

Unsteady effects in the flight of an insect

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UNSTEADY effects have frequently been invoked to explain the performance characteristics of insects and birds; their existence has been effectively proved in some cases. However, conventional aerodynamics principles are often considered sufficient for an understanding of most flapping flight. This point of view has been strengthened by the experimental results of Jensen on locust flight coupled with measurements of aerodynamic forces exerted by steady flows on detached wings. The instantaneous lift of locusts flying in a wind tunnel was determined, in order to compare the results to those obtained with steady flows. A piezo-electric probe was used to make these measurements. The air flow velocity was adjusted to be equal to that which would have been experienced by the freely flying insect. To obtain the true aerodynamic forces, the inertial forces must be subtracted from the gross forces measured. These inertial forces were calculated from the movement of the centre of gravity and from the mass of the different wing sections. The amplitude of the obtained lift curves is approximately twice as large as the one deduced from measurements on detached wings. These two different sets of results are only compatible if the existence of significant unsteady effects is acknowledged.

Dla wyjaśnienia charakterystyki lotu owadów i ptaków częste jest powoływanie się na efekty nieustalone; w pewnych przypadkach ich istnienie zostało efektywnie wykazane. Zazwyczaj jednak uważa się, że klasyczne zasady aerodynamiki powinny wystarczyć dla zrozumienia zasad lotu opartego na wahliwych ruchach skrzydeł. Ten punkt widzenia znalazł poparcie w doświadczeniach Jensena dotyczących lotu szarańczy, popartych pomiarami sił aerodynamicznych na oderwanym skrzydełku w przepływie ustalonym. Określono wartość chwilowego wyporu dla lotu szarańczy w tunelu aerodynamicznym i porównano ją z wynikami otrzymanymi dla przepływów ustalonych. W doświadczeniu użyto sondy piezoelektrycznej. Prędkość przepływu powietrza dostosowano do prędkości jaką rozwija owad w locie swobodnym. Dla uzyskania prawdziwych sił aerodynamicznych należy od siły całkowitej (zmierzonej) odjąć siły bezwładności. Siły te wyznaczono z ruchu środka ciężkości oraz mas poszczególnych przekrojów skrzydła. Amplituda otrzymanych krzywych wyporu jest w przybliżeniu dwukrotnie większa od amplitudy zmierzonej na oderwanym skrzydle. Zgodność tych dwóch różnych wyników uzyskać można jedynie przy założeniu istnienia poważnych efektów ruchu nieustalonego.

Для выяснения характеристики полета насекомых и птиц часто ссылаются на неуставившиеся эффекты; в некоторых случаях их существование эффективно доказано. Обычно однако считается, что классические принципы аэродинамики достаточны для понимания принципов полета, опирающегося на колебательные движения крыльев. Эта точка зрения нашла подтверждение в экспериментах Йенсена, касающихся полета саранча, подтвержденных измерениями аэродинамических сил на оторванном крыле в неуставившемся течении. Определено значение мгновенного выпора для полета саранча в аэродинамическом туннеле и оно сравнено с результатами полученными для установившихся течений. В эксперименте использован пьезоэлектрический зонд. Скорость течения воздуха согласована со скоростью которую развивает насекомое в свободном полете. Для получения действительных аэродинамических сил следует от полной силы (измеряемой) отнять силы инерции. Эти силы определены из движения центра тяжести и масс отдельных сечений крыла. Амплитуда полученных кривых выпора в приближении в два раза больше чем амплитуда измеренная на оторванном крыле. Совпадение этих двух разных результатов можно получить только при предположении существования значительных эффектов неуставившегося движения.

1. Introduction

UNSTEADY effects have frequently been invoked to explain the flight of insects and birds [1, 2]. Up to now, the necessity of taking into account these effects has been effectively demonstrated in a few cases [3].

