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# Flight Control in *Drosophila* by Visual Perception of Motion

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*Summary.* Apparent motion was simulated in the visual system of the tethered fruitfly *Drosophila melanogaster* by projecting moving stripe patterns onto stationary screens positioned in front of the lateral eye regions. The reactions of the animal were recorded under conditions of stationary flight in still air. It was found that visual stimulation modifies, independently, torque and thrust of the flight system. The responses appear suitable to counteract involuntary changes of direction and altitude in free flight.

Concerning the sensory system for visual flight control, the following was established:

1. Both eyes are functionally equal, and sensitive to pattern motion in any direction.
2. The motion detecting subunits possess a certain orientation on the eye surface, and discriminate between pattern motions that are progressive or regressive relative to this orientation.
3. Progressive and regressive stimuli elicit opposite responses in the flight system.
4. The subunit orientations are expected to group in at least two different directions that share a common line of symmetry with the internal eye structure.
5. A minimum of two contralateral and two ipsilateral nerve connections between the visual system and the motor system is required for the various torque and thrust responses.

Concerning the effect of pattern motion on the flight system, the following was found:

1. The motion detectors control only the magnitude of the force of flight. With the tethered animal in still air, the inclination of the force vector remains constant.
2. Consequently, the stroke plane and the wing pitch should be invariant to visual stimulation.
3. Possible influences of pattern motion on the wing-beat frequency were ruled out by frequency measurements.
4. The only major variables in wing articulation that respond to pattern motion are the wing-beat amplitudes on either side of the insect. In-flight photographs show that the difference and the sum of these amplitudes are, in fact, representative for the torque and the thrust of the flight system. The responses of the body posture may become important to flight performance at increased airspeed.

Comparative experiments with the housefly *Musca domestica* indicate that the principle of independent torque and thrust control by vision is adopted in at least two different species.

## *Introduction*

A common reflex in various insects is the tendency to follow the angular motion of visual objects within their visual field. This *optomotor response* may be regarded as part of the motion control system. Whenever the animal deviates from a straight course, its surroundings seem to rotate in the opposite direction. The tendency to turn with the surroundings may well compensate involuntary deviations from the previous course.

Quantitative studies on the relations between the visual *stimulus* and the optomotor *responses* in insects have contributed to the present knowledge of:

1. The factors that determine resolution and acuity of the compound eye.
2. The "one-quantum" effect in photoreceptors, and
3. The properties of nervous networks that enable the detection and integration of displacements in the brightness distribution of the surroundings.

The studies include investigations on the beetles *Chlorophanus* (Hassenstein, 1966; Reichardt, 1961; Varjú and Reichardt, 1967), *Lixus* (Bliss, 1963), and *Zophobas* (Wilson and Hoy, 1968), the bug *Oncopeltus* (ibid.), the bee *Apis* (Kunze, 1961), the grasshopper *Locusta* (Horridge, 1966; Palka, 1965; Thorson, 1966) the praying *Mantis* (Maynard and Howland, 1965), the dronefly *Eristalis* (Mittelstaedt, 1951), the blowfly *Calliphora* (G. Schneider, 1956; Burkhardt and Kaiser, 1968), the housefly *Musca* (Fermi and Reichardt, 1963; Reichardt, 1965; McCann and MacGinitie, 1965; v. Braitenberg and Taddei Ferretti, 1966; Reichardt, v. Braitenberg and Weidel, 1968), and the normal and mutant eyed fruitfly *Drosophila* (Götz, 1964—1965; Hengstenberg and Götz, 1967). The more recent references may be used to find important details in previous papers, as well as the related work of other authors. The work on the optomotor behavior of other compound-eyed animals, e.g. crabs (Kunze, 1964; Horridge and Sandeman, 1964; Shepheard, 1966; v. Campenhausen, 1967) is of special interest.

The present paper is mainly concerned with:

1. The information that originates from the nervous subsystems for the visual perception of motion.
2. The conveyance of this information to the flight-control system, and
3. The origin of torque, and the relations between torque and thrust in the fruitfly *Drosophila.*

## *Method*

The essentials of the technique for the stimulus-response analysis under "open-loop" conditions are outlined in Fig. 1a. The animal is mounted to a measuring device that is rigid enough to prevent changes of its orientation and position during the experiment. The *torque* around the vertical axis of the fixed flying insect is representative for the attempt to turn. Suitable torque recording devices have repeatedly been described in the literature. The comparatively weak reactions of the fruitfly *Drosophila melanogaster* require special instrumentation (Götz, 1964).

A specified stimulus may be generated by a periodic sequence of bright and dark stripes rotating (or oscillating) around the animal. In the present case the usual "striped drum" is replaced by a pair of independently controlled projectors. Each of the projectors is capable to generate continuous stripe motion on a translucent screen in the visual domain of only one eye. The arrows on the screens in Fig. 1a indicate actual directions of stripe motion. The pattern on the left screen is *progressing* from the frontal hemisphere, and the pattern on the right screen is *regressing* to the frontal hemisphere of the fly. A switchboard allows one to reverse or to stop the motion of the periodic pattern on either side.

The *spacial period* of the precision stripe patterns was about 48° throughout the following experiments. This value exceeds by far the 9.2° limit for the spacial resolution in the visual system of *Drosophila* as determined in earlier work. (An inversion of the apparent motion may, for instance, be encountered below this limit!). Furthermore the contrast of the selected 48°-pattern is almost completely transferred by the visual elements of the *Drosophila* compound eye. According to the size of their visual fields the losses are expected to be considerably below $10^{-3}$ (Götz, *loc. cit.*). This condition prevents the misleading effect of transfer increments in the visual elements that are directed toward the stripe-parallel edges of the screens (Palka, 1965). The *temporal period* of the stripe-pattern was 1 sec. This is about the optimum within the extended range of temporal resolution in the visual system of *Drosophila*. The average *luminance* of the screens was 12 cd/m$^2$ with an angular distribution approximating Lambert's law, and with a spectral composition corresponding to a color temperature of about 2,300° K. The contrast of the adjacent stripes was approximately 0.75. The stimulated area in the lateral part of an eye comprised always about 42% of the total eye surface, or roughly 300 out of 700 ommatidia. The stimulus is sufficient to elicit optomotor reactions, for instance in the female wild type of *Drosophila melanogaster* that was used in the present work. Head-to-thorax fixation has been applied in order to prevent spontaneous eye movements. The mounting technique is described in earlier work. Unless otherwise stated the room temperature was about 20° C.

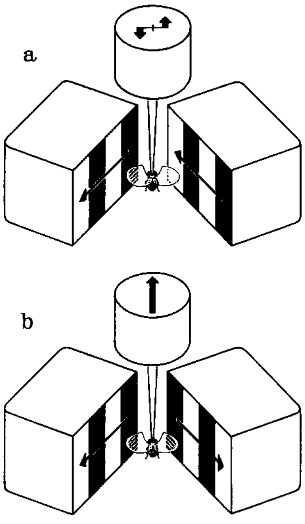

Fig. 1. Experimental arrangement with the flying *Drosophila* arbitrarely mounted to a *torque* meter (a), and to a *thrust* meter (b). The fly is confronted to the continuous stripe motion on the translucent screens of two stationary projectors. The arrows on the screens indicate actual directions of pattern motion. The force vectors on top of the measuring devices illustrate the belonging torque and thrust components of the tethered flight system. The counterclockwise stimulus motion in the situation (a) elicits, for instance, the expected counterclockwise torque: The animal tries to follow the angular motion of the stripes

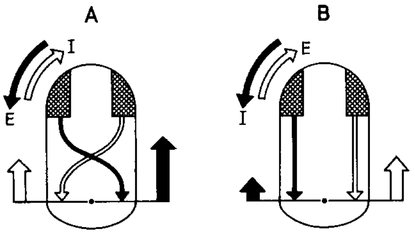

Fig. 2. Two functionally equivalent models for the description of the optomotor *torque* responses of the fruitfly *Drosophila*. Stimulus motion, for instance from the frontal to the lateral region of the left eye (curved black arrows) excites (*E*) in model ***A*** the contralateral part of the flight system, or inhibits (*I*) in Model ***B*** the ipsilateral part of the flight system. (The resulting thrust components are represented by the straight black arrows at the end of the baselines.) Unbalance of the thrust components on either side of the fly induces in both cases torque responses of the appropriate sign and magnitude. Note, however, the increased total thrust of the stimulated type-***A*** insect, and the decreased total thrust of the stimulated type-***B*** insect

The already mentioned correspondence between the directions of the stimulus and the response has been confirmed in numerous experiments with *Drosophila* (*loc. cit.*). Fig. 1a illustrates the response to counterclockwise stimulation. The torque evoked from the fixed flying animal is indicated by the pair of forces on top of the torque meter. The direction of the torque is positive in the mathematical sense and coincides with the positive direction of the pattern motion around the animal.

