restricted object darker than the surround, is also effective in eliciting a landing response. Brightening of the surround is not effective (Goodman, 1960).

This reaction, and the stimuli which trigger it, have been studied extensively only in Diptera. Using approaching disks of various contrasts and diameters, and approaching at various velocities, Goodman concluded that the effectiveness of the stimulus presented by an approaching object was a function of the product of three variables: the magnitude of change of intensity at successive ommatidia, the number of ommatidia so stimulated, and the rate of their successive stimulation.

In order to separate the effects of motion and overall change of illumination Braitenberg & Taddei Ferretti (1966) used a rotating black and white spiral as a visual stimulus. Such a stimulus was effective in triggering a landing response when the spiral was rotated in a sense which produced an illusion of expansion. Since the spiral remained at a fixed distance from the animal (*Musca*), the average illumination was constant. In a subsequent study (Fernandez Perez de Talens & Taddei Ferretti, 1970), the effectiveness of spiral patterns was measured as a function of various parameters such as pitch, stripe width, speed of rotation, and position in the visual field.

The basic difficulty with the use of an approaching object or a rotating spiral as a visual stimulus is that they are both quite complex. Neither the angular velocity nor the spatial frequency content are constant as a function of visual angle. In this paper methods are developed and applied which avoid these difficulties. The landing response of the milkweed bug, *Oncopeltus fasciatus*, is described. It is shown that certain features or components of more complex spatio-temporal visual patterns are sufficient to elicit a landing response. Based on this finding, further experiments are described

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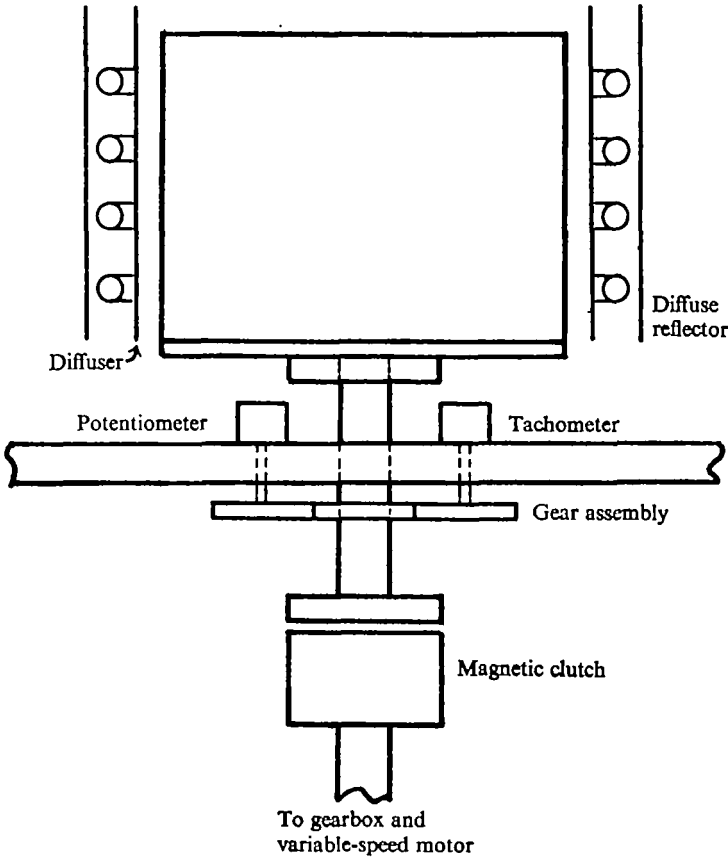


Fig. 1. Mechanical arrangement used for rotating-drum experiments.

and shown to be consistent with the hypothesis that common neuronal mechanisms underlie the triggering of the landing response and certain optomotor reactions.

Some initial results have been published (Coggshall, 1971).

#### MATERIALS AND METHODS

Adult laboratory-bred milkweed bugs, *Oncopeltus fasciatus*, were used in this study. A supply of dry milkweed seeds and water was continuously available in the colony. Both males and females, at least one week post-eclosion, were used.

The animal was fixed by the thoracic shield to a small wooden stick by a mixture of resin and beeswax. The head was fixed to the thorax by a small bridge of this mixture.

