Table 4. Offspring of XXY ♀♀ × + ♂♂
(see Fig. 2 and text)

	♂♂	♀♀
+ +	335	568
y w	25	-
w	1	-
y	1	-
	362	568

meiotic recombination between the two Y's can practically be excluded; it lies definitely under 2%.

The possibility of X–Y recombination in female meiosis has also been tested. The 362 male offspring of In(1)sc^{4L}sc^{8R},y sc^{4}sc^{8}w/In(1)sc^{4L} sc^{8R},y sc^{4}sc^{8}w/w$^+$Y y$^+$ ♀♀ × wild-type ♂♂ showed the expected genotypes (Fig. 2, Table 4) with the exception of two recombinants that, again, most probably result from exchange between one of the X's and a euchromatic section within the w$^+$Y y$^+$ chromosome.

Mitotic recombination has been induced by treating larvae 42–44 h after egg deposition with X-rays (100 kV, 8 mA, FD 10 cm, 1.7 mm Al-filter, exposure time 1.5 min, corresponding to 1480 ± 20 R); or with mitomycin C (1.5 ml 1.2 mM mitomycin C in 0.5% saccharose solution, 2.5 h feeding time). Three days after hatching adults were inspected for single and twin mosaic spots in their eyes. Control recombination frequencies depend upon the distance between centromere and marker, in our case almost the whole length of the X-chromosome; they lie below 0.5% [1]. On the y$^+$Y mal$^+$ chromosome see [7, 8], on zeste see [4].
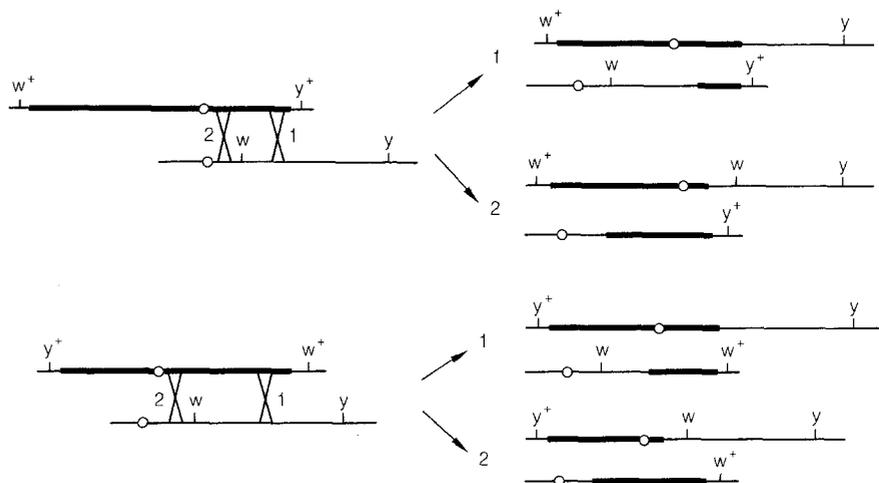

Fig. 2. Possible recombinations between X and Y in XXY females. Only the partner X of Y is shown; for X-constitution see text

In summary: The heterochromatin of the *Drosophila* Y-chromosome does not appear to engage in any recombination event, neither spontaneous nor X-ray- or mitomycin-induced, neither mitotic nor meiotic, neither in females nor in males, neither with X nor with Y as potential partner. Thereby it differs markedly from X-heterochromatin in which mitotic recombination takes place quite frequently.

This complete recombination incapability of Y-heterochromatin probably goes along with – or may be the source of – the genetic deterioration of the Y during its evolution where, from the very day of its origin, it remains limited to one sex and therefore, never becomes disomic from that point on. The molecular difference between Y-heterochromatin, X-heterochromatin, and euchromatin, accounting for their difference in recombination capability, is not known. The analysis of and comparison with neo-Y's might be helpful.

