Courtship-Like Tracking Behaviour in Wild-Type Female *Drosophila melanogaster*

Robert Cook

Max-Planck-Institut für biologische Kybernetik, Spemannstr. 38, D-7400 Tübingen

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Both male and female *Drosophila melanogaster* possess systems which enable them to track other walking flies visually. Males use this system predominantly in courtship; females, when of sufficient age but still unmated, have been observed to track other flies, at rates of up to 18 bouts per hour. This behaviour is most conveniently studied in groups of females. Although similar to the courtship tracking of males, female/female tracking lacks the "circling" component of courtship. The data suggest a functional relationship of female/female tracking to reproductive behaviour, although none has yet been identified. Bouts of tracking by females are most frequently terminated by the following female, especially when the target female remains motionless. Comparison of the tracking parameters of males and females has revealed differences in the velocity and pathlength of tracking bouts, and in the position of the fly with respect to the target. Males of Canton and Kapelle strains differ in the translatory component of their courtship tracking, but such a difference was not evident between females of these strains. Furthermore, tracking females do not allow their distance to the target to rise to that permissible in males, which suggests some sex-specificity in a part of the control system for tracking.

Introduction

The courtship of females by male *D. melanogaster* involves a tracking system which is largely dependent for its control inputs on the male's visual system [1, 2]. Although it is easier to study such tracking behaviour in males, since it is so readily evoked as part of courtship behaviour, it is not confined to this sex. As is clear from studies of the optomotor and fixation behaviour [3–6] of female, as well as male flies, visual object tracking is a property of both sexes. Such behaviour is important to both sexes for general environmental manoeuvres and course control, but can a more specific role for tracking in females be found? Female *D. melanogaster* do engage in chasing interactions with one another that could involve visual tracking behaviour, and a preliminary description is given by Cook [7]. The function of these chases is not yet fully clear; the interpretation that they reflect an "abnormal" manifestation of male courtship behaviour must be abandoned since the behaviour is seen readily in most wild-type strains. Rather it appears to be a "normal" social interaction among females, and thus probably has a distinct biological function.

The present report aims to describe the tracking behaviour involved, compare it briefly with that of males, and hint as to its possible function.

Experimental Methods

All flies were collected with cold anaesthesia. They were chilled to ca. 5 °C, before sorting on an aluminium plate at this temperature. Females were set in groups (usually of 10) in perspex vials of 33.5 mm internal diameter. The vials were 30 mm deep and contained standard yeasted medium up to 5 mm from the top. A clear plexiglass cover enabled the filming (8 f. p. s.) of behaviour on the surface of the food medium, at a luminance of 200 cd/m².

For some experiments the flies were marked individually to identify different experimental groups or individuals. Water soluble casein based paint of different colours (Pelikan/Plaka) was applied to the notum with a fine needle.

The study concentrated on females from two wild-type strains, Canton and Kapelle. The tracking behaviour of males has been found to differ between these strains [1, 2], so corresponding differences may be sought among the females.

Records were also made of the courtship behaviour of five free pairs from each strain, at the same frame rate (8 f. p. s.). The data were obtained with a Z-80 microprocessor system with video digitisation capability (Tecmar Inc., Cleveland, Ohio), which was programmed to track two *Drosophila* in real time, and store their contours for subsequent analysis. Once the axes of the flies had been calculated the data were input to the same programs as used for digitised filmed records. The flies were

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Reprint requests to Dr. R. Cook.

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illuminated from below to provide good contrast, with a luminance in the cell of 200 cd/m^2. The fly chamber was 30 mm diameter × 1 mm deep, with bevelled sides and perspex top. In such a cell courtship occurs normally apart from the absence of both attempted and actual copulation. Courtship of males to receptive females may thus be measured almost indefinitely. A small sample of courtship by Canton and Kapelle was also collected with the filming technique used for the females, as a check on the comparability of the results from the video system. The pooled results are presented at the relevant places for comparison.

Results

Functional aspects of female-female chasing

In observing this behaviour great care must be taken not disturb the flies mechanically or visually. Females can become refractory for chasing for an hour or more after being disturbed. Their age is also an important factor, and courtship-like chasing behaviour has never been observed in females under three days old, and usually at not less than five days. Kapelle females chase less frequently than Canton.

Non-chasing females clearly avoid other females when near them – they thus detect them, and respond with course control which avoids collision. Chased females even when virgin, often respond with extrusion of the genitalia (see Connolly and Cook [8], Cook [7].