Nevertheless, theories based on the principles of conventional aerodynamics [2, 4, 5] generally give results which are compatible with mean lift and thrust values observed [6]. Hence, it is often felt that in most cases, unless proved otherwise, flapping flight can be considered as a succession of steady states [7].

This postulate is supported by the comprehensive study made by WEIS-FOGH [8] and JENSEN [9] on the flight of the locust *Schistocerca Gregaria*, a four-winged insect whose main characteristics are roughly:

weight: 2 g.; span: 10 cm; stroke frequency: 20 Hz; flying speed: 4 ms^{-1} .

Jensen first measured the mean forces produced by insects suspended in a wind tunnel from a balance, and determined the different wing postures during a cycle by accurate cinematographic analysis; a feedback control system allowed to adjust the flow velocity in such a way that the absolute values of mean thrust and drag were equal, as in free flight. Then, the detached wings were placed in the boundary layer of a steady flow simulating the velocity gradient from base to tip due to the angular motion of the wings in a real flight; from measurements of the forces applied to detached wings under different conditions, Jensen succeeded in plotting the variations in lift and thrust occurring during a wing-stroke cycle.

He observed that average lift and thrust values calculated by integrating these curves were practically equal to the corresponding values measured in flight. He concluded that "the good conformity between the measured and the calculated forces makes it probable that the principles of steady-state aerodynamics can be applied to locust flight".

His work, which includes a considerable amount of delicate experiments and long calculations is still most unique. The results published in 1956 have often been mentioned to justify a quasi-steady type of analysis for the flight of different animals.

However, it is possible that the study of the *mean* values of the aerodynamic forces is insufficient to detect possible unsteady effects which are, by definition, transient phenomena.

In our work we measured the *instantaneous* lift in flying locusts to confirm whether the values obtained by Jensen on detached wings effectively correspond to the true values. We shall see that this is not the case.

Few direct measurements of instantaneous forces developed by insects have been taken hitherto [10-13]. Except in Wilkin's investigations on locust, the contribution of the inertial forces of the wings to the measured forces was not accounted for; furthermore, all measurements were taken either in an airflow in which the velocity was not equal to that which would have been assumed by the freely flying insect, or even in still air, yielding results of questionable validity, as pointed out by various authors [14].

In our experiments [15, 16], velocity matching was obtained by a method similar to

that used by WEIS-FOGH [8] and JENSEN [9], and inertial forces were determined. We restricted ourselves to lift measurements for which inertial corrections are relatively lower than for thrust.

2. Methods and materials

2.1. General

For tests, the locust (*Schistocerca Gregaria*) was placed at the outlet of an open throat, variable-speed wind tunnel. The values selected for ambient temperature (30°C), relative humidity (60%) and the angle made by the locust's body with the horizontal (7°) corresponded to the values determined by WEIS-FOGH [8] for normal flight.

The experimental system is shown schematically in Figs. 1 and 2.

