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Control of the flight of the dragonfly *Sympetrum darwinianum* Selys I. Dorsophotic response

By

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(With 5 Text-figures)

Flight is perhaps one of the most complicated forms of the animal locomotion. The complication demands very precise coordination among the various organs of the body. Sensory organs should supply a large amount of information relevant to the environmental as well as proprioceptive conditions, and the central nervous system should furnish precisely timed and accurately valued motor outputs to the individual effectors contributing to the wing movement, and to other body musculatures as well. Information provided by sensory organs will thus modulate the wing beat amplitude, angle of attack, flight posture of the body, and many other parameters of the flight activity, and will finally result in cessation or initiation of flight and any alteration of flight attitude which enables the animal to maintain the required condition of the flight under the various external and internal demands.

In insects, many forms of stimulation are known to induce their flight. One of such forms was described by Fraenkel (1932) as the 'tarsal reflex'. Sudden removal of contact to the legs instantaneously initiates wing movements of almost all of the insects tested except some beetles. Some forms of stimulus are exclusively effective to maintain the flight activity once it has commenced. Air current passing around the head is found to be effective to sustain the flight activity in *Schistocerca* (Weis-Fogh 1965) and in *Muscina* (Hollick 1940). Asymmetric impinging of the air jet on insect is also known to produce a certain reaction which seems to be contributing to the compensatory stabilizing mechanism of *Schistocerca* (Weis-Fogh 1949). Among other sensory inputs which may modify the flight parameters, the influence of light on the flight performance has also attracted attention of many investigators, because of the dominance of the surrounding light as an environmental factors governing the life of these insects. An effect on dragonfly was partially analysed by von Buddenbrock (1937) in terms of the

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'Lichtrückenreaktion', an orientation response depending on the direction of illumination falling on the upper part of the compound eye. Mittelstaedt (1950) also studied what part of the compound eye plays the decisive role in this response and revealed also the role of the head as an organ of balance in dragonfly. However, there has been almost no attempt to understand more fully about what kind of control mechanism is involved in this visual response. It appeared to be very important to analyse in full detail the control mechanism of flight muscles during the wing movement, pattern of processing of input information in thoracic ganglia, and possible innate pace setting mechanism in connection with delicate timing system of individual flight muscles.

Dragonfly seems to be a remarkably favourable material for the studies of this line because of the synchronous nature of the flight muscles, a relatively simple antagonistic arrangement of elevator and depressor muscles, and finally readily accessible nervous and muscular arrangements.

This paper, the first one of the studies on the dragonfly, will give a general description of dorsophotic response and related observations.

Material and Method

The dragonfly, *Sympetrum darwinianum* Selys which are quite abundant in Sapporo area from the middle of August to the end of October were collected and kept in a refrigerator at around 10°C (Neville 1960). Low temperature storage will prevent the dragonflies from exhausting by restless fluttering of their wings which is rather inevitable when a large number of them were confined in a small cage and left at room temperature. A brief recovery time for the low temperature immobilization, of a few minutes, was found to be sufficient for the restoration of normal activity of the specimens brought back to the room temperature. This technique of storing enabled us to use completely active individuals for more than 24 hours after field collection, if a precaution was taken to maintain a suitable humidity in the refrigerated cage. The animal tested was generally fixed on a thin metal rod with the aid of colophony bee-wax mixture at its sternum.

Observation of the amplitude and frequency of wings was performed with the aid of a stroboscopic light source (Toshiba SS4B with SX2B combined), and the same light source was used to give stimulation of a train of flashes in order to detect a possible effect of strong cyclic visual input. Ordinary single frame photographs as well as cinematographic recordings with or without the strobolight flashes were taken to analyse wing stroke amplitudes and wing stroke plane angles. Angle of attack of the wing was not quantitatively measured in the present experiment. The detailed study of this aspect will appear in a following paper. Measurement of the wing beat frequency was also performed electrophysiologically. A silver silver-chloride electrode of 100 μ in diameter exposed only at its tip was inserted into the first pleural muscle of mesothorax (I Ip_{m_1} , after Clark 1940). Activity of preferably one motor unit of the I Ip_{m_1} was then displayed on an oscilloscope simultaneously with signals of the strobolight source which serves as cyclic stimulation of the eyes during flight and recorded with a long recording camera. Illumination from various direction was given by forming an array of incandescent lamps with thin matt paper attached as diffuser and placed at an equal distance to provide the illumination of identical intensity, and by lighting one of them to give the illumination from either overhead or one side,

sometimes from beneath as well. Most commonly used intensity was 2000 luxes at the point of the eyes of insects, and weak illumination of 50 luxes was sometimes left through the experiment to maintain the background illumination which is found to be necessary to have uniform results and to facilitate visual observation.