1. Becker, H. J.: Z. Indukt. Abstamm. Vererb. *88*, 333 (1957)
2. Becker, H. J., in: The Genetics and Biology of Drosophila, Vol. 1c, p. 1019 (M. Ashburner, E. Novitsky, eds.). New York: Academic Press 1976
3. El Sayed, N.: Dissertation Univ. Assiut 1988
4. Gans, M.: Bull. Biol. France Belg., Suppl. *38*, 1 (1953)
5. v. Glasenapp, R.: Diplomarbeit Universität München 1975
6. Haendle, J.: Mutat. Res. *62*, 467 (1979)
7. Schalet, A.: Chromosoma *44*, 183 (1973)
8. Schalet, A.: Drosophila Info. Serv. *38*, 82 (1976)

Retinal Image Size Triggers Obstacle Avoidance in Flying Locusts

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Negotiating a complex 3-dimensional world at speed, efficiently, and without injury requires animals to have sensorimotor strategies that optimize the timing of locomotor maneuvers. In several instances it has been demonstrated that a successful strategy is to extract information from the optic flow field on the time remaining before the animal intercepts potential hazards in its environment.

Locusts flying in swarms successfully avoid collision with neighbors flying in different directions, often when there is very little time in which to maneuver. We have found that locusts avoiding simulated head-on collisions with obstacles in the flight path do not react at constant times before collision. Rather they appear to use the simpler strategy of initiating avoidance when obstacles subtend more than a certain angle in their fields of view.

The ability to determine when objects looming out of the distance will collide with an observer is of critical importance

whether the observer is stationary or in motion. With such information it is possible to prepare for the intercept or to take evasive action while time permits. Information on time to collision can be extracted from the expanding image of approaching objects even in the monocular optic flow field (at constant closing velocities the optical parameter τ specifies time-to-contact) [1]. There is evidence in various organisms [2, 3] that critical locomotor behaviors are executed at relatively constant times before collision, supporting the notion that τ, or its inverse (relative retinal expansion velocity), is being extracted and used to control timing of action. In particular, the nucleus rotundus of the pigeon's brain has been found to contain neurons that signal time-to-collision and it has been suggested that such neurons may initiate and control avoidance behavior [4]. However, evasive behavior does not always occur at a constant time-to-collision [5], and different detection strategies may underlie such behaviors.

A locust flying at around 3 m/s in a swarm with neighbors flying in different directions as little as 30 cm distant [6] is presented with a motor control problem of considerable urgency. The locust is flying in a space occupied with numerous potential obstacles moving at different relative speeds and directions. Even under such conditions locusts apparently do not collide with each other [7], indicating a robust and successful sensorimotor strategy for avoidance. Locusts will perform avoidance maneuvers to looming stimuli presented when they are tethered in a wind tunnel [8]. We have tested the idea that such maneuvers occur at a constant time-to-collision by timing their reactions when presented with obstacles of different sizes and different approach velocities.

Twenty adult female locusts, *Locusta migratoria*, were tethered with a rod waxed to their pronota and flown in an exhaust wind tunnel (20 cm² cross section, laminar wind speed 3 m/s) with a clear view out of the mouth of the tunnel. Each locust was flown for at least 15 min before an experiment started and sustained flight for the 2–4 h duration of an experiment. In order to simulate obstacles approaching in the flight path, targets were transported along a 2-m straight track that was aligned either directly down the sagittal midline of the locust, or parallel to the midline but

offset by 2 cm to the right or left. Progress of the target was monitored with three photosensors situated at different distances along the track. The targets were squares of cardboard covered with a spatially random pattern of uniform black and white pixels (pixel size 1 cm × 1 cm). Targets approached against a background covered with the same pixel pattern. For ten animals the size of the target was varied (5 × 5, 7 × 7, 9 × 9, 11 × 11 cm²; approach velocity constant at 2 m/s), and for the remaining ten the speed of approach was varied (1, 2, 3, 4 m/s; target size constant at 7 × 7 cm²). Each animal was presented with an approaching target nine times (thrice each down the midline or offset to right and left) with each of the different target characteristics (four different size *or* four different speeds). Thus, each animal received 36 presentations of a target. The total dataset for the 20 animals included 720 runs of a target to a locust. Presentations were separated by a least 2 min. Comparison with the results from counterbalanced trials in a separate group of animals showed that presentation order had no effect on the timing of the reactions. Presentation order was with increasing size (reaction times get shorter) or with increasing speed (reaction times get longer) in individual experiments. The wind tunnel was L-shaped allowing reactions of the animals to be videotaped from directly behind. The videotape of each of the 720 runs was analyzed frame-by-frame with a resolution of 60 frames/s (16.67 ms between frames) using PEAK Performance motion analysis software. The analysis started from the first photosensor (126 cm from the locust's head) and stopped when the target halted in the mouth of the tunnel (5 cm from the locust's head). Initial analysis showed that the transport mechanism was unreliable when speeds of 4 m/s were intended and these 90 runs were discarded.