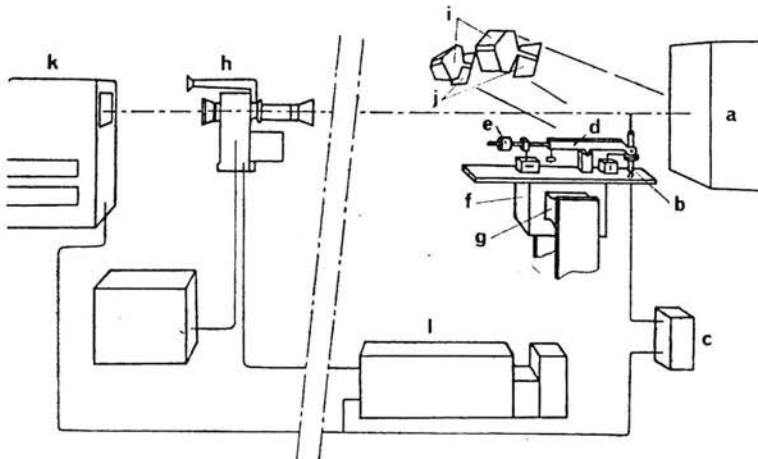


FIG. 1. Schematic diagram of the installation used to measure instantaneous lift in locusts. *a*, wind tunnel exit; *b*, force probe; *c*, charge amplifier; *d*, arm of balance for measuring average lift; *e*, balancing counterweight; *f*, metallic block; *g*, antivibration support; *h*, high-speed camera; *i*, projectors; *j*, heat-reflecting filters; *k*, oscilloscope; *l*, direct writing oscillograph.

2.2. Force probe system

For a rapid positioning of the insects, a thin soft iron disc was permanently cemented under the pterothoracic plastron of all locusts used in the tests; this disc fitted on a samarium-cobalt micromagnet (*m*, Fig. 2) cemented to the upper end of a 10 cm long rod (*n*) screwed into the probe body. We used a piezo-electric probe (*b*) combined with a charge amplifier (*c*). A special system (*o*, *p*, *q*) allowed to eliminate the spurious responses to transverse forces of the probe.

The probe-rod-cylinder system was able to oscillate about a horizontal axis perpendicular to the flow by means of the part (*r*) resting on two knives (*s*). In the absence of flow, with the locust at rest, the verticality of the support rod was adjusted by means of

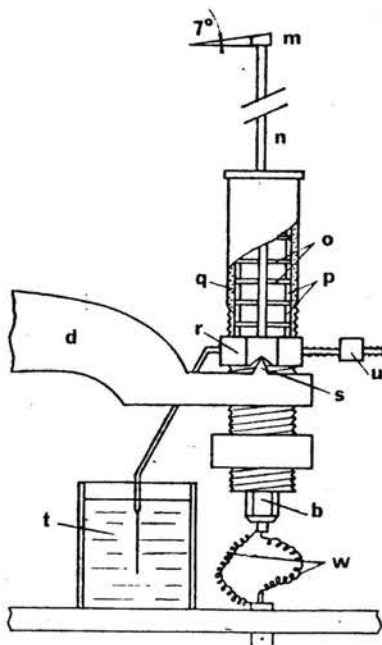


FIG. 2. Detail of mechanical assembly of force probe. *b*, probe; *m*, micromagnet for attaching insect; *n*, support rod; *o*, rubber pellets; *p*, pellet clamping rings; *q*, cylinder screwed on probe body; *r*, support of probe system resting on knife-edges; *s*, *t*, dashpot; *u*, balancing fly-weight; *w*, probe connection wires.

a fly-weight (*u*). When the locust was in flight, the flow velocity was adjusted to maintain the rod vertical. In this way, the absolute value of flow velocity was equal to that which would have been assumed by the freely flying insect.

2.3. Balance measuring average lift

The knife-edges supporting the probe unit were positioned at one end of the arm of a balance (*d*). The arm equilibrium was adjusted, before positioning the locust, by means of a fly-weight (*e*, Fig. 1). The new equilibrium position assumed during flight directly gave the difference between the average lift and the weight of the insect.

The balance-probe assembly, protected from the air-flow by a streamlined case, was installed on a heavy block (*f*) fixed to the wind tunnel frame by means of two antivibration supports (*g*).

2.4. High-speed camera and oscilloscope

The same camera (*h*, Fig. 1) was employed to film the insect and to record the force signal.

The light beams of two 800 W projectors (*i*) were focused on the insect by means of lenses coupled with heat-reflecting filters (*j*). The locust could be filmed at 1000 frames/s, giving about 50 pictures per wing cycle.

The signal produced by the charge amplifier (c) was fed to an oscilloscope (h) used without time base, and recorded on the film by means of a lens placed at the rear of the camera.

A direct-writing oscillograph (l) was used to monitor the regularity of the insect's flight before and after the wing-stroke cycle selected on the film for detailed analysis.