### *Neural Models*

The simplest structure of the various hypothetical nerve nets that are compatible with the previous observations, is represented by the two functionally equivalent models ***A*** and ***B*** in Fig. 2. The models illustrate the different organization of the flight control system in a schematic insect. The curved arrows at the periphery of the left eye indicate unilateral stimulation by progressive (black arrow) or regressive (white arrow) motion. The thrust of the motor system on either side of an insect is represented by the length and direction of the straight arrow at the right and left end of the baseline. Torque results from the unbalance of the two thrust components.

The action of the two models may be exemplified by the *black arrows* in Fig. 2. Progressive motion, presented to one eye, generates the appropriate torque either by excitation (*E*) of the *contralateral* motor system (model ***A***), or by inhibition (*I*) of the *ipsilateral* motor system (model ***B***). The efficiency of a pattern depends quantitatively on the strength of the visual stimulus, but qualitatively on the direction of motion. It is assumed that excitation is simply replaced by inhibition, and *vice versa*, as soon as the direction of motion is reversed. However under natural stimulation, in the usual striped-drum experiments, and in the situation of Fig. 1a there is almost always progressive motion on one side presented in combination with regressive motion on the other side. Hence it may be sufficient for the generation of the appropriate torque response if only progressive *or* regressive motion is monitored by the two sides of the bilateral visual system.

### *Torque*

Quantitative studies of the torque under selected conditions of unilateral and bilateral stimulation should allow one to decide whether the two sides of the visual system are equally and exclusively sensitive, either to the progressive components, or to the regressive components, or to the progressive *and* regressive components of the stimulus.

These and subsequent investigations have been performed at different values of the angle $\sphericalangle$**MA** that is defined in Fig. 3 as the vertical inclination of the line of pattern motion **M** relative to the animal's long axis **A**. The arrows and bars heading the columns of Fig. 4, 5, 12 and 13 denote 6 out of $3^2=9$ possible combinations of progressive (↓), regressive (↑), and missing (|) pattern motion on the two screens on either side of the insect in Fig. 1.

The results in Fig. 4 have been averaged from a total of 348 two-minute torque recordings with 8 flies. The first column at the left refers to the experimental situation of Fig. 1a. Bilateral application of a *counterclockwise* stimulus causes positive torque unless the line of motion is perpendicular to the animal's long axis ($\sphericalangle \mathbf{MA} = \pm 90°$). The two subsequent columns, however, show that the progressive as well as the regressive component of the counterclockwise stimulus are independently capable of inducing positive torque reactions. (The corresponding experiments with *clockwise* stimulation result in negative torque reactions of the same order.) The pronounced *non-additivity* of the torque controlling components was expected from the previous observation (*loc. cit.*) that the steady-state torque of the tethered fruitfly saturates at about $\pm 0.04$ dyne × cm. The three columns at the right refer to the stimulus free situation, and to the situations where both eyes receive equally progressive or regressive stimuli. The absence of significant reactions confirms the *lateral symmetry* of the motion detecting system.

With these results it now becomes *necessary* to assume that both sides of the motion detecting system are functionally equal and bidirectionally sensitive. The two models ***A*** and ***B*** in Fig. 2 match this postulate. Furthermore they have proved to be equally *sufficient* for the description of the torque response under the various conditions shown in Fig. 4.

The next step is to devise an experiment that allows one to eliminate at least *one* of the models.

### *Thrust*

Reexamination of Fig. 2 shows that diametrically opposed predictions can be derived from model ***A*** and ***B*** about the influence of a stimulus on the *total thrust* of the motor system. The thrust of model ***A*** is always increased by progressing stripes and decreased by regressing stripes, while the thrust of model ***B*** is always decreased by progressing stripes and increased by regressing stripes. In order to decide against model ***A***, model ***B***, or model ***A** and **B*** one has merely to check whether the total thrust of the tethered fruitfly is lowered, raised, or not changed when both eyes receive equal stimulation. Fig. 1b illustrates the experiment with progressive stripe motion on both sides.

In the following investigations the flying insect was mounted to a frictionless suspended vertical lever of high magnetic permeability. The horizontal displacement of the lever unbalances the magnetic fluxes through the two coils of a 50 kc-linear-variable differential transformer (LVDT). The demodulated differential signal from the coils controls a magnetic field strong enough to restore the position of the lever to a 0.5 μ-accuracy. The field generating current in the steady state is proportional to the horizontal forward component of the force of flight so that the total thrust in dynes can be directly read from the recordings of this current. The author is indebted to Mr. H. Wenking for the skillful electronic instrumentation.

The results in Fig. 5 have been averaged from a total of 462 two-minute thrust recordings with 14 flies. It is evident that visual stimulation modifies the thrust of the motor system. However, the influence depends in a remarkable way on the *vertical inclination* of the moving stripe patterns. The following statements can, for instance, be derived from the three columns on the right:

1. With $\sphericalangle \mathbf{MA} < 0$ (lower part of the figure) the results fit into model ***A***. It is found that progressing stripes increase, and regressing stripes decrease the thrust obtained under stimulus free conditions.

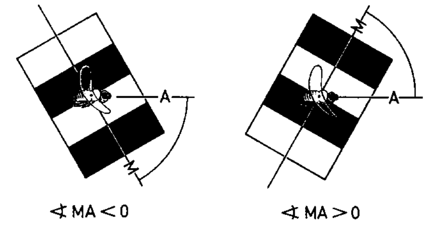

Fig. 3. The vertical inclination of the line of pattern motion **M** relative to the longitudinal axis **A** of the tethered fruitfly

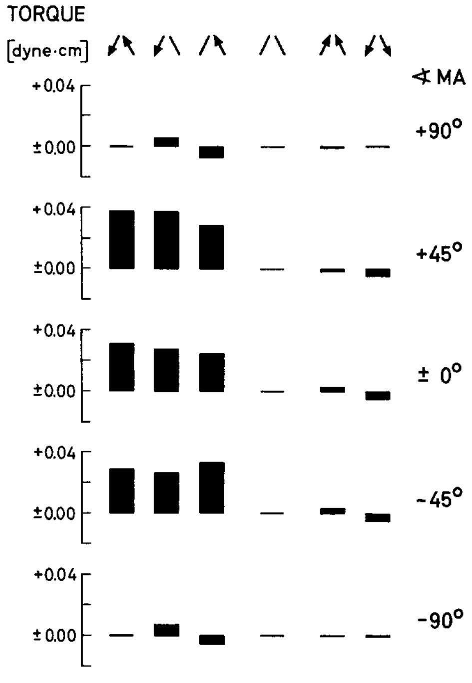

Fig. 4. The average optomotor *torque* reaction of *Drosophila* as a function of the composition and the inclination of the stimulus. The headings of the *columns* denote actual combinations of progressive (↓), regressive (↑), and missing (|) stripe motion on the two screens shown in Fig. 1a. The parameter ∢ **M A** of the *rows* specifies the inclination of the stripe projectors according to Fig. 3. Progressive and regressive stimuli, presented alternately to one of the eyes, are obviously discriminated, and elicit opposite responses in the fruitfly

2. With $\sphericalangle \mathbf{MA} > 0$ (upper part of the figure) the results fit into model ***B***. Here it is found that progressing stripes decrease, and regressing stripes increase the thrust obtained under stimulus free conditions.