When locusts are presented with targets as described above, they usually react by attempting to steer around the target using substantial forewing asymmetries and lateral deflections of the abdomen and the hindlegs [8]. Control experiments and consideration of the wind flow conditions at the time of reaction have demonstrated unequivocally that this behavior is visually induced and cannot be due to perception of turbulence created by the target [8]. The first indica-

tion that the locust has seen and is avoiding the simulated obstacle is an abrupt upward movement of the abdomen [8]. A full behavioral analysis of the dataset described above will be published elsewhere. Here, we are concerned with the timing of the avoidance maneuver which we measured as the time at which the abdomen started to move vertically. Using this measure, we calculated the following parameters at the time of reaction: distance from the head; time to collision; visual angle subtended by the edges of the target; angular velocity; angular acceleration; and relative retinal expansion velocity. We were particularly interested in time to collision and our results show that time to collision at the time of reaction was not constant (Fig. 1). The only other parameter that
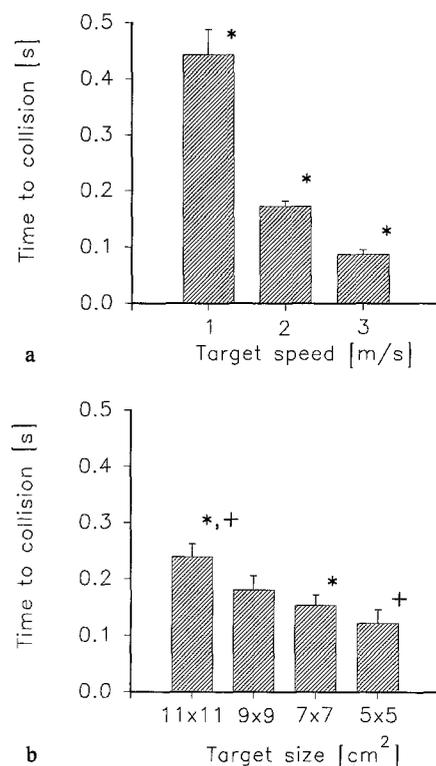

Fig. 1. At the time of the avoidance reaction, the time to collision was not constant either when approach velocity varied (a), or when the size of the target varied (b). In this and the following two figures each column and bar represents the mean and standard error of 90 runs (9 runs towards each of 10 animals). *Asterisks* and *crosses* indicate significant differences ($P < 0.05$) between the relevant columns, whereas a *bar* above columns indicates a lack of statistical difference between them. Significance was tested using t-tests of the difference between two columns and zero. P values were corrected using a sequential Bonferroni procedure [10] for multiple comparisons
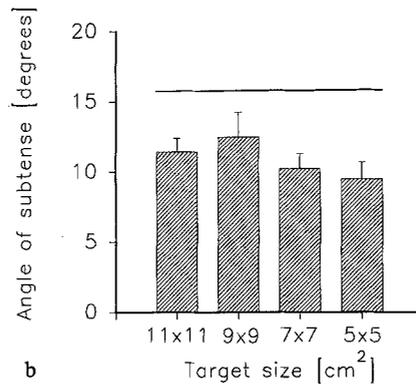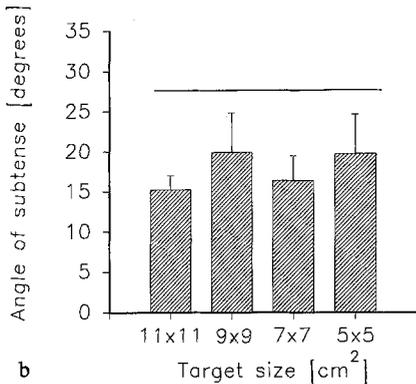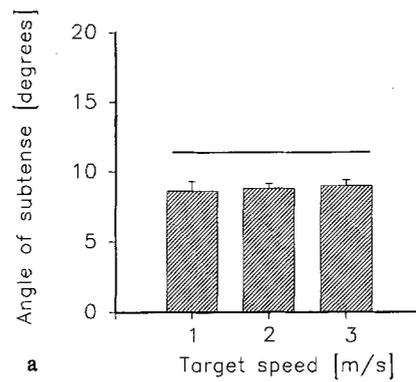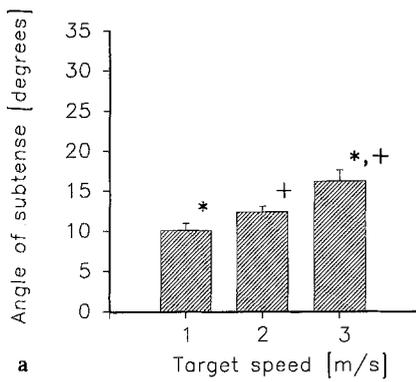
Fig. 2. At the time of the avoidance reaction, the angle the target subtended in the visual field was not constant when the target speed varied (a) but was constant when the size of the target varied (b)