There are several problems in obtained meaningful quantitative measures of rates of this behaviour, the most important being the fact that this is a social phenomenon. Chasing tends to elicit chasing, leading to periods when several flies engage in repeated interactions with one another. Under these conditions rates of chasing of 18 bouts per hour or more may be observed. Consequently it is dangerous to make comparisons between frequencies counted at different times or even at the same time in different cells. All the figures given here are based on experiments where different conditions were observed strictly simultaneously, and are thus at least nominally comparable.

Is chasing coupled to reproductive physiology?

Is the reproductive state of the female a determinant of chasing behaviour? Canton females were kept on normal medium for eight days from eclosion, then half were allowed to mate with Berlin males. The flies were then marked with black or white paint to enable the distinction of the reproductive state of the female. They were then placed into observation cells with food medium, mixing five virgins with five mated females per cell. The colour code was reversed for four of the nine cells set up to control for possible effects of the colours themselves. The cells were then observed for ca. 1 h at dusk on the subsequent six evenings. Of 138 chases observed, 121 were by virgins, and 17 by mated females ($p < 0.001$). The type of female chased was however distributed randomly, 68 chases being directed to virgins, and 70 to mated females. A replication for Canton, making observations on the first day after mating alone, yielded 113 chases by the virgins and none by the mated females. In the same test with 60 eight day old Kapelle females only 39 chases were recorded, all by virgin females. Females are thus strongly inhibited from initiating chases once mated, even when chased by other females.

It is not easy to interpret this result: behaviour could be changed directly by stimuli resulting from mating, or simply be inhibited by the switching on of other behaviours such as egg laying and intensive feeding. Keeping females on a protein-free diet could test this hypothesis, since such females mature very few eggs [9, 10]. However, 140 females kept from eclosion on 0.2 M glucose medium showed no chasing interaction at all, whether virgin or mated. Furthermore, virgins maintained on normal medium and then transferred to glucose only showed chasing for 1 day following the transfer. Conversely, 42 Canton females kept from eclosion on glucose and transferred to normal medium in groups of 7 on day 6 first displayed chasing behaviour on day 10, continuing subsequently at approximately "normal" levels. This dietary effect may be a trivial one: on the other hand it may reflect a further coupling of the tendency to chase with the female's reproductive biology.

Functional relationship to mating?

In experiments with marked virgin females a male may be introduced, with the minimum of disturbance to the females, to assess the possible role of virgin female chasing behaviour in the acquisition of a mate. In the tests performed thus far (12 cells of 7 females) the mean number of bouts of chasing observed for the first three females mated by the male does not depart from the expectation for random sampling of the females (mean = 3.5 ± 0.8 bouts, *cf.* 4.1 ± 0.54 bouts overall). A clear conclusion from these tests is that females showing high rates of chasing are nonetheless receptive to males, as implied by the crosses made previously (Cook [7]), although quantitative tests of receptivity have not been made. Three further points were noted in these tests: First, that the presence of a courting male does not inhibit female chasing. Females have been observed to chase another female whilst being courted themselves. Second, females have been observed to a), turn round upon and chase a courting male, and b), approach and chase a male (see also next paragraph). Thirdly, it was confirmed that chasing is rapidly inhibited by mating.

In a further test, the question was addressed whether females only chase other females, or whether males are also sufficient stimuli to elicit this behaviour. Since the presence of normal males hinders the assessment of female initiated interactions, decapitated flies were used. Equal numbers of decapitated virgin fermales and males were placed at random in observation cells with 11 day old intact Kapelle or Canton females, and chasing attempts by the latter subsequently recorded. Amongst 33 Kapelle females, 20 interactions were seen to the decapitated females and 12 to the males (N. S.). For 50 Canton females 52 interactions were observed to decapitated females and 17 to decapitated males ($p < 0.001$). Thus there seems to be some evidence that females discriminate the sex of the fly chased, and do so preferentially to females. However, the decapitated females are considerably larger than the males, and might thus simply present a more conspicuous target if the behaviour is visually controlled. Indeed, tests with *sine oculis* selected for total absence of ommatidia, no chasing behaviour was seen. Likewise, chasing behaviour has not been observed when normal females were illuminated with red light beyond the fly's spectral sensitivity, indicating the importance of visual control for this behaviour. However, no clear functional relationship of chasing behaviour to mating has emerged from these tests (see discussion for limitations of the method).