The statements are confirmed by the results with *unilateral* counterclockwise stimulation (second and third column from the left). There is about half as much thrust increment and decrement as in the experiments with *bilateral* stimulation (first and second column from the right). This shows that a fairly good *additivity* of the thrust controlling components is still preserved. (The invariance of the increments and decrements to lateral exchange of the stimuli was also established in the corresponding experiments with clockwise stimulation.) Simultaneous stimulation with progressing *and* regressing stripes (first column from the left) is not accompanied by any significant changes of the thrust.

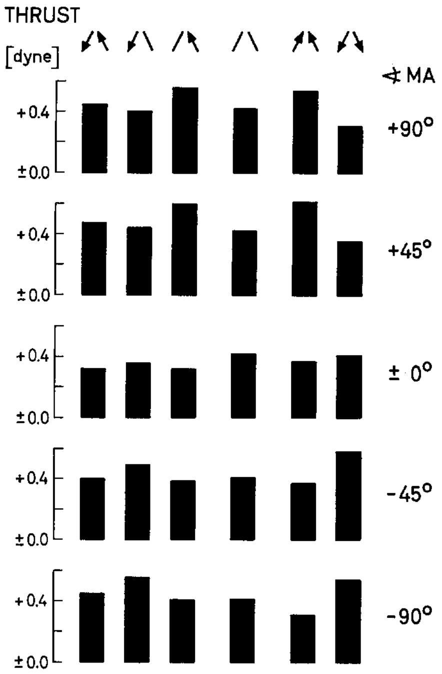

Fig. 5. The average optomotor *thrust* reaction of *Drosophlia* as a function of the composition and the inclination of the stimulus. Again, the headings of the *columns* denote actual combinations of progressive (↓), regressive (↑), and missing (|) stripe motion on the two screens shown in Fig. 1 b. The parameter ∢**MA** of the *rows* specifies the inclination of the stripe projectors according to Fig. 3. It depends entirely on this parameter whether the thrust under progressive stimulation exceeds the thrust under regressive stimulation, or *vice versa*

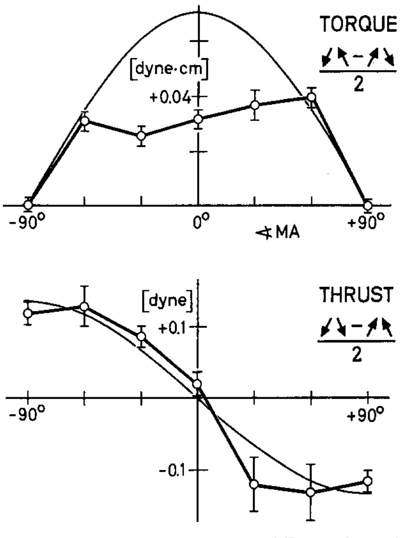

Fig. 6. Optomotor responses of *Drosophila* as functions of the stimulus inclination ∢**MA**, defined in Fig. 3. The upper diagram represents half the difference of the *torque* responses to counterclockwise (Fig. 1 a) and clockwise stimulus motion. The lower diagram represents half the difference of the *thrust* responses to bilaterally progressive (Fig. 1 b) and bilaterally regressive stimulus motion. The given means and the standard errors of the means refer to a total of 176 recordings from 17 flies. The two response curves are approximated by simple trigonometric functions of ∢**MA**. Comparison shows that the stimulus inclinations for zero-torque and zero-thrust responses are about orthogonal to each other. Motion detectors of different orientation on the eye surface are, therefore, necessarely involved in the visual flight control of the fruitfly

The answer to the problem raised in the beginning of this section is ambiguous. Neither of the two models, ***A*** and ***B***, together with their equivalent derivatives is compatible with *all* the results of the thrust experiment. It is the vertical inclination of the stimulus, ∢**MA**, that determines whether the thrust of the motor system in *Drosophila* can be described exclusively by model ***A*** or by model ***B***.

The previous observations suggest that the sensory system for visual flight control is composed of motion detectors with different vertical inclinations. The question whether or not these differences really exist is important for further analysis and will be treated in more detail.

### *Directional Orientation of the Motion Detectors*

Consider a hypothetical motion detector in the lateral region of an insect eye that faces the screen of a stripe projector. The situation is illustrated in Fig. 3. As in *Drosophila*, the detector may increase (+) as well as decrease (—) the output of the motor system. The inclination of the stimulus motion on the screen relative to the inclination of the motion detector on the eye surface may determine the sign of the response, and the reversal of the pattern movement may always produce the opposite sign.

It is evident that the response of any such system has to cross zero if the direction of the presented motion is tilted around into the reverse position. Therefore one has to postulate the existence of at least two opposed directions on the eye surface where progressive as well as regressive stimulation is uneffective. A single detector is expected to be non-receptive in the two directions orthogonal to its orientation. However, the postulate extends to complex devices comprising motion detecting subunits of uniform or different orientation if these devices are compatible with the previous assumptions.

The vertical inclination of uneffective pattern motion can readily be determined from the *zeros* of the torque or thrust responses in the angular domain of ∢**MA** that was defined in Fig. 3. Fig. 6 gives the means and the standard errors of the means obtained from a total of 112 torque and 64 thrust recordings with 17 fruitflies. The values represent half the difference of the *torque* responses to counterclockwise and clockwise stimulation, and of the *thrust* responses to progressive and regressive stimulation on either side.

The *torque* responses in Fig. 6 can roughly be described by the function cos (∢**MA**) which is clipped at the saturation levels of about ± 0.04 dyne × cm. The *zeros* of the torque responses occur with pattern motion that is *perpendicular* to the animal's long axis. The *thrust* responses in Fig. 6 are comparable with the function — sin (∢**MA**), and saturation effects are less conspicuous in this case. The *zeros* of the thrust responses occur with pattern motion that is *parallel* to the animal's long axis.

The different angular positions of the zeros in the torque and thrust curves lead to the following conclusions. The sensory system for visual flight control in *Drosophila* is *not* restricted to motion detectors of uniform vertical inclination. The motion detectors involved in torque and thrust responses are necessarely oriented in at least two *linearly independent* directions on the eye surface. A neural model that matches all previous results is, therefore, impossible to devise under the restraint of a planar representation such as models ***A*** and ***B*** in Fig. 2.

It is feasible to derive from Fig. 6 *separate* two-dimensional models for the torque and for the thrust response, so that the three-dimensional combination of these two models is consistent with all previous results. The motion detectors of the *torque* subsystem should be oriented *parallel* to the animal's long axis **A**. In order to modify the torque, but not the thrust, a stimulated detector has to inhibit one side of the motor system and simutlaneously excite the other. This is achieved by superposition of the models ***A*** and ***B*** in a plane parallel to axis **A**. The motion detectors of the *thrust* subsystem should be oriented *perpendicular* to axis **A**. In order to modify the thrust but not the torque, a stimulated detector has simultaneously to inhibit or to excite both sides of the motor system. The combination of the two systems consists of at least *four* contralateral and *four* ipsilateral connections, each of them capable of exciting as well as inhibiting one side of the motor system.

