References and Notes

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Flight Behavior of a Fly Alighting on a Ceiling

Abstract. Salient features in the maneuvers executed by a house fly (*Musca domestica*) in ascending to land on the underside of a horizontal surface have been observed in photographs exposed in a continuous-writing high-speed framing camera. Details of the action and the instrumentation required to record it are described.

The high-speed camera has been widely used by entomologists to study the flight mechanism of insects (*1*). In recent years engineers have become increasingly interested in the maneuvering ability demonstrated by many kinds of insects. The difficult maneuver of landing on a ceiling is of interest to both the entomologist and the engineer, but the spontaneity of the action makes it a difficult one to record by conventional high-speed motion picture techniques. Eyles (*2*) studied the problem and concluded that the fly "performed a 'half roll' in alighting, coming to rest at a slight angle to the direction of flight." More recently, Curran (*3*) reported an entirely different maneuver in which the fly made surface contact with its forefeet first, then swung its other four feet into contact with the ceiling.

To study this problem further, through high-speed photography, I chose a continuous-writing drum-type framing camera (Beckman and Whitley Dynafax), which exposes 224 frames on a 33-inch length of film supported on the inside of a rotating drum of 11-inch diameter (*4*). The camera was operated at 9500 frames per second. Exposure illumination of as much as 300,000 ft-ca was provided by an electronic light source (Beckman and Whitley model 357). This source produces a rectangular pulse of light 22.35 msec in duration, corresponding to one rotation of the camera drum. The exposing light was triggered by the fly when its body eclipsed a horizontally collimated light beam focused on a phototube. The height from the ceiling of the electric-eye trigger could be adjusted to permit initiation of illumination from the exposing light source at various stages of the action. Experiments were conducted indoors at a low ambient-light level, so the camera could be operated continuously for several minutes with the lens uncovered without exceeding the exposure threshold of the film.

House flies (*Musca domestica*) were introduced into the bottom of a light-tight box, whereupon they were attracted upward toward the light transmitted by a translucent ceiling illuminated from the opposite side by a 40-watt lamp. The camera was focused on the illuminated ceiling through a glass port in the side of the box. Experiments were conducted with two ceiling surfaces: galvanized window screen and tracing paper. Selected frames from a typical film strip are shown in Fig. 1.

A blinding flash is required to photograph the action at short exposure time, and there is reason to suspect that the fly's mechanism of reaction to this stimulus may interfere with the normal performance of its landing maneuver. To eliminate doubt on this point, confirming experiments were performed with sunlight as a source of light for exposure. A conventional high-speed camera of roll-film type was mounted inside the box, with the lens aimed vertically toward the back-lighted ceiling. Operated at 650 frames per second, this camera requires 2 seconds to reach running speed and then continues to run for 5½ seconds until the film is expended. It had been previously determined under simulated operating conditions that the chances of recording a fly's landing during the operating time of the camera were one in five, at a 0.05 significance level, if six flies were released into the box simultaneously with the starting of the camera. On the basis of these preliminary data five 100-

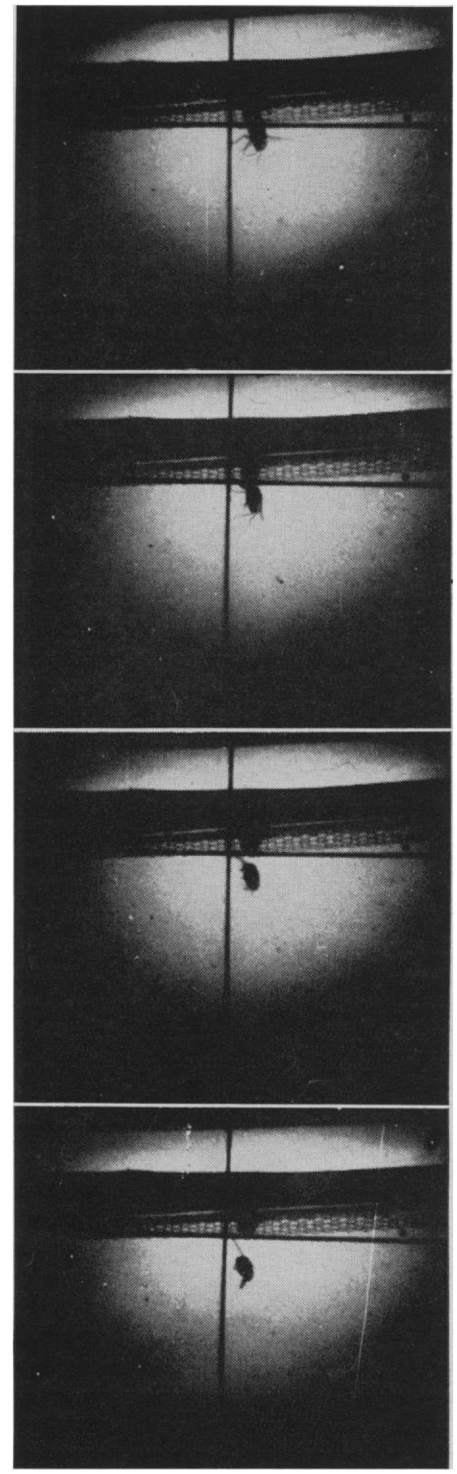
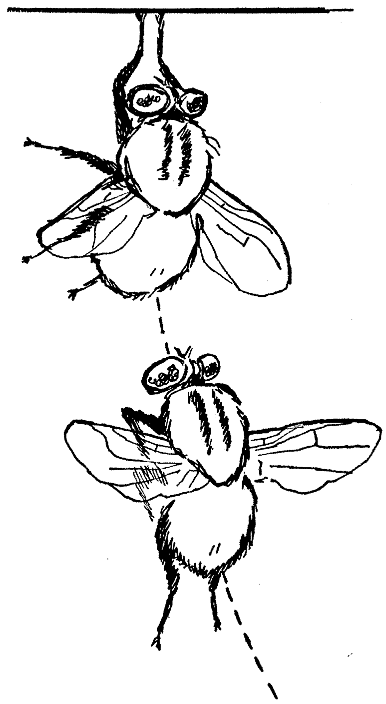


