onstrated that single pulses of light repeated at 24 h intervals do entrain the rhythm of traverse frequency, as though the pulses "reset" the ryhthm to its new phase 0 (circadian time 0, CT 0; see [1, 2]), after which the rhythm immediately initiates its endogenous oscillation with the maximum in the rhythm occurring about 12 h (CT 12) after the pulses [6]. Our recent experiments reveal that the rhythm of traverse frequency previously entrained to the skeleton photoperiod of 12 h, when transferred to a continuous darkness after either the first or the second pulse, initiates the free-running oscillation with the first maximum in the rhythm occurring around 12 h after the pulse no matter which was the first or the second pulse. It is, therefore, thought that the rhythm of traverse frequency is almost equally reset to its new CT 0 by each pulse of the skeleton photoperiod of 12 h which falls immediately after the time when the traverse frequency reaches its maximum, thus demonstrating "bistability".

The observations above also indicate that the "Ψ-jump" in the rhythm of traverse frequency in the population of *Paramecium* occurs in the narrow range of skeleton photoperiods between 11 and 13 h which is evidently represented by the fact that times of occurrence of the steady-state maxima in rhythms in skeleton photoperiods $\leqq 11$ h parallel the evening pulses, and those in skeleton photoperiods $\geqq 13$ h parallel the morning pulses. These facts also indicate that the time between light pulse and the maximum traverse frequency is determined to be ≈ 12 h. In effect, in asymmetric skeleton photoperiods the dominant maxima always occur during the inter-pulse interval when the interval is longer than 12 h so that the subejctive night for the *Paramecium* population always corresponds to the longer interval. These results, therefore, suggest that the pulses of the skeleton photoperiods as well as single pulses repeated at 24-h intervals basically cause only a discrete phase-shift in the rhythm of traverse frequency of the *Paramecium* population.

The fact that the maxima and minima in complete photoperiods are delayed parallel to each other with the increasing duration of the complete photoperiod, but not exactly parallel to the duration of the complete photoperiod, clearly indicates that the continuing components of complete photoperiods acts to decelerate the angular velocity of the rhythm of traverse frequency. These facts also provide evidence that the effects of skeleton photoperiods of less than 11 h in the population of *Paramecium* do not obviously mimic the effects of corresponding complete photoperiods, as they do in multicellular animals such as *Drosophila* [2, 3].

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Spatio-Temporal Integration of Motion

A Simple Strategy for Safe Landing in Flies

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When approaching a landing site the fly initiates landing at a certain distance. To account for the underlying release mechanism of this behavior different models have been derived from experiments on tethered flies and from free-flight studies. The integration model [2,3] claims that the output signals of direction-sensitive movement detectors are spatio-temporally pooled and subsequently processed by a threshold unit. In contrast, the flow-field model [11] proposes that landing is triggered by the relative retinal expansion velocity of the landing site, a mechanism which provides, for different flight velocities, a constant time-to-collision. Although settled on different levels of explanation, the integration model and the flow-field model can be distinguished experimentally because they differ considerably with respect to the predicted dependence of the landing distance on parameters of the landing site and its environment.

According to the integration model, the landing distance should depend on the size and structure of the landing site, because both parameters affect the number of activated movement detectors. Due to spatial integration the movement signal increases with the apparent size of the landing site. Furthermore, due to temporal integration landing distance is expected to increase with increasing distance the fly is approaching the landing site from. Finally the landing distance should also be affected by the environment because motion of the object and of the environment are not separately treated by the

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integration model. Any motion within the visual field is assumed to contribute to the spatio-temporally integrated motion output of the landing system.

The flow-field model of landing denies dependence of the landing distance on size and structure of the object. It also expects the landing distance to be independent from the start distance of the fly because only instantaneous signals are assumed to control landing. Furthermore, according to the flow-field model the landing system only evaluates the retinal motion of the landing site irrespective of the environment. However, under physiological conditions both models lead to similar predictions with respect to the dependence of the landing distance on the relative speed of fly and landing site: the faster the fly is approaching the object, the higher the relative retinal expansion velocity of the landing site (flow-field model), the higher the output signals of the movement detectors (integration model) and, therefore, the longer the distance between fly and object at which the fly is expected to initiate landing according to either of these models. To distinguish between these two models we compared each model's predictions derived from previous studies with the results obtained by using moving discs to simulate in tethered flight the approach towards a landing site.