However, a reduction of the connections to a *minimum* of *two* contralateral and *two* ipsilateral channels can be achieved with the equivalent model in Fig. 7, which is shown in perspective from the upper left side. This "minimum model" is merely a three-dimensional combination of the two models ***A*** and ***B*** in Fig. 2. The motion detectors of the subsystem ***A*** are directed to the lower frontal region while the motion detectors of subsystem ***B*** are directed to the upper frontal region of the fly. Both directions are located symmetrically to the animal's long axis.

The action of the model is exemplified by the black arrows in Fig. 7. The curved arrows indicate the effective stimulus components when progressive motion from below ($\sphericalangle \mathbf{MA} = -90^\circ$) is presented to the left eye. No torque response, but an increase in the total thrust is required and obtained in this case. The stimulus excites, via subsystem ***A***, the contralateral side and, via subsystem ***B***, the ipsilateral side of the motor system.

The described model with the minimum number of four necessary channels is consistent with all previous results. It implies that the signals for torque *and* thrust control originate from *common* motion detectors and propagate along *common* lines. This demonstrates that the independent entities, torque and thrust, do not necessary require autonomous control systems. Obviously, the "minimum model" meets the postulate that the motion detectors should be arranged in at least two *linearly independent* directions on the lateral eye surface. However, here the directions must be located *symmetrically* with respect to the animal's long axis. They can *not* coincide with the zero-response directions in Fig. 6, since each detector must modify, simultaneously, torque *and* thrust. The orientation of the detectors may possibly correspond to the *hexagonal* structure of the facet eye, and therefore reconcile this structure with the *orthogonal* array of the sensory systems for torque and thrust control.

As was mentioned in the introduction to this paper, the well known optomotor *torque* response of *Drosophila* and many other insects can be interpreted as an aid in straight-course navigation. The entirely different optomotor *thrust* response that has been discovered in the present work with *Drosophila*, may serve similar purposes. However, the attempt to interpret this phenomenon will be postponed until more is known about the properties of the thrust generating motor system.

### *Parameters of Flight Control*

In order to modify the force of flight on either side of the motor system, the visual stimulation must change the *wing articulation* and/or the *body posture.* Table 1 gives a list of the major variables in flight performance. The asterisks indicate whether or not a variable is expected to influence significantly the *magnitude*, the *direction*, or the *position* of the *force vector* **F** during tethered flight in still air. The problem of this and subsequent sections is to determine which of the variables, and which of the vector parameters, are under control of the motion detectors.

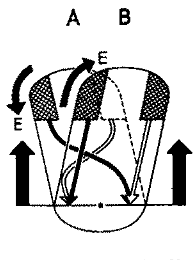

Fig. 7. "Minimum model" for the description of the optomotor *torque* and *thrust* responses of the fruitfly *Drosophila.* The model is shown in perspective from the upper left side, and can be regarded as a spacial arrangement of the models ***A*** and ***B*** from Fig. 2. The motion detectors of the subsystem ***A*** are directed to the lower frontal region while the motion detectors of the subsystem ***B*** are directed to the upper frontal region of the insect. Both directions are located symmetrically to the longitudinal axis of the insect (Fig. 14). The curved black arrows illustrate the effective stimulus components when progressive stimulus motion from below ($\sphericalangle \mathbf{MA} = -90^\circ$) is presented to the left eye. No torque response, but an increase in the total thrust is required and obtained from the model in this special case

Table 1. *The expected main effects of the major variables in flight performance*

| Flight variables | | Force vector | | | |
|---|---|---|---|---|---|
| | | Magnitude | Direction | | Position |
| | | | Vertical | Horizontal | |
| Wing articulation | stroke amplitude | * | | | |
| | stroke frequency | * | | | |
| | stroke plane | (*) | * | (*) | |
| | wing pitch | (*) | * | (*) | |
| Body posture | abdomen | | * | * | * |
| | hind legs | | (*) | (*) | * |
| | halteres *etc.* | | | | |

The force vector is not accessible for *direct* measurement. However, the properties of this vector can be derived *indirectly* from a set of ordinary thrust experiments. Consider the situation where a fly is tethered to a thrust compensator and exposed to bilateral pattern motion with a certain inclination relative to the animal's long axis **A**. Fig. 8 illustrates two different situations where $\sphericalangle \mathbf{MA} = -45^\circ$. It is assumed that both eyes receive equal stimulation (progressive *or* regressive) so that horizontal deflection of the force vector **F** is not encountered in these experiments. The *vertical* component $\mathbf{F_V}$ of vector **F** represents the total *lift* of the motor system under the conditions of tethered flight in still air. The *horizontal* component $\mathbf{F_H}$ represents the total *thrust* under these conditions, and only this component can be recorded with the thrustmeter. Obviously the components of a given vector **F** are not invariant. Their magnitudes and signs depend on the inclination of the animal's long axis **A** relative to the horizontal direction **H**. This is demonstrated for two arbitrary values of $\sphericalangle \mathbf{AH}$ in Fig. 8. The components obtained in these two cases are entirely different, even if the force vector **F** is constant with respect to the fly's coordinate system. Note that the stripe projectors must be turned together with the fly in order to preserve the effective inclination $\sphericalangle \mathbf{MA}$ of the stimulus on either side.

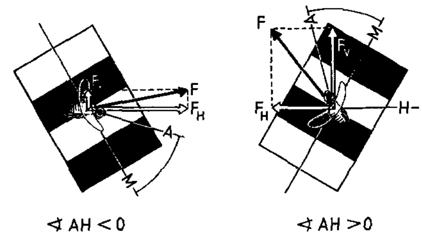

Fig. 8. The horizontal *thrust* component $\mathbf{F_H}$, and the vertical *lift* component $\mathbf{F_V}$ of a given force of flight **F** depend on the inclination $\sphericalangle \mathbf{AH}$ of the animal relative to the horizontal direction. The figure illustrates two different situations where the composition and the inclination of the stimulus is kept constant with respect to the animal's long axis **A**

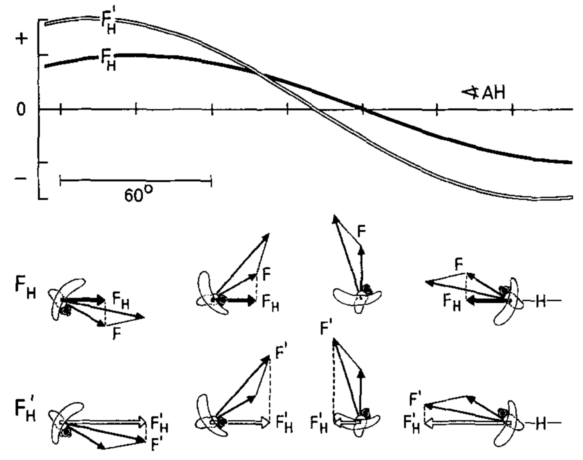

Fig. 9. The thrust components $\mathbf{F_H}$ and $\mathbf{F'_H}$ of two arbitrary force vectors **F** and **F'** at different inclinations $\sphericalangle \mathbf{AH}$ of the tethered animal. The *magnitude* |F| and the *inclination* $\sphericalangle \mathbf{FA}$ of an unknown force vector can be determined from the maximum value and from the zero position of the corresponding experimental thrust curve

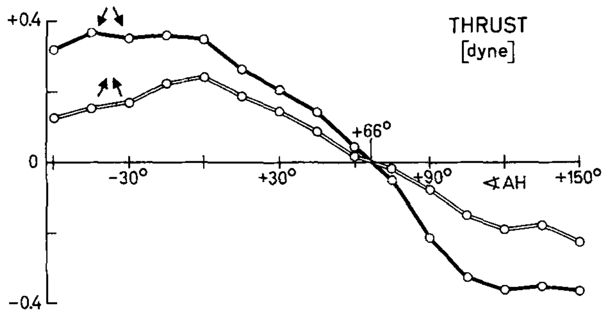

Fig. 10. Thrust reactions of a fruitfly as a function of its inclination $\sphericalangle \mathbf{AH}$. The animal was alternately exposed to bilaterally progressive pattern motion (black curve), and to bilaterally regressive pattern motion (white curve). The effective inclination $\sphericalangle \mathbf{MA} = -45°$ of the stimuli was maintained throughout the experiment by the procedure shown in Fig. 8. The different thrust maxima and the common zero positions of the two curves indicate the variable *magnitude*, and the constant *inclination* of the force vector during tethered flight in still air