2.5. Procedure and use of recordings

To determine the vertical aerodynamic forces (lift: L), the inertial forces (F_I) due to the accelerations of the wings must be subtracted from the raw forces (F_z) measured by the probe. The vertical components of the inertial forces were determined as follows.

Before the test, white paint marks were made on the wings at the points indicated in Fig. 3 to visualize better the movements of the wings. A single reference point (a) was

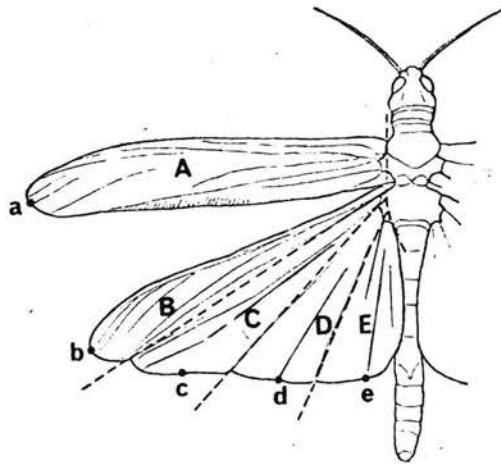


FIG. 3. Unfolded wings of *Schistocerca Gregaria*. Positions of the reference points (a-e) and partition of the wings (dashed lines) used for movement analysis and determination of inertial forces.

marked near the tip of the forewings. For hindwings, whose fan structure permits significant flexing perpendicular to the ribs, four reference points (b-e) were marked on the trailing edge.

Immediately after a wind tunnel test, the animal was weighed and killed. The wings were separated from the body and the hindwings were cut into segments B-E (Fig. 3), corresponding to the four reference points above. The position of the centre of gravity of each wing or wing segment was determined as the location indicated by the point of a needle on which horizontal equilibrium was achieved. This element was pierced at the centre of gravity, photographed for subsequent distance measurements, and weighed.

The test film was projected and analysed frame by frame. For each picture of the selected wing cycle, the positions of the different wing reference points were marked on the screen; the curves obtained by connecting these points represented the projection of the movement of the reference points on a plane perpendicular to the flow (Fig. 4).

The vertical movement $z_i = f_i(t)$ of the centre of gravity of each wing segment of mass m_i was deduced from these curves. Each z_i was expressed analytically by a Fourier

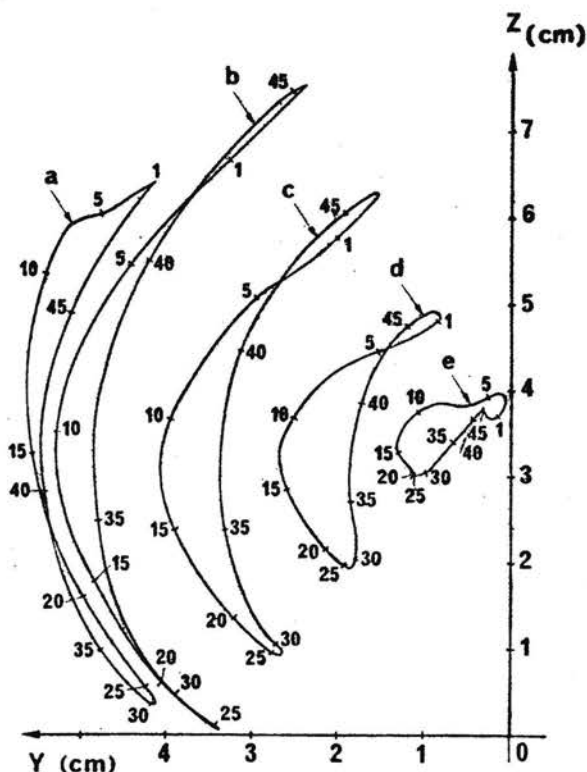


FIG. 4. Projection on a plane perpendicular to the flow of the movement of reference points, *a-e*, of the left-hand wings during a typical flight. Each curve is plotted from 50 points. *Z* axis: vertical; *Y* axis: horizontal perpendicular to the flow direction.

series expansion, and twice differentiated to obtain the total inertial force (taken to be positive when directed upward):

$$F_I(t) = - \sum_{i=1}^n m_i \frac{d^2 z_i}{dt^2},$$

where n is the number of reference points for the two pairs of wings.