Approximately 25% of the animals mounted as above flew longer than 5 min. Occasionally one would fly several hours, but approximately  $\frac{1}{2}$  h was more usual.

Rarely, an animal would start flight spontaneously upon loss of tarsal contact. However, with most animals flight was induced by moving the animal with a quick downward motion. Wind on the head was ineffective in inducing flight. In some initial experiments an air-stream flowing past a flying bug was created by placing a vacuum tube behind the animal. This had the advantage of leaving the frontal visual field clear.

For presentation of stimuli. However, further investigation revealed that flight in a wind stream lasted no longer, on the average, than flight in still air.

Spirals and striped patterns were made from high-contrast graphic arts film. In all rotating-drum experiments a striped pattern with an angular period of  $22.5^\circ$  was used. Since the interommatidial angle for *Oncopeltus* (estimated from histological sections) is about  $5^\circ$ , this was well above the expected cut-off wavelength of the spatial frequency transfer function associated with the compound-eye receptor mosaic (Gavel, 1939; Götz, 1965).

The striped pattern was mounted within a Plexiglas cylinder which was rotated by a variable-speed motor coupled through a gear box and a magnetic clutch. The angular position and instantaneous angular velocity were monitored with a  $360^\circ$  potentiometer and a tachometer coupled to the shaft rotating the drum (Fig. 1). The rise-time to an angular speed of  $20^\circ/\text{sec}$  was approximately 0.1 sec after energizing the magnetic clutch.

Illumination was provided by four General Electric Circline FC 12 T 10 cool-white fluorescent lamps using direct current. A diffuse reflector was placed behind the lamps, and a frosted diffusing screen was placed between the lamps and the rotating drum (Fig. 1). This provided bright vertical stripes (luminance approximately 7.3 lamberts) alternating with dark stripes with a contrast of 0.9 or greater. This brightness is near the range encountered by a bug in the daylight (luminance of open sky is approximately 2.5 lamberts; Hodgman, 1954), in open fields which constitute its natural environment (Andre, 1934). Luminance of the interior pattern surface was measured with a small-spot photometer (photomultiplier tube RCA 6199, S-11 spectral response) which was calibrated against a secondary standard kept by the Visibility Laboratory of the Scripps Institute of Oceanography, San Diego, California.

The field of view of the insect was restricted by the placement of flat black shields within the drum (see Sections II of Results).

## RESULTS

### I. General description

During flight the front and middle pairs of legs are tightly flexed beneath the thorax. The rear pair of legs lie on either side of, and more or less parallel to, the abdomen. Upon presentation of an adequate visual stimulus the first two pairs of legs are extended in the landing response (Fig. 2). For the front pair of legs this extension occurs primarily at the femur-tibia joint, with the femur remaining essentially fixed. The tarsi are also extended. The second pair of legs are extended in a similar manner, and in addition the femur is slightly lowered. The rear legs retain their positions parallel to the abdomen.

Intermediate leg positions are observed. They consist of legs partially extended, or of some legs extended and some folded. However, these intermediate positions are quite labile and pass within a few seconds to one of the two above-described states. Thus, the landing response in *Oncopeltus* is not a graded response. This is in contrast to the situation in Diptera, where the occurrence of intermediate leg positions appears to be a function of the input stimuli (Goodman, 1960).

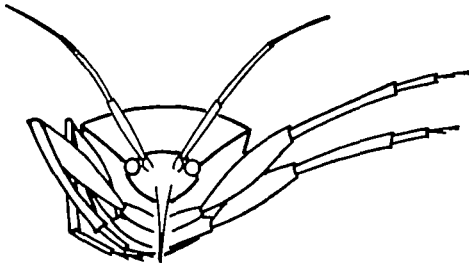


Fig. 2. Composite drawing: right legs in normal flight position, left legs in landing position. The rear pair of legs lie alongside the abdomen for either case.