It is evident from Fig. 8 that the recorded thrust $\mathbf{F_H}$ represents, in magnitude and sign, the *horizontal projection* of the force vector **F**. The corresponding relationship

$$\mathbf{F_H} = |\mathbf{F}| \cos(\sphericalangle \mathbf{FH}) \tag{1}$$

can be rewritten as

$$\mathbf{F_H} = |\mathbf{F}| \cos(\sphericalangle \mathbf{FA} + \sphericalangle \mathbf{AH}) \tag{2}$$

where |**F**| denotes the *magnitude* and $\sphericalangle \mathbf{FA}$ the vertical *direction* of the unknown force vector. In order to determine these two parameters one must increase the inclinations of the fly (and of the projectors) by steps, and record the thrust $\mathbf{F_H}$ as a function of $\sphericalangle \mathbf{AH}$. Fig. 9 illustrates this procedure for two subsequent experiments with different stimulation. It is assumed that the corresponding force vectors, **F** and **F'**, differ by magnitude *and* direction as indicated in the upper and lower rows of this figure. The resulting horizontal components, $\mathbf{F_H}$ and $\mathbf{F'_H}$ are represented by the black and the white curve, respectively. The figure reflects the general expectation that the *amplitude* as well as the *phase* of the curves will be changed under the influence of visual stimulation.

This, however, is apparently not the case with *Drosophila*. Fig. 10 shows the thrust reactions of a fly that was alternately exposed to progressive (black curve), and regressive (white curve) pattern motion on either side. The inclination of the stimulus, $\sphericalangle \mathbf{MA} = -45°$, was constant throughout the experiment, and sufficiently apart from the zeros of the torque and thrust controlling devices. Either of the experimental curves can be evaluated by comparison with Eqs. (1) and (2), or with Fig. 9.

The *magnitude* |**F**| of the unknown force vector is given by the *peak* value of the curve, and it is evident that this parameter is under control of the motion detectors. The *direction* $\sphericalangle \mathbf{FA}$ follows from the *zero* of the curve. The inclination angle $\sphericalangle \mathbf{AH}$ at this point denotes the position of the fly where the force vector is vertically oriented, or $\sphericalangle \mathbf{FH} = +90°$, so that

$$\sphericalangle \mathbf{FA} = 90° - [\sphericalangle \mathbf{AH}]_{\mathbf{F_H}=0}. \tag{3}$$

The coincidence of the zeros in Fig. 10 indicates a remarkable economy in the flight control system of *Drosophila*. The vertical direction of the force vector relative to the animal's long axis is invariant to the visual stimulation. The statement has been confirmed in experiments with two other flies at different temperatures (Table 2). The mean direction of the force vector during tethered flight in still air was about $\sphericalangle \mathbf{FA} = 24°$ throughout these experiments.

The varying influence of gravity on the antennae, wings, halteres, abdomen, and hind legs in these experiments may cause directional changes of the force vector. These changes must necessarely result in deviations of the measured curves from a sinusoidal pattern. The existence of minor changes cannot be excluded from the experiments in Fig. 10. Note however that the statement derived from the coincidence of the zeros is not impaired by these effects. Since

Table 2. *The influence of stripe motion on the vertical direction of the force of flight* ($\sphericalangle \mathbf{FA}$) *in Drosophila*

| Temperature [°C] | Direction [degrees] | | | Difference [degrees] |
|---|---|---|---|---|
| | $\swarrow\searrow$ | $\nearrow\nwarrow$ | $\wedge$ | $\swarrow\searrow - \nearrow\nwarrow$ |
| 15 | 26.0 | 20.0 | 24.0 | +6.0 |
| 20[a] | 23.5 | 24.5 | 24.5 | −1.0 |
| 28 | 25.0 | 22.5 | 25.0 | +2.5 |
| Means | 23.9 (±0.6) | | | +2.5 (±2.1) |

[a] See Fig. 10.

the influence of gravity must be constant for a given position of the animal, it is impossible to encounter different directional changes at the point of coincidence.

The capability to control the magnitude of the force vector without changing its direction can be attributed to only two of the variables given in Table 1, *viz.* the *wing-beat frequency*, and the *wing-beat amplitude*.

### *Wing-beat Frequency*

It is well known that the wing-beat frequency of *Drosophila* and other flies is not invariant to parameters of the environment (CHADWICK, 1953; PRINGLE, 1957—1965; VOGEL, 1966/67; NACHTIGALL and WILSON, 1967).

A measure of the wing-beat frequency is the repetition rate of the periodic signals from a microphone in posterior position to the tethered fruitfly. (This can be demonstrated by the in-phase illumination of the wing-beat from a stroboscopic light source that is triggered by the sound signals.) The repetition rate has been sampled under the various conditions of the torque and thrust experiments.

Table 3 gives the means and standard errors of the wing-beat frequency $f$, and of the simultaneously recorded magnitude of the force vector $\mathbf{F}$ as obtained with four female fruitflies. The inclination $\sphericalangle \mathbf{AH} = -24°$ of the tethered animals was derived from the results in Table 2. The position ensures the horizontal alignment of the force vector, so that the force of flight $|\mathbf{F}|$ is directly read from the recordings of the thrust $\mathbf{F_H}$. The inclination $\sphericalangle \mathbf{MA} = -45°$ of the stimulus relative to the animal's long axis corresponds to the experimental conditions in the previous section.

Table 3. *The influence of stripe motion on the frequency of the wing-beat (f), and on the magnitude of the force of flight* ($|\mathbf{F}|$) *in Drosophila*

| Temperature [°C] | Frequency [cycles/sec] | | Difference [rel. units] |
|---|---|---|---|
| | $\swarrow\searrow$ | $\nearrow\nwarrow$ | $\frac{\swarrow\searrow - \nearrow\nwarrow}{\wedge}$ |
| 15 | 147<br>(±4) | 147<br>(±5) | ±0.00 |
| 20 | 169<br>(±4) | 164<br>(±5) | +0.03 |
| 28 | 209<br>(±4) | 200<br>(±7) | +0.04 |

| Temperature [°C] | Force of flight [dynes] | | Difference [rel. units] |
|---|---|---|---|
| | $\swarrow\searrow$ | $\nearrow\nwarrow$ | $\frac{\swarrow\searrow - \nearrow\nwarrow}{\wedge}$ |
| 15 | 0.28<br>(±0.03) | 0.17<br>(±0.02) | +0.49 |
| 20 | 0.35<br>(±0.02) | 0.24<br>(±0.04) | +0.40 |
| 28 | 0.48<br>(±0.06) | 0.35<br>(±0.04) | +0.31 |

The results in Table 3 confirm the frequency enhancing effect of the temperature that has already been reported by CHADWICK (1953). As expected from theoretical considerations (*e.g.* VOGEL, 1967) the almost linear increase of the wing-beat frequency $f$ is accompanied by an increase of the force of flight $|\mathbf{F}|$ that is roughly proportional to $f^2$. Flight control via the wing-beat frequency comes, therefore, into the scope of possible mechanisms.

However when alternatively exposed to progressive ($\swarrow\searrow$), and regressive ($\nearrow\nwarrow$) stimulation the animals do not significantly change their wing-beat frequency. The parameter $f$ proves to be almost invariant to the pattern movement, and is certainly not responsible for the comparatively large changes of the force of flight. The major influence of pattern movement on the wing articulation in *Drosophila* is, therefore, necessarely confined to modifications of the wing-beat amplitude.