Translation control in tracking

The general properties of tracking bouts by Canton and Kapelle females are summarised in

Table I. Tracking bouts by male and female *D. melanogaster.* As described in the text, technical differences in the recording method are controlled for by the pooled sample of Canton and Kapelle males (last line).

Strain	Sex		No. of seqs.	Total time [s]	Mean pathl. of chased fly [mm]	Mean Seq., duration [s]	Mean velocity of chased fly [mm s⁻¹]	k (s⁻¹)		Mean D (tail-to-head) [mm]	Mean abs. ang. vel. of target [deg. s⁻¹]
	Chaser	Chased							95% C.I.		
Kapelle	♀	♀	46	428	22 ± 2	9.3 ± 1.4	2.7 ± 0.1	20	16.5 – 22.5	1.27 ± 0.01	134 ± 3
Kapelle	♂	♀	19	211	85 ± 21	11.1 ± 2.5 [a]	7.6 ± 0.1	9	8.3 – 10.1	1.72 ± 0.03	97 ± 3
Canton	♀	♀	49	564	26 ± 4	11.5 ± 1.3	2.3 ± 0.0	23	18.5 – 29.9	1.12 ± 0.01	154 ± 3
Canton	♂	♀	27	246	47 ± 13	9.1 ± 1.7 [a]	7.5 ± 0.1	5	4.0 – 5.4	2.85 ± 0.08	106 ± 4
Canton + Kapelle	♂ [c]	♂	14	105	77 ± 13	7.5 ± 1.2 [b]	12.8 ± 0.1	13	10.3 – 16.0	1.72 ± 0.04	113 ± 5

[a] Sequences shortened for technical reasons.

[b] Sequences shortened because flies climbed onto side of chamber.

[c] 6 sequences of Canton and 8 of Kapelle combined. Individual gains not sig. diff. ($k = 14$ and 12 respectively).

Table I. All sequences of female/female behaviour in this analysis are complete, that is they are entire records from the inception of chasing to its termination. Data on free male/female courtship of these strains is also given, but here the sequences are not all complete. For technical reasons the records were sometimes interrupted, leading to shorter bout lengths. These data are nonetheless presented for comparison since they only reduce the differences between males and females in tracking seen in Table I. They also confirm the strain differences in gain found by Cook [1] between Canton and Kapelle males tracking females moved at controlled velocities.

There is a conspicuous difference in the mean velocity of females courted by males and chased by females, making general comparison of the conditions difficult.

The considerably shorter mean pathlengths for females tracked by females can hardly be accounted for by velocity limitations in the chasing females, but by differences of sensory control or strategy. Tracking bouts by females are slow and strictly limited in duration. Those of males are fast and may be of almost unlimited duration, under the constraints of the present experiment.

In spite of the differences in mean velocity the distributions do overlap entirely (Fig. 1 a). In Fig. 1 b are shown the distance/velocity relationships for these flies, including also a small sample of male courtship tracking (Canton and Kapelle males pooled), filmed at 8 f. p. s. exactly as the females. The reciprocal of the slope of these curves gives the gain (k) (Table I) of the translatory component of tracking (see Cook [1]). The females have high gain compared to the males, and show no comparable strain difference. However, as noted by Cook [2], gains can not be compared without consideration of the velocity distributions on which they are based, and high gain can simply reflect a cut-off in the system, where tracking stops when a certain velocity or distance is exceeded. This can in turn be related to the operative ranges of different sensory modalities. In this case the gain values of the females are influenced by the highly reliable data points at low velocity. If the region from 11−17 mm s^{-1} is considered alone the gain falls to 6.67 s^{-1}. This figure is still within the range found for normal males.

A complementary approach is to assess the distance maxima during ongoing tracking (*i. e.* not maxima at which tracking terminated). It is clear from observation that males can sometimes lag a female by 20 mm or more and then catch up without breaking off courtship. Females do not behave in this way. The mean maxima for head-to-tail distance in continuous tracking are given in Table II. They are significantly lower for both Canton and Kapelle females than their respective control males. Whereas this measure is also not fully independent of the velocity distribution of the tracked female (but males