When a non-flying bug hangs in mid air with no tarsal contact, the legs dangle down and are usually continuously active with small-amplitude movements. On initiation of flight, either by downward motion or occurring spontaneously, the first two pairs of legs immediately assume the fully extended landing position and the rear pair take up their position beside the abdomen. As flight continues the first two pairs of legs are gradually folded into the characteristic flight posture. This folding can take up to 30 sec or more to complete. A brief puff of air on the antennae greatly facilitates this transition, causing the legs to 'snap' into the flight posture. After removal of the antennae the legs are still folded gradually, but a puff of air on the head no longer facilitates the process.

The landing response is induced by a variety of spatio-temporal visual stimuli. Those involving movement will be treated in the succeeding sections. In addition to moving stimuli simple dimming of the surround illumination will also induce the landing response, as it does in Diptera (Goodman, 1960). Brightening of the surround does not induce a landing response. The landing response occasionally occurs with apparent spontaneity. This is usually, but not always, followed by termination of flight.

There is a clear habituation of the landing response, both to movement and to dimming. The response becomes habituated sooner with weak stimuli. There is also a maximum stimulus above which the response never becomes habituated. This maximum, and the time course of decay of habituation, are highly variable from one animal to another and from trial to trial in individual animals. However, if 4-5 min of continuous flight elapse between stimuli, no habituation effects are observed. Habituation was not seen in *Lucilia* (Goodman, 1960), but was noted in *Musca* (Fernandez Perez de Talens & Taddei Ferretti, 1970).

## II. *The nature of sufficient visual stimuli*

An object approaching at constant velocity readily induces a landing response in *Oncopeltus*. Each point on the approaching surface has a certain angular velocity with respect to the bug's eye (Fig. 3). This angular velocity is given by

$$\dot{\Theta}_a = (v/x) (\frac{1}{2} \sin 2\Theta_a), \quad (1)$$

where  $\Theta_a$  is the visual angle,  $\dot{\Theta}_a$  is the angular velocity,  $v$  is the linear velocity of the approaching surface, and  $x$  is the distance from the object to the insect. The factor  $\frac{1}{2}$

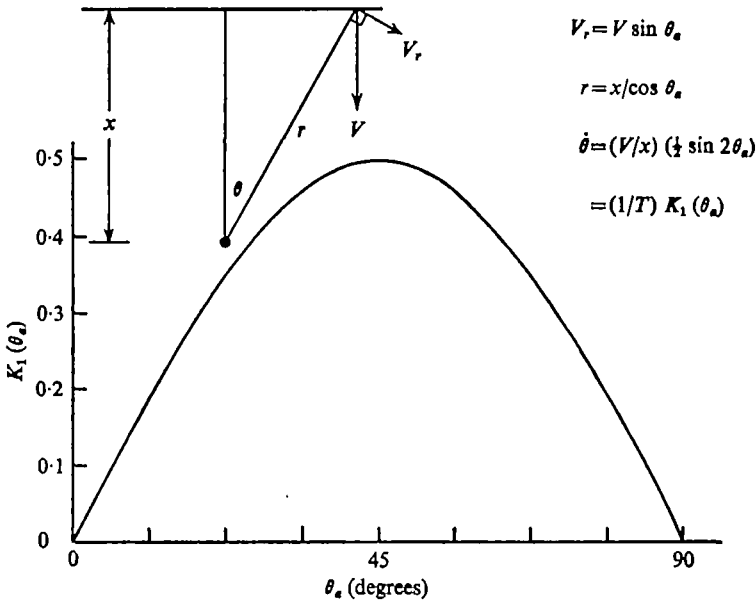


Fig. 3. Angular distribution of angular velocity associated with an approaching surface.

$\sin 2\theta_a$  is plotted in Fig. 3, along with the geometry and equations used in deriving (1). It is perhaps more revealing to write (1) in terms of the time-to-collision,  $T$ :

$$\dot{\theta}_a = (1/T) (\frac{1}{2} \sin 2\theta_a). \tag{2}$$

Two points should be noted. For a given distance of object-to-insect (or at a given instant in time) different visual angles, and thus different ommatidia, experience different angular velocities. In addition, angular velocities at all visual angles increase rapidly as the time-to-collision becomes less (equivalently, as the distance between object and insect approaches zero).