Fig. 1. Selected frames from a film strip showing the approach phase of the landing maneuver. The cross-hairs visible in the photographs serve as a reference for velocity measurements.



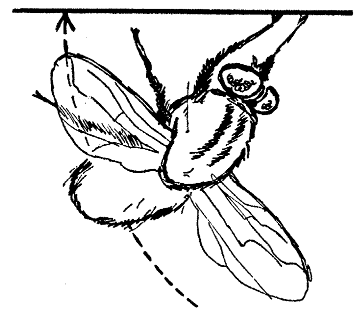


Fig. 2. (Left) The ascent toward the landing surface; (right) the actual landing phase. These sketches illustrate essential details lost in the reproduction of the original photographs.

foot rolls of film were exposed, and one confirming record of a landing maneuver was obtained.

Analysis of all the films exposed to date by the methods outlined reveals that the landing maneuver is essentially comprised of two phases: (i) the ascension, or approach, and (ii) the actual landing operation. The general mechanics of the approach are quite clear in the photographs. In each case the fly ascended toward the ceiling in a near-vertical flight path at a typical velocity of 25 cm/sec. The frequency of wingbeat varied between 144 and 240 cy/sec. A large supination twist of the wings at the beginning and at the end of the downstroke provided the required thrust for vertical climbing. When the fly approached within about a body's length of the ceiling, all its legs were extended outward—the forelegs reaching forward. Continued vertical motion head-on into the ceiling brought the two forefeet into contact with the landing surface with sufficient momentum (¼ gcm/sec) to firmly attach the pulvilli and to aid in the execution of phase ii of the landing maneuver. With its forefeet firmly bound to the landing surface, the fly swung its body forward sufficiently to bring its other legs into contact with the surface. Independent fluttering of the wings served to stabilize the body during this movement. The origin of the forward torque required to swing the body upward is not entirely clear in the photographs, but the probable components are vertical momentum, centrifugal force resulting from an inside-loop approach path, and wing movement (see Fig. 2).

Some variations in the landing maneuver were observed. In one case the fly went into a rolling movement immediately before "touching down" with its forefeet. The final phase of the maneuver resembled a sidewise handspring or "cartwheel" in which the other four feet were brought into contact with the landing surface. This variation probably accounts for the "half roll" interpretation reported by Eyles (*2*). Qualitatively our findings agree with those of Curran (*3*), who did not report any quantitative data.

Neither the exposing flash nor the nature of the landing surface appear to have any marked effect upon the general mechanics of landing, as recorded by the camera.

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Staggerer, a New Mutation in the Mouse Affecting the Cerebellum

Abstract. The "staggerer" mutant is recognized by its staggering gait, mild tremor, hypotonia, and small size. Symptoms develop during postnatal weeks 1 to 4 and remain stationary thereafter. The cerebellar cortex is grossly underdeveloped, with too few granule cells and unaligned Purkinje cells. Genetic linkage studies and neuropathological findings distinguish staggerer from other known mutants.

Several dozen independent mutations are known to affect neurological function in mice (*1*). These mutants are potentially of great value for the study of brain structure and development and for the analysis and therapy of neurological disease. However, they are unlikely to be used extensively for these purposes until the phenotypes are defined more fully. In almost no instance has there been a description of pathology which accounts for the clinical neurological findings. We recently recognized a gross brain lesion in a hitherto undescribed mutant and correlated the clinical and neuropathological features.

The mutation occurred spontaneously in a stock of obese mice at the Jackson Memorial Laboratory in 1955. The parents were normal in appearance. The segregation data given later in this report prove the mutation to have been due to a single recessive gene. Clinically the mutation somewhat resembles reeler (*rl*) (*2*), and the name "staggerer," symbol *sg*, is suggested (*3*).

The staggerer mutant mouse is first distinguishable from normal littermates between postnatal days 8 and 12. Of 20 affected animals in seven successive litters, three were detected with certainty on postnatal day 8, five on day 9, two on day 10, two on day 11, and eight on day 12. The mutants are identified most readily in the second postnatal week by their abnormal gait, which is more shuffling and hesitant than the gait of normal littermates. Forward progress is interrupted every few steps by a lurching motion to one side or the other. The mutants remain stationary more of the time than the normal mice, and a mild unsustained tremor sometimes accompanies the initiation of motor activity. At rest the hind limbs often are held abducted and everted about 45 degrees. Sometimes the mutants walk backward with hind limbs splayed outward. Of the mutant mice observed, about 50 percent weighed