### *Wing-beat Amplitude*

The role of the wing-beat amplitude (stroke amplitude, stroke angle) as a possible parameter of flight stabilization in *Drosophila* and other flies has repeatedly been investigated and discussed (*e.g.* CHADWICK, NACHTIGALL, PRINGLE, VOGEL, WILSON, *loc. cit.*). It has been emphasized in the review article of CHADWICK (1953) that the articulation of the two wings is apparently restricted to common *frequencies*, but not to common *amplitudes*. This is of interest in the present work, since the individual adjustment of the wing-beat amplitudes on either side would meet the requirements for simultaneous torque and thrust control.

The influence of pattern motion on the wing-beat amplitudes of *Drosophila* can be investigated by in-flight photography. The tethered flies were mounted in working distance to a photomicroscope with the stroke plane in almost horizontal position ($\sphericalangle \mathbf{AH} \approx +60°$). Again, the stimulus was provided by the stripe projectors. However, scattered light from the additional illumination of the wings diminuished the effective contrast of the moving stripes in these experiments. Ordinary high-speed panchromatic film (400 ASA/27 DIN) was exposed for 1 sec, or about 180 wing-beats, and the photographs of the wing-beat envelopes were evaluated by means of an appropriate ocular-goniometer.

Fig. 11 shows photographs of the wing-beat envelopes under the influence of counterclockwise ($\swarrow\nwarrow$), and clockwise ($\nearrow\searrow$) stimulus motion in the plane of the animal's long axis ($\sphericalangle \mathbf{MA} = \pm 0°$). The pictures indicate slight asymmetries of the wing-beat amplitudes (or of the corresponding force components) on either side that are apparently correlated to the stimulation. The resulting torque elicits, obviously in both cases, the expected *positive* optomotor response, *i.e.* the tendency to follow the angular motion of the surroundings.

The investigation of wing-beat envelopes has been repeated under the various conditions of the torque and thrust experiments. Fig. 12 shows the average wing-beat amplitudes as obtained from a total of 352 in-flight photographs taken with 15 tethered fruitflies. The general scheme of the figure relates to Figs. 4 and 5. Again, the headings of the columns denote the

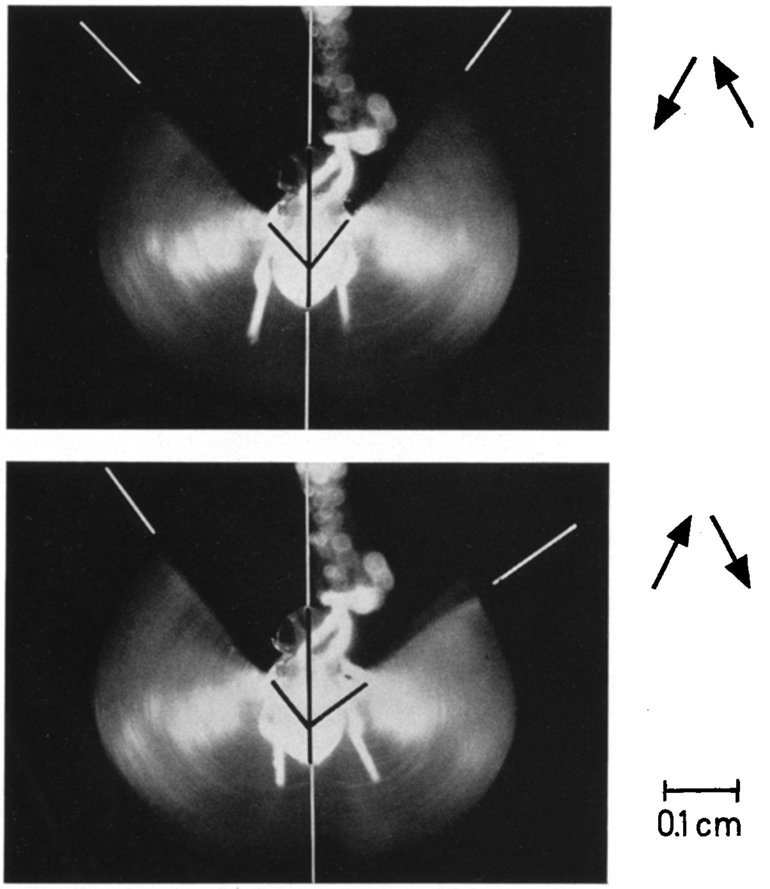

Fig. 11. Wing-beat envelopes of the tethered fruitfly under the influence of counterclockwise (Fig. 1a) and clockwise stimulus motion. The slight asymmetries of the wing-beat amplitudes indicate, in both cases, the appropriate torque response: The animal tries to follow the angular motion of the stripes

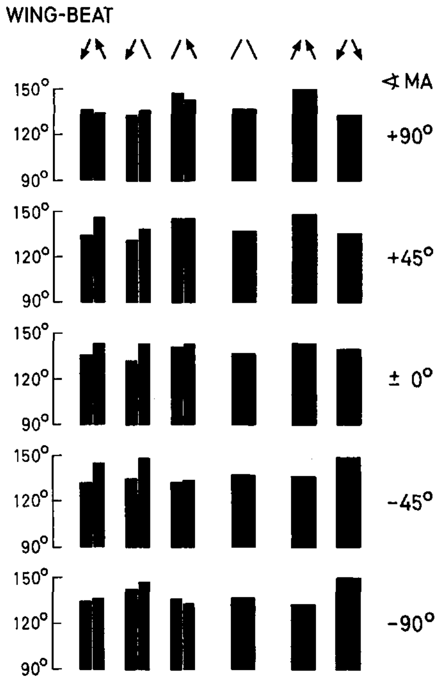

Fig. 12

Fig. 12. The average *wing-beat amplitudes* of *Drosophila* as functions of the composition and inclination of the stimulus. The headings of the columns and the parameter ∢ **MA** of the rows correspond to the notations in Figs. 4 and 5. Split bars indicate the average angular amplitudes of the left and the right wing when the two eyes receive different stimulation. The standard errors of the means are in the order of ±2.5°. Nevertheless it is possible to reconstruct the general properties of the *torque* and the *thrust* responses from the *differences* and the *sums* of the wing-beat amplitudes on either side of the fruitfly

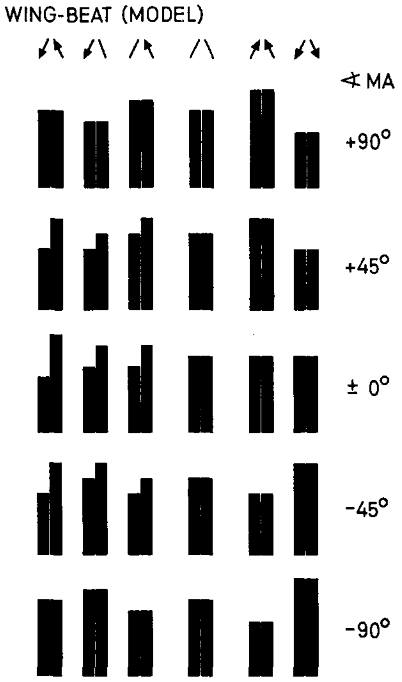

Fig. 13

Fig. 13. The expected *wing-beat amplitudes* according to the "*minimum model*" in Fig. 7. The increments and decrements on either side of the flight system are represented on an arbitrary scale as functions of the composition and inclination of the stimulus. The headings of the columns and the parameter ∢ **MA** of the rows correspond to notations in previous figures. The results resemble the experimental data in Fig. 12, and suggest that the various torque and thrust reactions of the tethered fruitfly in still air can possibly be described by the "minimum model" in Fig. 7 acting exclusively upon the wing-beat amplitudes

direction, and the parameters of the rows denote the inclination of the stimulus motion on the two projector screens. The bars representing the angular wing-beat amplitudes under asymmetrical stimulation have been split in order to illustrate separately the average reactions on either side of the motor system.