If, in addition, the approaching object is darker than the general surround illumination, then as the object approaches there is a corresponding reduction in the total illumination reaching the eye. This in itself is capable of triggering a landing response in *Oncopeltus* as well as in other insects. Thus the visual correlates associated with an approaching object are, in general, quite complex and contain at least two types of stimuli known to be effective in inducing a landing response.

Black and white striped spirals, rotating in a sense so as to produce the illusion of approach for a human observer, are also effective in inducing a landing response in *Oncopeltus*. The spiral remains at constant distance from the animal and the total surround illumination remains constant. However, such a stimulus is still rather complex. The distribution of angular velocities associated with an arithmetic spiral rotating at a constant angular velocity is

$$\dot{\theta}_s = (v_T/d) \cos^2 \theta_s, \tag{3}$$

where  $\theta_s$  is the visual angle,  $\dot{\theta}_s$  is the angular velocity,  $d$  is the distance from the spiral to the insect, and  $v_T$  is the radial velocity of the stripe edges. The geometry, the function  $\cos^2 \theta_s$ , and equations are shown in Fig. 4. Note that, in contrast to the

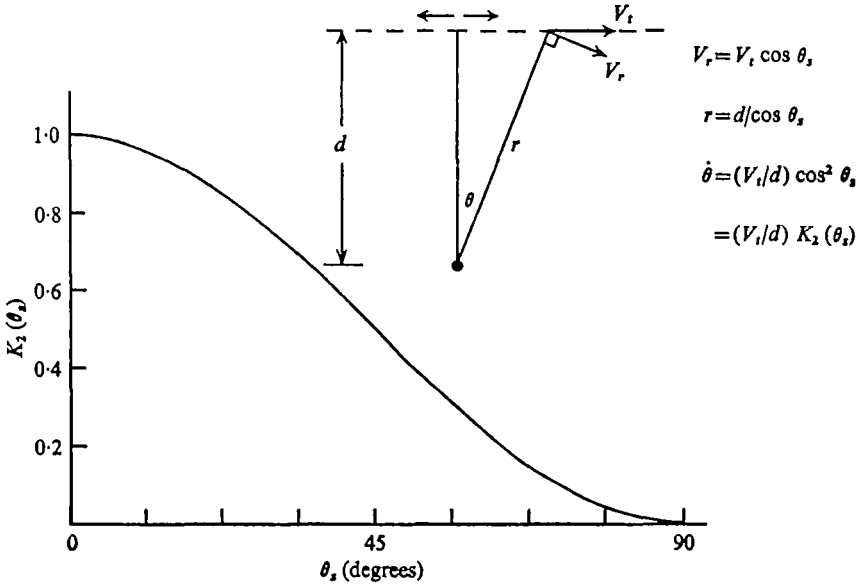


Fig. 4. Angular distribution of angular velocity associated with a rotating spiral

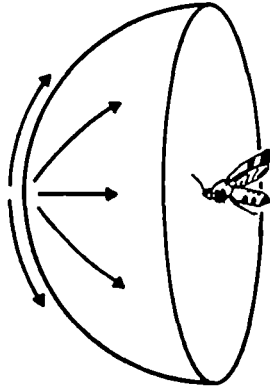


Fig. 5. Directions of movement of small-field patterns effective in triggering a landing response.

situation for an approaching object, the angular velocity distribution is not a function of time. However, the angular velocities are still a function of the visual angle.

Since the spatio-temporal patterns associated with approaching objects and rotating spirals are both effective in inducing a landing response, and each contains a component of *angular velocity to the periphery*, it was hypothesized that the insect's visual system was extracting this particular component from the more complex patterns. This was tested by the following experiment. Tethered, flying bugs were placed at the centre of a Plexiglas hemisphere. Square black discs with edges subtending 5, 10 or 20° of visual angle were moved on the surface of the hemisphere along arcs of great circles passing through the point directly in front of the bug. When moved on the sphere's surface, they remained constant in size and an essentially constant angular velocity could be maintained. Only those discs which moved from the centre out to the periphery were effective in triggering a landing response. The 10° and 20° discs readily elicited a landing response, whereas the 5° disc rarely triggered a response. Movement