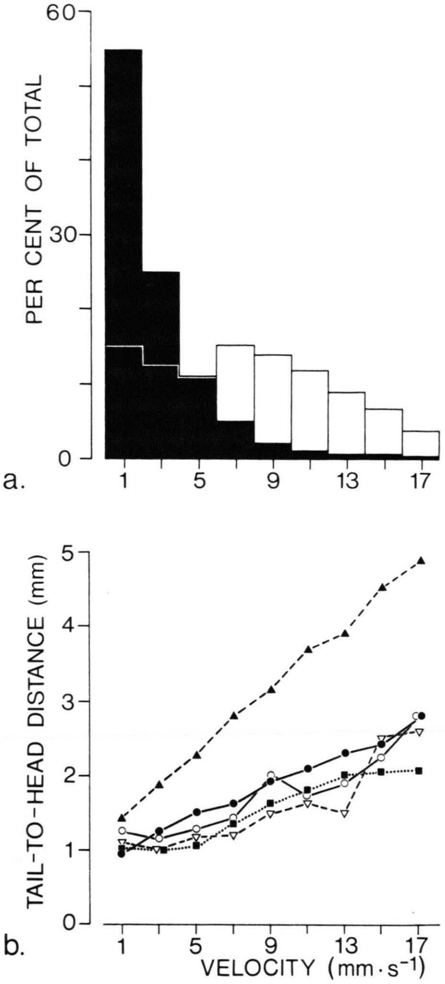


Fig. 1 a. Frequency distribution of velocity of chased female in chases by males and females. Black and white columns refer to females and males respectively. b. relationship of tail-to-head distance between flies to velocity of leading fly for tracking by females and males. Solid symbols refer to tracking by males, open symbols to that by females. Triangle = Canton, circles = Kapelle, and squares denote a small sample of Kapelle and Canton males, measured with the same technique as the females.

Table II. Mean maximum tail-to-head distance between flies per tracking sequence.

Strain	Sex		*N*	Mean max D [mm] ± SEM	
	Chaser	Chased			
Kapelle	♀	♀	46	2.8 ± 0.2	$t = 3.94$ d.f. $= 63$ $p < 0.002$
Kapelle	♂	♀	19	4.7 ± 0.6	
Canton	♀	♀	49	2.3 ± 0.2	$t = 3.16$ d.f. $= 74$ $p < 0.01$
Canton	♂	♀	27	4.9 ± 1.0	

can show high distance peaks with slowly moving females) it is an indication that large fluctuations in distance are not permissible in females.

It is somewhat difficult to assess the causality of breaks in tracking by females, to determine whether they are "intentional" or due to limitations of sensory input. Males with reduced visual input make movements interpreted as searching behaviour (see Cook [2] and refs. therein). Normal males in light sometimes turn away from courted females, or are "distracted" by other objects. Females make no such searching movements on termination of chasing, but they often turn away apparently spontaneously. The termination of chasing was observed for 100 filmed cases where this could be observed clearly (pair stayed on food medium and was not disturbed by other flies). Four categories best described this, three of which are due to the behaviour of the female chased, the other to that of the chaser. They are defined as follows, together with the frequency of each:

1. Decamping (9): The chased female flies or jumps away.
2. Distance loss (21): The chasing female ceases to follow the target female during straight chase.
3. Angular loss (8): The chasing female to follow the target female during rotatory tracking
4. Turning away (62): The chasing female herself turns away for no apparent reason.

From these data it may thus be concluded that chases are broken largely by the chasing female, rather than by limitations of sensory control. It was noticed however that turning away mainly occurs when the chased female is motionless or nearly so. Thus movement of the target fly may help to maintain this tracking behaviour. On finer analysis of these phenomena it could transpire that such behaviour reflects the outcome of "contests" between the females, with females which stand their ground through chasing until the chaser ceases being the "winners", and those which run until no longer chased the "losers".

Control of position around the female

Female/female tracking behaviour is distinguishable from male courtship by its distribution around the female, especially at low velocities. Under these conditions, males make circling movements around the female, (see Cook [1], Figs. 2a and b). Such movements are absent in female chasing behaviour. The positioning of the male with respect to the female is shown for these experiments in Fig. 2. The data were classified, on the basis of the velocity of the target female, into the categories 0–1 mm s^{-1} and 6–17 mm s^{-1} inclusive. In contrast to males, females do not position themselves by the head of the target female, even at low velocities of 0–1 mm s^{-1}. However, neither do they orientate so directly behind the female as do males especially at low velocity (the distributions for females at 0–1 mm s^{-1} are significantly different from the corresponding distributions for males ($p < 0.001$)). Indeed, in Canton a clear bimodality is seen, with peaks at > ± 30 deg from the midline behind the female. For Kapelle females the spread at ± 90 deg of the midline is clearly greater than that for males. In all cases there is a velocity effect which aligns the following fly more directly behind the target female (distributions for females differ significantly between 0–1 mm s^{-1} and 6–17 mm s^{-1}, $p < 0.001$).