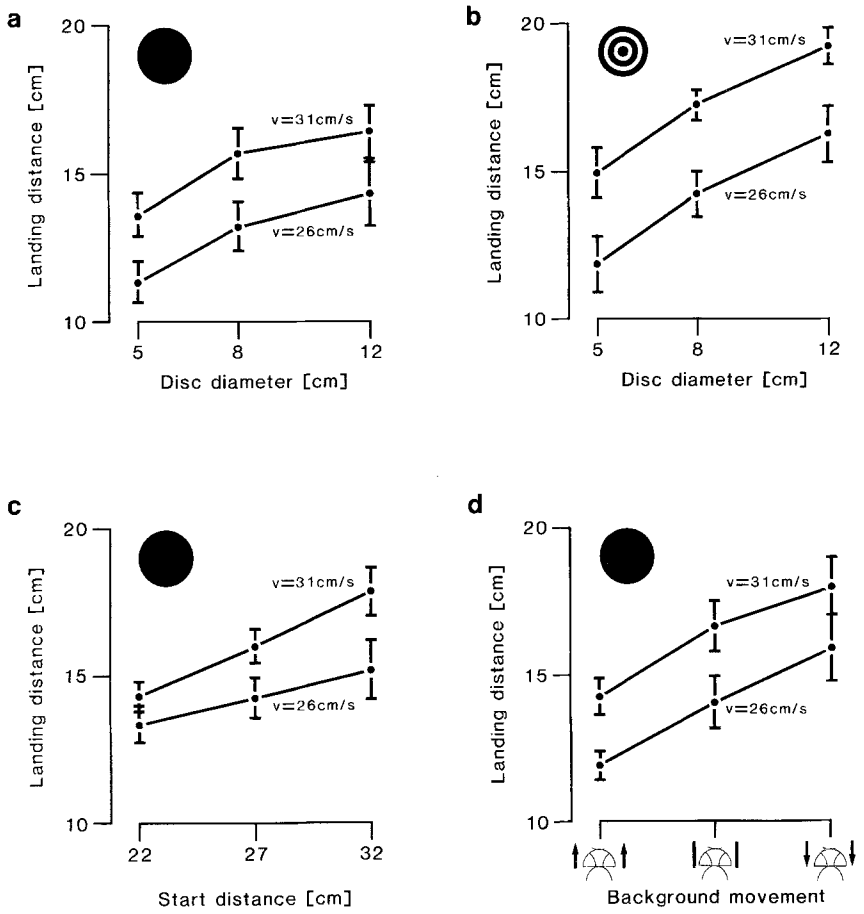

Fig. 1. Discs of various size and structure were moved towards flies in tethered flight. The distance at which the flies initiate landing was determined by a photo-electric which monitored the foreleg lift response. Discs were started in a distance of 32 cm from the fly (a, b, d) and had a diameter of 8 cm (c, d). The landing distance was found to depend on the speed of the approaching disc (a – d) as well as on its size (a, b). Furthermore structured discs released landing earlier than black discs (compare a with b). The landing distance also depends on the start distance from which the discs were moved towards the flies (c) and from the movement of the environment (d). *Inset* shows the discs which were used in each experiment. Each data point represents the mean ± SEM of 20 flies, each tested 5 times per stimulus

All experiments were performed with female houseflies (*Musca domestica*). A small cardboard triangle was glued with wax to their head and thorax and the ocelli were covered. For the experiments shown in Fig. 1 flies were placed at the end of a homogeneously illuminated plexiglass tunnel in which discs of various size and pattern could be moved towards them. Discs were mounted on the pen-holder of a plotter (HP7475) which allowed computer control of speed and position. Movement of the fly's leg was detected by a photoelectric which became interrupted whenever the fly extended its forelegs. This signal was taken as an indicator for the landing response [1]. A translucent windshield excluded any wind stimulation due to the moving disc. Pattern projectors generated optic flow with a temporal modulation of 1 Hz at the walls of the tunnel. The "landing distance", i.e., the distance between disc and fly at which the fly lifted its forelegs was calculated from known speed and start position of the disc and from the delay of the response. In the experiment shown in Fig. 2, flies were mounted on a force-transducer [7] in front of two photo-electrics to monitor simultaneously the lift of the forelegs (upper trace), the forward shift of the wings (middle trace) and the thrust (lower trace). In this experiment, landing was released by motion from the front to the back displayed on oscilloscope screens in front of both eyes of the animal.