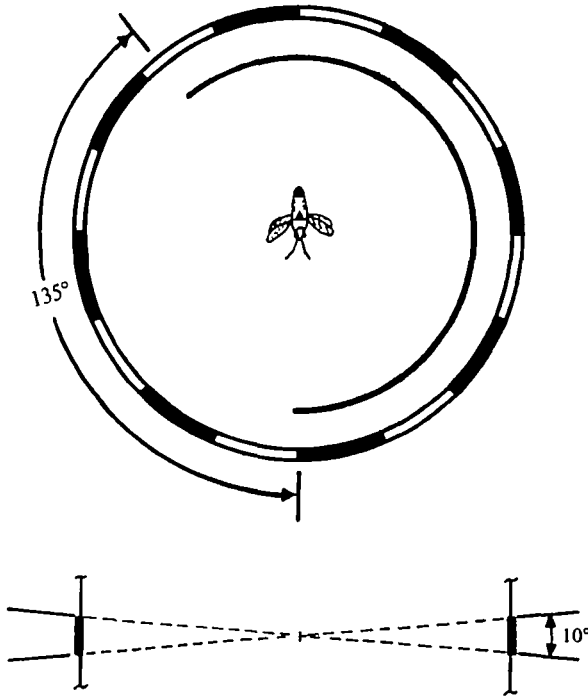
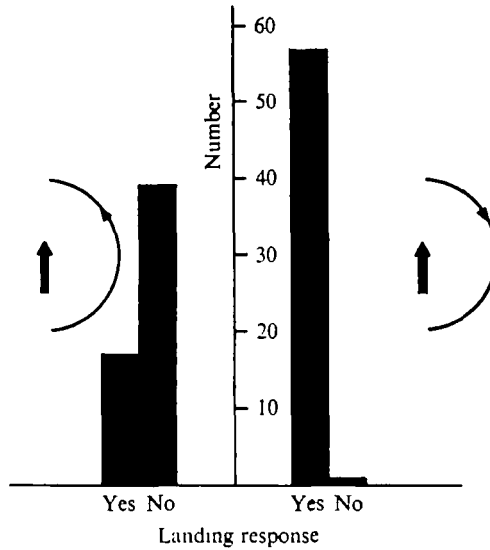


Fig. 6. Stimulus configuration for experiments using a rotating black and white striped drum.

from the periphery to the centre did not trigger a landing response. Symmetric movement was not required. Horizontal, vertical, or oblique movement was effective, as long as it was directed to the periphery (Fig. 5). For these stimuli, habituation was particularly evident. The bug often failed to respond on a second trial which immediately followed the first. If 5 min elapsed between trials, no habituation was noted.

After demonstrating that small peripherally moving spots were sufficient to evoke the landing response, an attempt was made to estimate the range of angular velocities for which they were effective. The equipment used was the motor and magnetic clutch system described in Methods. A  $10^\circ$  or  $20^\circ$  black disc was placed directly in front of a bug and then moved horizontally at constant angular velocity for one-half revolution. It was noted whether or not a landing response occurred. This was done for various velocities over a range of approximately  $1\text{--}60^\circ/\text{sec}$ . The only clear-cut result, with three bugs, was that there was a minimum velocity below which the landing response was never given. This was  $50^\circ/\text{sec}$  and  $30^\circ/\text{sec}$  for the  $10^\circ$  and  $20^\circ$  discs, respectively.

Optomotor reactions in *Oncopeltus* can occur at much lower angular velocities (Bliss *et al.* 1964). The optomotor turning reactions of insects in general tend to be reduced at low and high velocities, and in general have a single maximum at an intermediate angular velocity. This maximum usually occurs for a contrast frequency (ratio of angular velocity to wavelength of stripe pattern) of about 1 Hz (Götz, 1964). For *Oncopeltus* the maximum reaction lies between  $10^\circ/\text{sec}$  and  $20^\circ/\text{sec}$  using a pattern wavelength of  $18^\circ$  (Bliss *et al.* 1964) which corresponds to contrast frequencies of 0.55 Hz and 1.1 Hz respectively.



g. 7. Effectiveness of progressive rotation versus regressive rotation using a rotating black and white striped drum.