Control of angular tracking

Implicit in the results presented in the previous section is the expectation that females do not orientate so precisely to the target female's genitalia as males. That this is the case may be seen in the upper portion of Fig. 3, showing histograms of the error

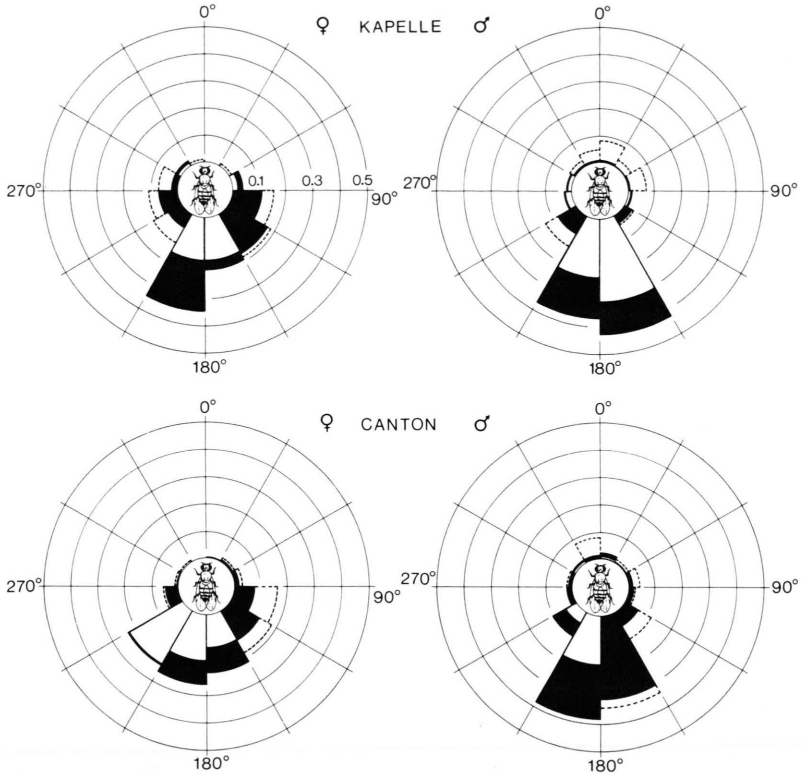
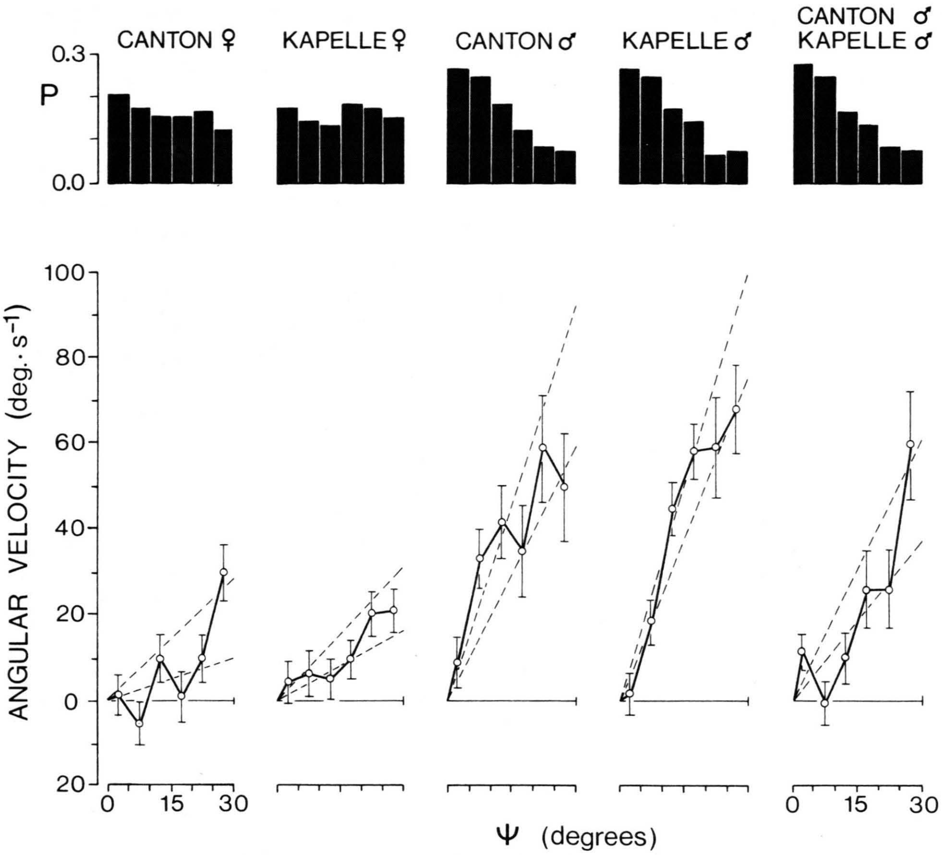