Fig. 3. At an assumed time of detection (65 ms before the time of the avoidance reaction), the angle the target subtended in the visual field was constant both when the approach velocity varied (a) and when the size of the target varied (b). Although the means of the columns in (a) are slightly larger than the means of the columns in (b), there is no significant difference between the columns in (a) and (b). Note that the 2-m/s column in (a) and the 7 × 7 cm² column in (b) have the same experimental conditions of approach velocity and target size and the insignificant difference between the means must represent differences in the two groups of animals or other undetected differences in experimental conditions

showed some measure of constancy at reaction was the angle subtended by the target. This was constant for the runs in which target size was varied but not for those in which target approach velocity was varied (Fig. 2). However, whereas time to collision may be a parameter particularly significant at the time of *reaction*, angle of subtense is likely to be more significant at the time of *detection*. Between detection of the image as a hazard and the behavioral reaction to avoid there will be an inevitable delay imposed by neural processing. Such a delay would have equal effects on the parameters measured for the runs with variably sized targets approaching at a constant velocity, but would have markedly different effects on the same parameters when the approach velocity is varied (slower targets travel shorter distances in the same delay). We recalculated the parameters listed above at a projected time of detection assuming a processing delay of 65 ms such as has been described for auditorily evoked avoidance steering

and visually evoked correctional steering during locust flight [9]. When this is done, only the angle of subtense of the target at an assumed time of detection was found to be constant for size and speed variations of the target (Fig. 3). Indeed, there was no significant difference in image size at an assumed time of detection between the animals receiving variations in target size and those receiving variations in approach velocity. We conclude that in this experimental situation, which simulates collision avoidance during flight, locusts do not react at a constant time to collision. Rather it appears as if they initiate avoidance

when the obstacle in the flight path exceeds a retinal image size of around 10 °. This sensorimotor strategy is simple but simplicity is desirable when speed of reaction is to be optimized rather than precise timing.

Studies in other species have shown reactions at constant times to collision but these may reflect a different behavioral goal. For example, in studies of diving gannets and landing flies [2, 3], intercept with the obstacle/target is desired and timing of locomotor behavior according to a projected time of intercept would be eminently appropriate. In the case of the locust, and that of escaping flies [5], only collision avoidance is required and an intercept is highly undesirable. Given this one might predict that the neurons signaling time to collision in the pigeon brain [4] will be found to be involved in controlling landing or similar behavior rather than escaping looming predators during flight.

1. Lee, D. N.: Phil. Trans. R. Soc. Lond. [Biol.] 290, 169 (1980)
2. Lee, D. N. Reddish, P. E.: Nature 293, 293 (1981)
3. Wagner, H.: ibid. 297, 147 (1982)
4. Wang, Y., Frost, B. J.: ibid. 356, 236 (1992)
5. Holmqvist, M. H., Srinivasan, M. V.: J. Comp. Physiol. 169, 451 (1991)
6. Waloff, Z.: Bull. ent. Res. 62, 1 (1972)
7. Uvarov, B.: Grasshoppers and Locusts, Vol. 2 (1977)
8. Robertson, R. M., Reye, D. N.: J. Exp. Biol. 163, 231 (1992)
9. Robert, D., Rowell, C. H. F.: J. Comp. Physiol. 171, 53 (1992)
10. Rice, W. R.: Evolution 43, 223 (1989)