The results (Fig. 1) indicate that the landing position depends on the velocity of the disc as predicted by both theories: the higher the velocity the longer the landing distance. But landing distance also depends on the size of the disc (Fig. 1a), as has also been found in previous studies [6]. The size-dependence is even more pronounced if structured discs were used (Fig. 1b). Size-dependence of the landing distance is not predicted by the flow-field model but can be easily explained by the integration model: the number of stimulated movement detectors increases linearly with the diameter of a black disc (only the periphery of the disc activates movement detecors) and with the square of the diameter of a structured disc (the whole area of the disc activates movement detectors). Landing distance also increases with in-

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creasing start distance of the disc (Fig. 1c). This cannot be understood if any instantaneous signal triggers landing as postulated by the flow-field model. It is easily explained if one assumes temporal integration of movement detectors' output signals. Finally the landing distance also depends on the movement of the environment of the disc (Fig. 1d): when the pattern ist moving across the retina from the front to the back flies land earlier than with the pattern moving in the reverse direction. This demonstrates that the movement of the environment influences the response of the fly to the potential landing site and suggests that the release mechanism simply pools the motion from a considerable portion of the fly's visual field.

Comparison of the results obtained under free-flight and tethered flight conditions is complicated by the use of different behavioral indicators for the onset of landing: in free-flight studies the onset of prelanding deceleration was assumed to represent the beginning of the landing phase, whereas in open-loop studies the beginning of this phase was always associated with the foreleg lift response. To test whether the discrepancy between our results and the predictions of the flow-field model are due to this difference, leg-, wing- and thrust-response were measured simultaneously. Flies were mounted on a thrust meter [7] in front of two photoelectrics. One detected leg lift, the other detected forward shift of the wing stroke plane, a mechanism which is known to produce a pitch torque in *Drosophila* [13]. In free flight pitch leads to a reduction of the fly's forward velocity [12]. Landing was released by motion from the front to the back displayed on oscilloscope screens in front of both eyes of the flies. An example of such an experiment is shown in Fig. 2. 750 of these traces, obtained from five flies, were measured and the latencies of all three variables were determined. Using various pattern velocities the latencies ranged from 60 up to 1200 ms and were found to be covariant with a coefficient of $r = 0.61$ (leg- vs. wing-response) and $r = 0.68$ (leg- vs. thrust-response). Although, unlike the leg response, the amplitudes of both thrust and pitch response gradually depend on pattern velocity, the covariance of the latencies of all three output variables

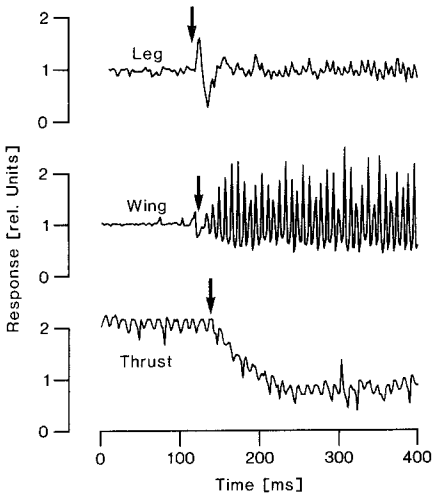

Fig. 2. Simultaneous recording of leg, wing, and thrust response of a single fly. *Arrows* indicate the onset of the responses. The forelegs can be seen crossing the photoelectric at the same time when the wings become shifted forward. Simultaneously the fly reduces its thrust. Note the modulation of the second trace with wing beat frequency after the onset of landing.

strongly suggests a common *release* mechanism. Thus, it seems that the same visual processing system is evoking the landing response in both tethered- and free-flying animals.

Because the landing distance was found to depend on the size, structure, and start distance of the landing site and on the movement of its environment as has been predicted by the integration model we can reject the hypothesis of a constant time-to-collision postulated by the flow-field model: it is the spatio-temporal integral of the movement detectors' output signals which triggers landing. Compared to determination of the relative retinal expansion velocity spatio-temporal integration seems to be less demanding with respect to the computational expenditure. It requires the movement detector signals which are also used for optomotor course-control [3], and simply pools them in space and time. Beside this economical consideration, it seems noteworthy that motion information is indeed retinotopically represented in the fly's nervous system [5], and motion-sensitive neurons pooling the output signals of spatially distributed movement detectors have already been thoroughly investigated in the third visual ganglion of the fly [8]. Spatio-temporal integration might be modified in order to reduce its dependence on parameters other than the fly's speed. That is, partial independence from the environment of the target could be provided in free flight by appropriate adaptation of the movement detection system [4, 9, 10]. Moreover, effective tailoring of the spatial sensitivity distribution [3] might minimize the size-dependence. In addition, non-visual input like wind could increase threshold for landing and by this way cancel the contribution of large-field movement from the front to the back which will be always present when the fly is cruising around. However, the fly does not calculate the time-to-collision, although this appears desirable from an engineering point of view. Obviously the landing problem for the fly is not to initiate landing at a constant time before it touches ground, but, simply, to land safely. The mechanism proposed by the integration model reliably fulfills this criterion.

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