Fig. 2. Circular histograms showing the positioning of females and males around the target female, considering also velocity and strain. The radial axis is proportion of total frames in sample. Black segments refer to target female velocity of 6–17 mm s^{-1}, and white segments to the range 0–1 mm s^{-1}. Moving radially from the centre the first shade encountered (black/white) corresponds to the lower of the two proportions for that segment.

angles (ψ), measured as the angular deviation of the following fly's body axis from the target female's genitalia. In view of the different velocity distributions for female chasing and male courtship, the low velocities (0–1 mm s^{-1}) were excluded from the analysis. This means at least that the records are not confounded by stationary targets, where all the variation in error angle is determined by the tracking individual, and not by the angular velocity of the target. In the lower part of this figure is shown the turning speed of the fly as a function of error angle to the target (the angular tracking function). This is identical with the functions given by Cook [2], and analogous to the D (ψ) of Reichardt and Poggio [11], the turning tendency function of Horn [12], and error angle/angular velocity functions shown by Land and Collett [13] and Collett and Land [14]. These functions demonstrate a less rapid and more variable reduction of error angle by females. The lower mean translatory velocity for the case of chasing females does not lead to a correspondingly lower target angular velocity with respect to the following fly. In fact, the mean absolute target angular velocities for the females are higher than for the males (see Table I). This measure is independent of the following fly's turning response, but strongly dependent upon its position with respect to the fly being tracked. The more laterally distributed positioning of females (see previous section) thus probably explains the greater target angular velocity to which they are subjected. High angular velocity (100 deg s^{-1}) of a moving target with respect to a stationary walking fly leads in general to a similar flattening of the D (ψ) profile in open loop experiments [6]. Furthermore, the D (ψ) for males and females do not differ, at least in the lower part of the eye (Bülthoff, pers., comm.). It is thus most likely that the difference measured here reflects either the different angular velocity inputs or a difference in the motivation and function of tracking between males and females. Broadening of the subjective target alone could be expected to reduce the steepness of the angular tracking function, for example if the female were tracking the whole fly rather than the genitalia. Since the head was not immobilized in any of these experiments, the difference could also reflect the degree to which error angles are compensated by the head alone.



Firg. 3. The control of orientation in the tracking of males and females of the strains studied. Above are shown histograms of error angle (ψ) of the chasing to the target fly, taking the genitalia of the latter as the target. In the corresponding positions below are shown the mean (± SEM) angular velocity of turning of the chasing fly associated with each class of error angle. The broken lines show the 95% confidence intervals for the slope of the regression of angular velocity on ψ in each case. The diagrams demonstrate that females control their orientation less precisely than males, with consequently flatter error angle histograms. The right hand column refers to the small sample of Canton and Kapelle males measured with the same technique as the females.

Discussion

Contrary to previous suggestions [7] there is now no reason to view chasing behaviour by females as a mistake in wiring and/or triggering which releases male courtship behaviour, although the great similarities to courtship remain uncontested. In wild-type females, unlike the mutants studied previously [7], wing extension is rarely seen, reducing the similarity to male courtship.