Stability of the frequency of the wing beat against an influence of the almost synchronous strobolight flashes was tested because of a possible disturbance of the strobolight on the flight performance of the dragonfly. Removing a tarsal contact and/or pinching the abdomen were effective to induce the flight activity. Air current was given by a blower at a speed of 2.0 meter per second which was sufficient to maintain the flight activity. It was also noticed that the turning of the light on or off itself sometimes generated the flight initiating response.

Results

Normal flight parameters: Wing beat frequency was measured both stroboscopically and electrically. Wing beat frequency was primarily determined by the frequency of stroboscopic flashes which was necessary to freeze the wing beat. Since innate frequency setting mechanism of wing beat could be somehow affected by invasion of visual information of a close frequency, the frequency of the wing beat was also monitored by recording electrical activities of a flight muscle $IImp_1$. The measured wing beat frequency by those two methods agreed well regardless of wide range of illumination intensity. The wing beat frequency averaged 30 cycle per second ranging from 24 to 36 c.p.s. For one second or little more from the onset of the flight activity the frequency stays 2 to 3 c.p.s. lower than the maximum value which the insect will attain afterward. Then preceding the cessation of the flight the frequency gradually start to fall to a final low of again 2 to 3 c.p.s. less than the maximum.

Wing beat amplitudes were recorded by taking single frame photographs of the animal in flight with light reflecting pieces of aluminium foil attached on the tip of hindwings and in the middle of forewings. Measurements of wing position I were made on the photographs and are expressed as degrees from the lower vertical about the longitudinal body axis (Weis-Fogh and Jensen 1956). Of 20 individuals measured in normal condition and with the body axis of 0° to the horizontal, average values for wing positions were: I_{max} . for forewing, 150° , for hindwing, 130° , I_{min} . for forewing, 65° , for hindwing, 65° . Stroke plane angle of same group averaged 35° from the vertical (Fig. 1). I_{max} . of 115° and I_{min} . of 70° were reported by Neville (1960) in the forewings of *Aeshna cyanea* (Mueller).

Sudden decrease in illumination intensity was found to induce an increase in amplitudes of both wings.

Effects of asymmetric illumination: When the light intensity falling on the eyes of a dragonfly was asymmetric, it is noted that the wing amplitude of the darker side becomes invariably larger than that of the brighter side. The effect was ascertained by both stroboscopic and cinematographic observations. 2000 luxes light falling on the one side, while the other side was illuminated with 50 luxes, produced the

wing amplitude difference of about 30 degrees between two sides. Generally Γ_{\max} increases by about 10 degrees in both the fore and hindwings of the darker side, while the values of Γ_{\min} decreases by about 10 degrees in these wings. There is also an increase of about 10 degrees in the Γ_{\min} of the brighter side bringing the amplitudes of the wings of the both wings of the brighter side little less than the normal values (Fig. 1)

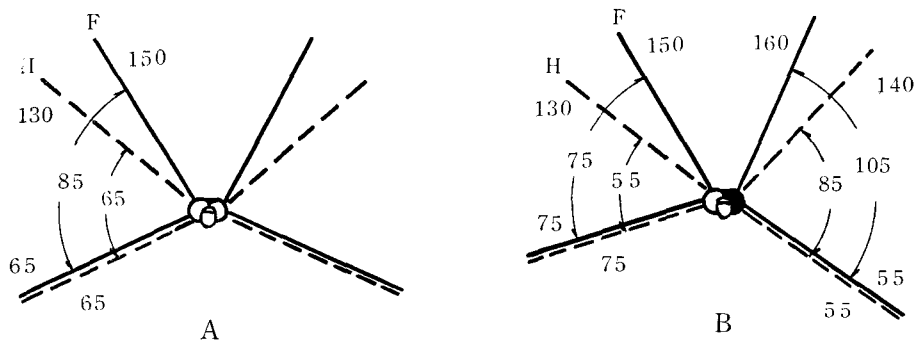


Fig. 1. Average wing positions (Γ) and wing amplitudes in normal (A) and asymmetrically illuminated (or occluded) (B) dragonflies. Darker or occluded side is indicated by blackened eye in B.