The already mentioned deficiencies of pattern contrast, and sampling time in these experiments lead to an average standard error of the mean wing-beat amplitudes of ±2.5 degress. Although the single values in Fig. 12 are not very reliable the ensemble represents quite well the *torque* in Fig. 4 by the *difference*, and the *thrust* in Fig. 5 by the *sum* of the wing-beat amplitudes on either side of the motor system.

This becomes more evident if the results of Fig. 12 are compared with the modifications of the wing-beat amplitudes that are expected on the basis of the "*minimum model*" for the torque and thrust responses of *Drosophila*. Fig. 13 illustrates, on an arbitrary scale, the effects of this model under the various conditions of Fig. 12. The increments and decrements of the wing-beat amplitudes on either side are derived from the wiring pattern in Fig. 7 by superposition of the outputs of the motion detectors with appropriate orientation and position. For each of these outputs the magnitude and sign depends on the inclination of the stimulus motion relative to the orientation of the detector. It is assumed that the outputs are small compared to the saturation level, and therefore still proportional to the cosine of the angle between these two directions.

A variable parameter of the "minimum model" is the inclination of the detectors relative to the animal's long axis, and a ±45°-divergence of their orientation has arbitrarely been chosen in the present case. It can be shown that the deviation from this value is merely imposing different factors upon the torque and the thrust components of the wing-beat responses in Fig. 13. (A *decrease* of the divergence to, for instance, ±30° would raise all torque responses by the factor 1.22, and lower all thrust responses by the factor 0.70. An *increase* of the divergence to ±60° would, in reverse, lower all torque responses by the factor 0.70, and raise all thrust responses by the factor 1.22.) The actual inclination of the "minimum model" detectors can, therefore, in principle be determined from precise data of sufficiently small wing-beat responses.

Indirect evidence from previous sections has led to the conclusion that the major influence of pattern motion on the *wing articulation* in *Drosophila* is necessarely confined to modifications of the wing-beat amplitudes. Now it is evident that these modifications exist, and that they are sufficient for the generation of appropriate torque as well as thrust responses. However there are still other variables which could possibly be under control of the motion detectors (Table 1). The in-flight photographs of Fig. 11 show the effect of counterclockwise, and clockwise stimulation on the position of the hind legs, and similar effects are observed with the position of the abdomen. The observations suggest that the *body posture* also is, actively or passively, involved in visual flight control. However, the truncation of the *hind legs*, as well as radical changes of the *abdominal volume* by appropriate nutrition have no significant influence on the torque and thrust reactions in still air. With increasing airspeed the variables may, of course, become important parameters of flight performance. It is improbable that the relatively small *halteres* contribute as effectors to the visual flight control (Pringle, 1957).

The torque responses in the present experiments can, in fact, be almost completely attributed to the differences of the wing-beat amplitudes on either side of the tethered fruitfly. This is shown by comparison of the results in Fig. 6. One side of the flight system in *Drosophila* produces, under optimal stimulation, one half of the maximum *torque* response (about 0.02 dyne × cm), or one half of the maximum *thrust* response (about 0.06 dyne). The thrust is roughly proportional to the square of the down-stroke velocity. The thrust increment originates, therefore, mainly from the distal part of the laterally extended wing, where the down-stroke velocity is about its maximum. The resultant of the *thrust increment* passes through this region. Estimates of its perpendicular *distance* to the center of the fly are based on Fig. 11, and range between 0.2 and 0.3 cm. The increment of the wing-beat amplitude in the *thrust* experiment is, therefore, capable of generating torque in the order of

$$0.06\,\text{dyne} \times 0.25\,\text{cm} = 0.015\,\text{dyne} \times \text{cm}\,. \qquad (4)$$

This value is comparable with the 0.02 dyne × cm maximum torque response per wing which was derived from *torque* recordings.

The previous results support the view, that the various torque and thrust reactions of the tethered fruitfly in still air can, so far, completely be described by the "minimum model" in Fig. 7 acting exclusively upon the wing-beat amplitudes.

## *Discussion*

It is evident from Fig. 6 that the visual subsystems for *torque* control, and *thrust* control conform to directions on the eye surface that are *parallel*, and *perpendicular* to the longitudinal axis **A** of the fruitfly. This imposes certain constraints on the orientation of the motion detectors on the eye surface. It was expected that these detectors group in at least two directions that are either parallel and perpendicular, or symmetrically located to the axis **A**.

The results suggest that the direction **A** corresponds to a distinct direction in the array of the ommatidia on the lateral eye surface. This is, in fact, the case as seen from Fig. 14. Moreover, the axis **A** has proved to be parallel to the line of symmetry of the *internal* eye structure that was determined in the flies *Musca* (Kirschfeld, 1967) and *Drosophila* (Franceschini, 1968). However, the orientation and distribution of the motion detectors on the eye surface is still unknown.

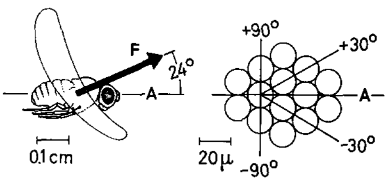

Fig. 14. The position of the longitudinal axis **A** of the female fruitfly *Drosophila* is plotted on the left side in relation to the body markers, and on the right side in relation to the array of the ommatidia on the lateral eye surface. The uniform orientation of the hexagonal array facilitates a fairly precise determination of the direction **A**. The vector **F** denotes the force of flight of the tethered fruitfly in still air. The inclination ∢ **FA** of the force vector has proved to be invariant to visual stimulation (Table 2)

The role of the thrust response in the flight control of *Drosophila* may find a possible explanation in the light of the present results. It has been shown that the motion detectors control the magnitude but not the inclination of the force of stationary flight in still air. Consequently the increase of *thrust* by pattern motion from below is accompanied by an appropriate increase of the *lift* unless the inclination of the animal undergoes considerable changes. This lift response is obviously suitable to counteract involuntary changes of the altitude.

It is conceivable that the visually stimulated altitude-control reflex replaces the wide-spread "lift-control reaction" of insects (Weis-Fogh, 1964), which is not found in *Drosophila* (Vogel, 1966). The torque and thrust experiments of Fig. 6 have, therefore, been repeated with the housefly *Musca domestica*. Fig. 15 gives the means obtained from a total of 125 torque and 155 thrust recordings with only 1 housefly. As in Fig. 6, the values represent half the difference of the *torque* responses to counterclockwise and clockwise stimulation, or of the *thrust* responses to progressive and regressive stimulation on either side of the fly. Besides of the increased scale factors, and the missing saturation of the torque response the figure resembles the essential details of Fig. 6. It can be concluded, that the principle of independent torque and thrust control is adopted even in flies with a considerably more elaborate flight control system than is found in *Drosophila*.

Recently it became feasible to identify electrophysiologically, and to localize anatomically certain properties of the visual flight control system in insects. Fundamental progress on the investigation of the interneural basis of optomotor behavior has been made in the work on the moth *Sphinx* (Collett and Blest, 1966), and on the flies *Calliphora* and *Musca* (Bishop, Keehn, and McCann, 1968). The neuro-muscular basis of flight control has been investigated in the flies *Muscina*, *Sarcophaga*, and *Calliphora* (Smyth and Yurkiewicz, 1966), (Nachtigall and Wilson, 1967). Further studies on flight performance in the wind tunnel include, for instance, the work on the fruitfly *Drosophila virilis* (Vogel, *loc. cit.*), and confirm the outstanding simplicity of the flight control system in *Drosophila*.