The main hypotheses now held as to the function of chasing behaviour by females fall into two classes. In the first of these, chasing behaviour is seen as regulating socially relevant phenomena such as feeding and/or egglaying. It is similar in several respects to the "aggressive" behaviour described in males by Dow and Schilcher [15] and Skrzipek *et al.* [16]. The latter authors observed strain differences in the low rate of occurrence of "aggressive" behaviour, and that such encounters occur exclusively on food. Females have not been seen to engage in stand-up fights such as described for males, and it seems unnecessary to refer to their behaviour as "aggressive" without detailed knowledge of its function. By chasing other flies virgins may be dominating a food resource either for their immediate or future needs. However, such a suggestion raises the question of why chasing is not seen in young females, where competition for food resources could actually exclude some individuals from the maturation and deposition of eggs. In fact, chasing really begins once the females are old enough to be sexually receptive. Its disappearance with mating also points to sexual receptivity as a precondition for chasing, and seems to exclude the possibility that it is designed to reduce the density of eggs or avoid the mixing of different families. Indeed, it is a common observation that, at least in the laboratory, high densities of larvae improve feeding conditions by breaking up the medium.

The suggestion that chasing is related to sexual receptivity leads to the second hypothesis, that chasing enhances the female's chances of aquiring a mate. Two main possibilities pertain here. Females might increase the chance of mating by approaching and contacting other flies, which will often be males. Whereas this would surely be an effective method, it again seems unlikely considering the active mate seeking usually characteristic of *Drosophila* males. They will usually copulate 3 or 4 times in immediate succession if virgin females are available, although the later matings are less fertile [17]. This suggests that a better strategy for the female is not only to arouse a male to courtship (for example by the emission of pheromones [18–20]), but also to ensure that other females are not available for copulation. This could be achieved either spatially, by chasing females from the site at which a male is most likely to be found (food), or functionally, for example by engendering a short or long term reduction in the sexual receptivity of other females. The latter possibility is currently being tested since rather little is known about the effects of aberrant courtship stimuli on subsequent sexual receptivity. In this case the most obvious abberation for the target female is the lack of wing vibration, licking and circling. "Groping" with the forelegs [7] is supplementary to normal courtship. It is relevant to note that the target female's response to chasing is often extrusion, hitherto interpreted as a rejection response to courtship (see Connolly and Cook [8]). The orientation of the chasing female to the abdominal region is consistent with this view. Bastock and Manning [21] demonstrated that males inhibit each other from courtship by wing flicking, and it could be of similar adaptive advantage if females were to modulate each other's receptivity. This hypothesis is held in spite of the finding that females which chase frequently do not necessarily acquire a mate first. But this test is inadequate in at least three respects: First, the number of individuals may not be high enough to detect what may be a very small effect. Second, the spatial relationships between the flies are undoubtedly disturbed by the introduction of the male – a more refined method is necessary. Thirdly, the system is too closed: chased females may not readily leave the effective food site, leading to repeated contests which do not allow a natural resolution.

In summary, it can not yet be excluded that 1). female chasing is a response specific to other females and 2). it serves a function which increases the probability of mating, should a male become available.

Tracking parameters

Consideration of the tracking behaviour of females leads to the tentative conclusion that the system employed by females is not fundamentally different to that used by males in courtship. Nonetheless, a number of differences are evident which may be attributed either to motivational differences (function specific effects) or to limitations in the visual system of the females. Of these, the difference in positioning around the target female is likely to be a function specific effect. The lower mean maximum tracking distance on the other hand, with its tendency to increase apparent translation gain in tracking, may reflect additional inbuilt sex differences in the visual system. Experiments have already been reported [22] in which courtship tracking by bilateral gynandromorphs (mosaic boundary approximately at midline) was compared as a function of the sex of the eye (and putative sex of the visual system) that mediated it. The mean maximum tracking distance was lower for the female eyes in both gynandromorphs measured, although the gain was higher. This result is clearly consistent with the hypothesis of sex specific differences in the reception and/or processing of visual information. Wehrhahn [23] has already drawn this conclusion for *Musca domestica,* where there are clear sex differences in the external structure of the visual system. Female/female chases in *Musca* are also slower and under coarser angular control than those by males. The external eye of *D. melanogaster* shows no marked sex differences apart from in the number of ommatidia (fewer in males); but in retinal organisation differences have been reported (for *Drosophila*: Franceschini, pers. comm., for *Musca*: Franceschini *et al.* [24]). Sexual dimorphism for interneurons involved in visual information processing has also been reported for *Musca* (Hausen and Strausfeld [25]). It is possible, but not yet demonstrated, that corresponding differences occur in the visual system of *Drosophila.* If this is so it may provide an interesting opportunity to analyse the sex-specific portion of the visual system genetically; the difference in tracking behaviour between Canton and Kapelle males (Cook [1], and confirmed here for free flies) is not found between females of these strains: this difference may thus reside in the male-specific portion of the tracking system.

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