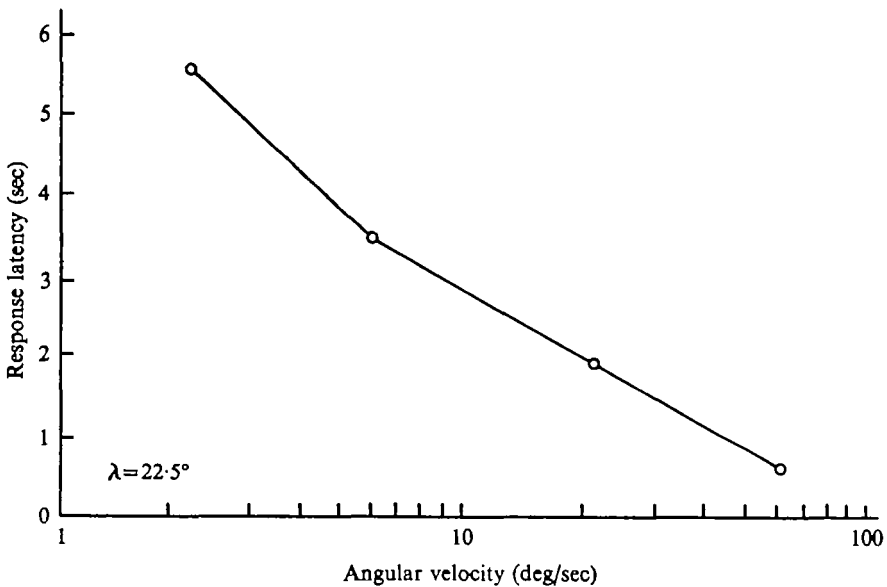


Fig. 8. Average response latency as a function of angular velocity for progressively rotating black and white striped drum.

Additional experiments were carried out using a black and white striped rotating drum as a visual stimulus. The bug was placed in the centre of the drum. The total left  $180^\circ$  visual field was shielded. On the right, approximately  $135^\circ$  of the pattern (wavelength =  $22.5^\circ$ ), starting directly in front of the animal, was visible. The vertical extent of the pattern was limited to  $\pm 5^\circ$  with respect to the horizontal (Fig. 6). The first experiment tested the effectiveness of the drum as a stimulus for the landing response. A bug was presented with either a progressive (front-to-back) or regressive