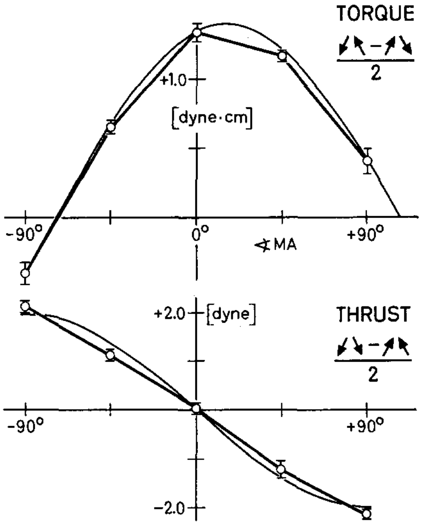

Fig. 15. Optomotor responses of *Musca* as functions of the stimulus inclination ∢ **MA**, defined in Fig. 3. The upper diagram represents half the difference of the *torque* responses to counterclockwise (Fig. 1a) and clockwise stimulus motion. The lower diagram represents half the difference of the *thrust* responses to bilaterally progressive (Fig. 1b) and bilaterally regressive stimulus motion. The given means and the standard errors of the means refer to a total of 280 recordings from only 1 fly. The two response curves are approximated by simple trigonometric functions of ∢ **MA**. They resemble the essential details of the *Drosophila* response curves in Fig. 6. The principle of independent optomotor torque and thrust control is, therefore, obviously adopted also in the elaborate flight system of the housefly

However, the studies on the optomotor speed control in *Calliphora* (P. Schneider, 1965), and on the optomotor landing response in *Musca* (v. Braitenberg and Taddei Ferretti, 1966) indicate that the optomotor reactions are probably not restricted to the steady state torque and thrust responses that have exclusively been studied in the present work.

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**References.** Bishop, L. G., D. G. Keehn, and G. D. McCann: Studies of motion detection by interneurons of the optic lobes and brain of the flies *Calliphora phenicia* and *Musca domestica.* (In preparation.) — Bliss, J. C.: Visual information processing in the beetle *Lixus*. Published in D. K. Pollack *et al.* (eds.), Optical processing of information. Washington: Spartan Books 1963. — Braitenberg, V. v., and C. Taddei Ferretti: Landing reactions of *Musca domestica* induced by visual stimuli. Naturwissenschaften **53**, 155 (1966). — Burkhardt, D., u. W. Kaiser: (In preparation). — Campenhausen, C. v.: The ability of *Limulus* to see visual patterns. J. exp. Biol. **46**, 557—570 (1967). — Chadwick, L. E.: Insect flight. Published in K. D. Roeder (ed.), Insect physiology. New York: John Wiley & Sons 1953. — Collett, T. S., and A. D. Blest: Binocular, directionally sensitive neurons, possibly involved in the optomotor response of insects. Nature (Lond.) **212**, 1330—1333 (1966). — Fermi, G., u. W. Reichardt: Optomotorische Reaktionen der Fliege *Musca domestica*. Kybernetik **2**, 15—28 (1963). — Franceschini, N.: (In preparation). — Götz, K. G.: Optomotorische Untersuchung des visuellen Systems einiger Augenmutanten der Fruchtfliege *Drosophila*. Kybernetik **2**, 77—92 (1964); — Die optischen Übertragungseigenschaften des Komplexauges von *Drosophila*. Kybernetik **2**, 215—221 (1965); — Behavioral analysis of the visual system of the fruitfly *Drosophila*. Pasadena: Proc. Symp. Information Processing in Sight Sensory Systems, p. 85—100 (1965). — Hassenstein, B.: Kybernetik und biologische Forschung, p. 705—715. Handbuch der Biologie I/2. Frankfurt a. M.: Athenaion 1966. — Hengstenberg, R., u. K. G. Götz: Der Einfluß des Schirmpigmentgehalts auf die Helligkeits- und Kontrastwahrnehmung von *Drosophila*-Augenmutanten. Kybernetik **3**, 276—285 (1967). — Horridge, G. A.: Optokinetic memory in the locust. J. exp. Biol. **44**, 255—261 (1966). — Horridge, G. A., and D. C. Sandeman: Nervous control of optokinetic responses in the crab *Carcinus*. Proc. roy. Soc. B, **161**, 216—246 (1964). — Kirschfeld, K.: Die Projektion der optischen Umwelt auf das Raster der Rhabdomere im Komplexauge von *Musca*. Exp. Brain Res. **3**, 248—270 (1967). — Kunze, P.: Untersuchung des Bewegungssehens fixiert fliegender Bienen. Z. vergl. Physiol. **44**, 656—684 (1961); — Eye-stalk reactions of the ghost crab *Ocypode*. Published in R. F. Reiss (ed.), Neural theory and modeling, p. 293—306. Stanford: Stanford University Press 1964. — Maynard, D. M., and H. C. Howland: Dynamics of the optomotor response in mantids. 9th Internat. Ethological Conference, Zürich, 1965. — McCann, G. D., and G. F. MacGinitie: Optomotor response studies of insect vision. Proc. roy. Soc. B, **163**, 369—401 (1965). — Mittelstaedt, H.: Zur Analyse physiologischer Regelsysteme. Verh. dtsch. Zool. Ges. Wilhelmshaven **8**, 150—157 (1951). — Nachtigall, W., and D. Wilson: Neuro-muscular control of dipteran flight. J. exp. Biol. **47**, 77—97 (1967). — Palka, J.: Diffraction and visual acuity of insects. Science **149**, 551—553 (1965). — Pringle, J. W. S.: Insect flight. Cambridge: Cambridge University Press 1957; — Locomotion: Flight. Published in M. Rockstein (ed.), The physiology of insecta. New York: Academic Press 1965. — Reichardt, W.: Autocorrelation, a principle for the evaluation of sensory information by the central nervous system. Published in W. A. Rosenblith (ed.), Sensory communication, p. 303—317. New York: John Wiley & Sons 1961; — Quantum sensitivity of light receptors in the compound eye of the fly *Musca*. Cold Spr. Harb. Symp. quant. Biol. **30**, 505—515 (1965). — Reichardt, W., V. v. Braitenberg u. G. Weidel: Auslösung von Elementarprozessen durch einzelne Lichtquanten im Fliegenauge. Kybernetik. (In the press). — Schneider, G.: Zur spektralen Empfindlichkeit des Komplexauges von *Calliphora*. Z. vergl. Physiol. **39**, 1—20 (1956). — Schneider, P.: Vergleichende Untersuchungen zur Steuerung der Fluggeschwindigkeit bei *Calliphora vicina*. Z. wiss. Zool. **173**, 114—173 (1965). — Shepheard, P. R. B.: Optokinetic memory and the perception of movement by the crab *Carcinus*. Published in C. G. Bernhard (ed.), The functional organization of the compound eye. Oxford: Pergamon Press 1966. — Smyth, T., and W. J. Yurkiewicz: Visual reflex control of indirect flight muscles in the sheep blowfly. Comp. Biochem. Physiol. **17**, 1175—1180 (1966). — Thorson, J.: Small-signal analysis of a visual reflex in locust, I and II. Kybernetik **3**, 41—53 and 53—66 (1966). — Varjú, D., u. W. Reichardt: Übertragungseigenschaften im Auswerte-System für das Bewegungssehen. II. Z. Naturforsch. **22b**, 1343—1351 (1967). — Vogel, S.: Flight in *Drosophila*. I. Flight performance in tethered flies. J. exp. Biol. **44**, 567—578 (1966); II. Variations in stroke parameters and wing contour. J. exp. Biol. **46**, 383—392 (1967). — Weis-Fogh, T.: Biology and physics of locust flight. VIII. J. exp. Biol. **41**, 257—271 (1964). — Wilson, D. M., and R. R. Hoy: Optomotor reaction, locomotry bias, and reactive inhibition in the milkweed bug *Oncopeltus* and the beetle *Zophobas*. Z. vergl. Physiol. **58**, 136—152 (1968).

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