To avoid spurious oscillations of acceleration functions, due to measurement uncertainties concerning wing positions, the Fourier series were limited to five harmonics. Then the gross force curve $F_Z(t)$, reconstructed from the positions of the oscillograph spot in each picture of the film, was frequency-limited in the same manner as for the wing-stroke curves.

Figure 5 is an example of the curves obtained for the total vertical force and of the corrected curves giving the variation of lift force during a wing stroke.

Among the different causes of errors which have been considered [16], some are liable to modify details in the shape of the curves, but none of them can change significantly the amplitude of lift variations. Our conclusions are based on the latter.

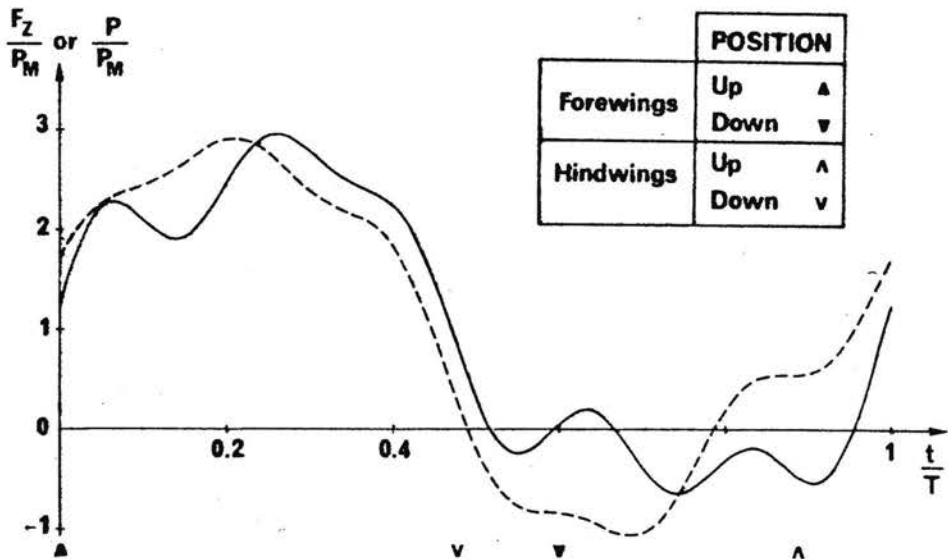


FIG. 5. Flight I. Gross vertical force F_z (dashed line) and real lift L (solid line) normalized by average lift L_A , as a function of time t normalized by period T . The pass band is limited to the fifth harmonic.

3. Results and discussion

We analysed completely one wing cycle in recordings corresponding to six different flights in which the average lift L_A differs from the weight of the locust by less than 15%. Qualitative analysis of the force signal and of wing movements relative to other flights showed that the same general characteristics were observed in all cases.