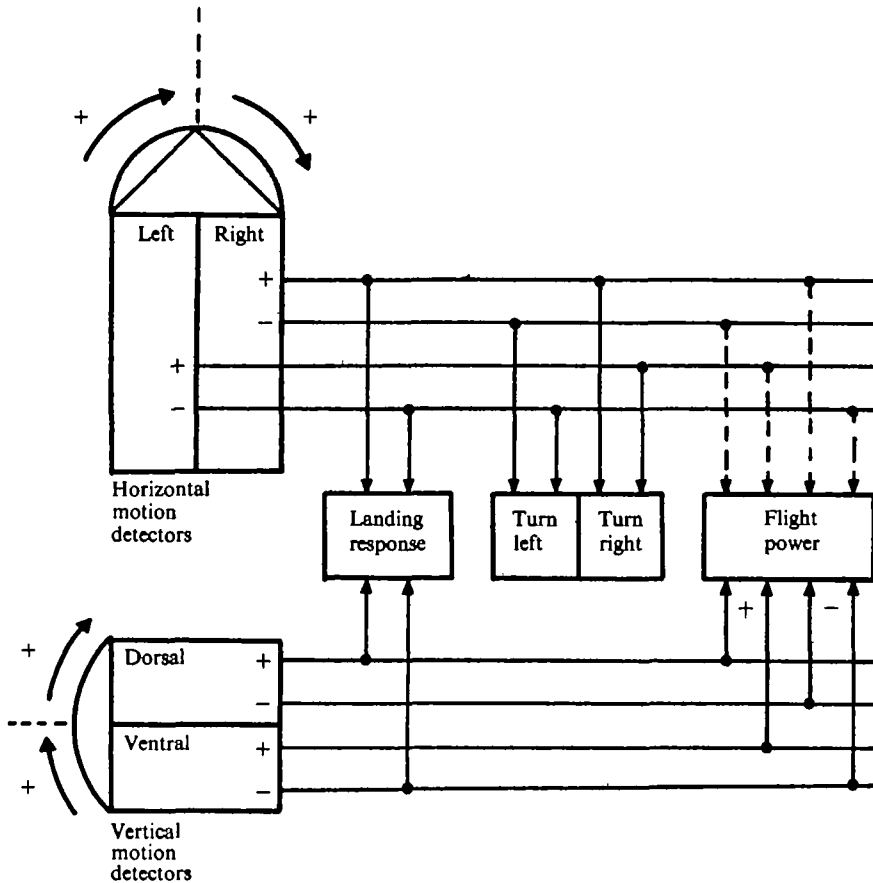


Fig. 9. Diagram suggesting how neuronal motion detectors may provide common inputs to landing response, optomotor turning, and flight-power neuromotor system. (Arrows indicate directions arbitrarily taken as positive.)

(back to front) rotation selected alternatively. At the beginning of each trial the angular velocity was zero and then went to  $18^\circ/\text{sec}$ , which corresponds to a contrast frequency of 0.8 (for the  $22.5^\circ$  pattern used). At least 5 min elapsed between trials. It was recorded whether or not a landing response occurred during two full revolutions of the drum. A total of 56 trials using progressive rotation and 58 using regressive rotations was used. Ten bugs in all were used.

The results are shown in the histogram of Fig. 7. The progressively rotating drum is clearly a very effective stimulus, while regressive motion is much less effective. (It cannot be absolutely excluded that the responses to regressive motion are due to the field of view of the left eye overlapping the midline and/or undetected light reflexions.)

For triggered responses one possible measure of the effectiveness of the triggering stimulus is the latency between the onset of the stimulus and the occurrence of the triggered event. In the next set of experiments the same visual stimulus configuration was used. The latency was measured from the start of progressive rotation until the occurrence of the landing response. This was done over a velocity range of approximately  $2\text{--}65^\circ/\text{sec}$ , with 15 trials at each velocity setting. At lower velocities the

response was rarely elicited. At higher velocities the rise time of the velocity of the rotating drum became a significant portion of the response latency. The average response time is plotted for each velocity in Fig. 8. It is clear that the landing response can be elicited over a wide range of angular velocities. Further, the latency for the response continues to decrease, presumably indicating a stronger stimulus, at velocities for which the strength of the optomotor turning reaction declines.

#### DISCUSSION

In the preceding account it has been demonstrated that simple peripherally directed angular motion is *sufficient* to elicit a landing response from the milkweed bug *Oncopeltus fasciatus*. (It is not a *necessary* stimulus, since dimming of the surround illumination will also elicit a landing response.) This greatly simplifies the requirements placed on a neuronal system for detecting imminent collision.

There is now considerable electrophysiological evidence that neurones exist in the optic lobes and brains of insects which are selectively activated by unidirectional angular motion in the visual environment. Such unidirectional motion-detecting units have been recorded in Diptera (Bishop & Keehn, 1966, 1967; Bishop, Keehn & McCann, 1968; McCann & Dill, 1969; Mimura, 1971), in Lepidoptera (Collett & Blest, 1966; Collett, 1970, 1971; Swihart, 1969), in Orthoptera (Horridge *et al.* 1965; Northrop & Guignon, 1970), in Hymenoptera (Kaiser & Bishop, 1970) and in Heteroptera (Coggshall, unpublished observations using *Oncopeltus*). In general, these units have large monocular receptive fields which may be either ipsilateral or contralateral. Units with binocular receptive fields are also observed. The directions of maximum sensitivity (at least in Diptera) form an approximately orthogonal set orientated more or less horizontal and vertical (Bishop *et al.* 1968).

Since the landing response is also elicited by simple angular motion, this increases the confidence with which one may hypothesize that these or similar units contribute to triggering this response, as has been suggested by Bishop & Keehn (1966).