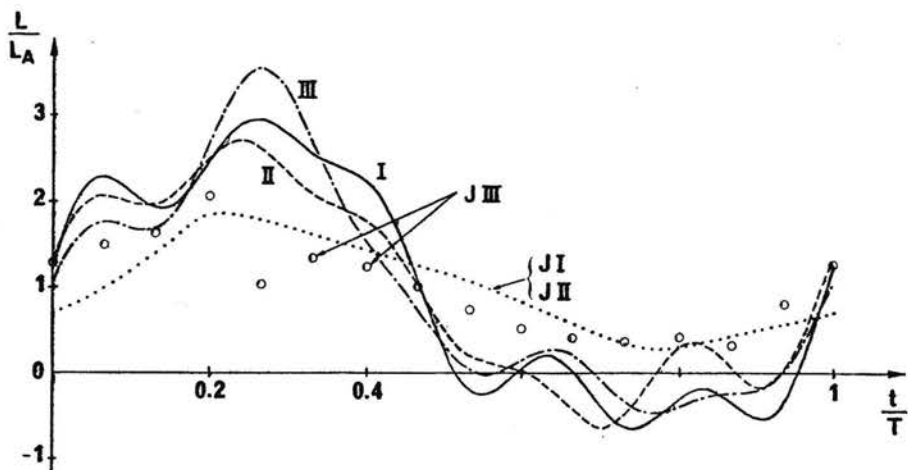


FIG. 6. Variations in lift during a wing-beat cycle. Dotted line and circles: Jensen's results derived from normal flights J I and J II, and from the very high performance flight J III, respectively. Other curves: flights I-III of the present study (see table 1). Coordinates as in Fig. 5.

We only present the results obtained for three typical flights and a comparison with Jensen's data. The principal parameters of the flights are given in Table 1. The lift curves are shown in Fig. 6. The instantaneous lift and the time are normalized with the mean lift L_A and with the stroke period respectively; this enables us to make a comparison between insects whose weight, mean lift, and wingbeat frequency are different.

Table 1.

flight No.	present experiments			Jensen's experiments		
	I	II	III	JI	JII	JIII
flight velocity (m/s)	3.4	3.9	3.6	3.5	3.6	3.2
wingbeat frequency (Hz)	21.9	20.1	19.3	17.5	18.3	21.2
insect weight (g)	1.75	2.12	1.95	2.3	2.04	1.69
average lift L_A (g)	1.97	2.28	1.68	2.23	2.26	2.74
relative lift L_A /weight	113%	107%	86%	97%	111%	162%
relative amplitude ($L_{max} - L_{min}$)/ L_A	3.5	3.3	3.9	1.6 (mean)		$\approx 1.7^*$

* This result is derived from figure III, 17 in the article by Jensen (1956). Note that in this figure ordinate represents the lift normalized by the weight of the insect and not by the average lift as stated in the text of the article.

Our results are significantly different from Jensen's in essentially two aspects:

- 1) direct measurements show that lift is negative at certain moments during the upstroke,
- 2) the lift variations are far greater than those observed from measurements on detached wings.

The amplitude of these variations may be characterized by the difference between maximum and minimum instantaneous lift L , normalized by average lift L_A . The values of this "relative amplitude" are given in Table 1 for the different flights. It may be observed that its mean value is greater than 3.5 in our curves, and less than 1.7 in Jensen's curves, even if the latter include the very high performance flight J III.

Hence the relative amplitude obtained by direct measurements on insects in flight is about twice as that obtained by measurements in steady-flow conditions.

If our results are correct, this large discrepancy in the amplitudes can be explained in two ways:

- 1) The lift values calculated by Jensen are not exact. But in this case it would be fortuitous if the mean aerodynamic forces that he measured and calculated coincide; therefore, a quasi-steady type of analysis could not be justified by this equality.

- 2) Jensen's results are correct. In that case they are compatible with ours only if the existence of important unsteady effects is acknowledged.

Let us note that this second alternative is further enhanced by the fact that Jensen's results do not preclude the existence of significant unsteady effects. The equality of measured

and calculated forces merely shows that if they exist, these effects successively produce increases and decreases in the aerodynamic forces which practically offset each other in the course of a cycle. This may be observed to occur, for example, in the case of profiles oscillating in a constant velocity flow, when the average angle of attack approaches the stalling angle; experiments and computations carried out at high Reynolds number, but reduced oscillation frequencies comparable to those of the locust showed that instantaneous lift and drag values are alternately higher and lower than steady values at the corresponding angles of incidence [17].

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