The landing response usually occurs within a few seconds after presentation of the stimulus. The dynamics of the responses of motion-sensitive units have been studied to some extent, especially in flies. Bishop *et al.* (1967), using moving black and white stripes as a stimulus, found that the units respond maximally to the onset of motion with a rise time of 0.5–0.8 sec. The firing rate decays to steady state in approximately 2 min. The units continue to respond as long as the stimulus is present. They respond to velocities at least as low as 1°/sec. The steady-state firing rate increases with angular velocity up to about 100°/sec (contrast frequency approximately 7 Hz.) Mimura (1971), using a spot of light (approximately 1.15° diameter) moving in the dark, found that the motion-sensitive units he recorded attained maximum steady-state discharge rates at velocities between 23°/sec and 86°/sec with rise time of less than 1 sec. Assuming that the landing response is triggered by units with properties similar to those studied, then for the stimulus configurations used in this study the landing response occurs during the transient portion of their response.

One can propose a simple model consisting of a central state of excitation which increases monotonically as a function of input from certain motion-sensitive units and a triggerable motor-sequence generator. When the central state reaches a certain

level of excitation, the motor-sequence generator is triggered and the appropriate motor commands for a landing response are generated. Clearly, if the triggering threshold remains constant (no habituation, for example) then a monotonic increase in transient discharge rate as a function of angular velocity implies a monotonic decrease in latency for a landing response.

Chapple (1966) recorded the effects of simple visual stimuli on motoneurone discharges in the metathoracic leg nerves of a dissected *Oncopeltus* preparation. However, the rear legs do not participate in the landing response, and it is difficult to relate his results to neuromotor output associated with the landing response produced by an intact flying animal.

Previous behavioural studies have also suggested that the same neural mechanisms mediate certain optomotor turning reactions and the landings response (Goodman, 1960; Braitenberg & Taddei Ferretti, 1966). McCann & Foster (1971) find that the reaction of motion-detection units compares closely with that of optomotor flight-torque reactions when studied as a function of pattern intensity, angular orientation of the pattern, and position of maximum sensitivity in the visual field. In addition it is known that moving patterns in the visual environment can influence flight-power behaviour (Kennedy, 1939; Schneider, 1965; Smyth & Yurkiewicz, 1966; Götz, 1968).

Fig. 9 illustrates how information from motion-sensitive neurones may be processed to provide the appropriate inputs to motor control centres. For example, progressive (front-to-back) horizontal motion in the right visual field induces an optomotor torque which would turn the animal to the right and trigger a landing response. Regressive motion in the right visual field would induce a tendency to turn left but would not trigger a landing response. Both progressive and regressive horizontal motion, either symmetrical or unsymmetrical, influence the wing-beat frequency and pattern of wing articulation during a wing-beat cycle in *Oncopeltus*. Presumably these produce a change in thrust, lift, or both. However, no quantitative data is available, and for this reason these connexions are indicated using dotted lines.

Götz (1968) has established that vertically orientated motion affects primarily the wing-beat amplitude in *Drosophila* and therefore the magnitude but not the direction of the thrust vector. Upward-directed motion increases thrust, downward decreases it. However, upward motion *only* in the *dorsal half* of the visual field induces a landing response in *Oncopeltus*, while downward motion is effective only in the ventral half. It appears that there is a distinction to be made between dorsal and ventral portions of the eye with regard to processing vertically orientated motion. In Diptera the dorsal and ventral parts of the eye show a mirror symmetry with regard to the pattern of rhabdomeres in each ommatidium (Dietrich, 1909). Also in Diptera the dorsal and ventral portions of the eye are of different embryological origin (Becker, 1956). Stimulus configurations for further behavioural and electrophysiological studies should be designed having regard to these distinctions.

#### SUMMARY

1. The landing response of the milkweed bug *Oncopeltus fasciatus* consists primarily of extension at one leg joint (femur-tibia) of each of the front four legs upon presentation of the appropriate visual stimulus.

2. Small-field peripherally directed angular motion in the frontal visual hemisphere is sufficient to elicit the landing response.
3. Movement *from* the periphery is not an effective stimulus.
4. Response latency to a large-field peripherally moving striped pattern decreases monotonically with increasing angular velocity.
5. This decrease is consistent with what is known of the dynamics of motion-detecting neurones in other insects.
6. It is suggested that motor mechanisms controlling the landing response, optomotor turning reactions and flight-power behaviour receive inputs from a common neural motion-detection system.

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