There is no detectable change in the stroke plane angle of the wings of both sides under the asymmetric illumination, except a slight change in the path of the wing tips. In darker side, the path becomes more wider in fore and aft direction in a barely detectable extent.

Changes in amplitude by the difference in visual stimulus was also determined by blinding of the one compound eye as well as the lateral ocellus with black enamel. When one of the compound eye was painted black, the insect shows the enhancement of the wing beat amplitude of the occluded side in the same way as in the case of asymmetric illumination.

The occlusion of either lateral or median ocellus has no apparent effect on the wing beat amplitude. This finding was confirmatory to the result of Mittelstaedt (1950) in the static control of wing posture in *Anax imperatur* Leach. Only when the compound eye of one side of the animal was blinded with coating, there was an unbalanced change in wing amplitude.

If one observe more closely the behaviour of the dragonfly under the asymmetric illumination, it will be noted that the head of the dragonfly will first start to rotate in a direction bringing the uppermost ommatidia to the direction of incident light, then the wings will follow this by changing their amplitudes.

Recording of nerve impulses: The sensory information was recorded as the electrical activity of the connectives between the first and second thoracic ganglia by placing two silver silver-chloride electrodes placed separately on each connectives.

And the nerve impulses were recorded from them when the asymmetric illumination was given by decreasing the light intensity falling on an compound eye leaving the other side illuminated continuously.

There is an increase in impulse frequency recorded from the connective of the darker side, which shows a certain extent of adaptation, though the frequency remains higher than normal. There seems to be a slight 'on' effect when the light intensity is brought back to the original level, but this is not profound and long lasting as the 'off' response. The simultaneous recording of the activity of the contralateral connective shows barely recognizable increase in impulse frequency. The large increase in frequency of ipsilateral side seems to indicate that the optic input as well as the sensory hair input controls the wing parameters through the ganglionic conversion of the tonic input into the phasic output of definite regularity to the flight musculatures. Further details of the nature of this processing mechanism of information in the ganglia will be discussed in another paper.

Stability of wing beat frequency: Preliminary checking of a possible interference of the flashes used to measure the wing beat frequency on the stability of wing beat

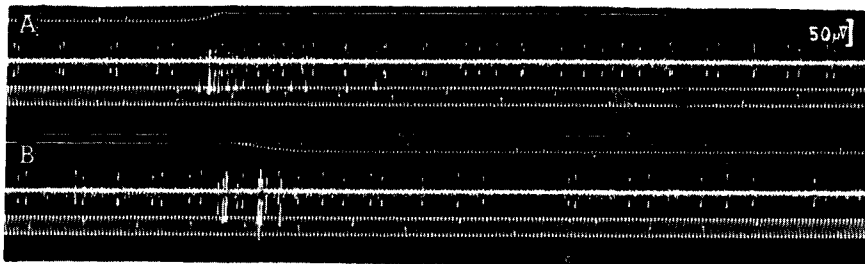


Fig. 2. Electrical activity of the right side connective between the 1st and 2nd thoracic ganglia, when the illumination of the ipsilateral compound eye was turned off (A) and on (B). Top trace: illumination, middle trace: nervous activity, bottom trace: 50 c.p.s.

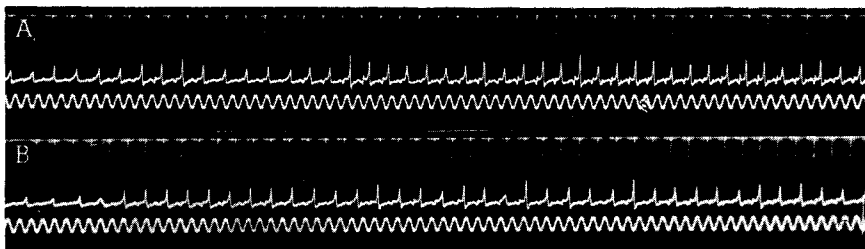


Fig. 3. Electrical activity of a motor unit of the mesothoracic first pleural muscle (IIpm₁) recorded during the cyclic stimulation of the eyes with strobolight flashes of 30 c.p.s (A) and 31.5 c.p.s. (B). Top trace: flash, middle trace: motor unit activity, bottom trace: 50 c.p.s.

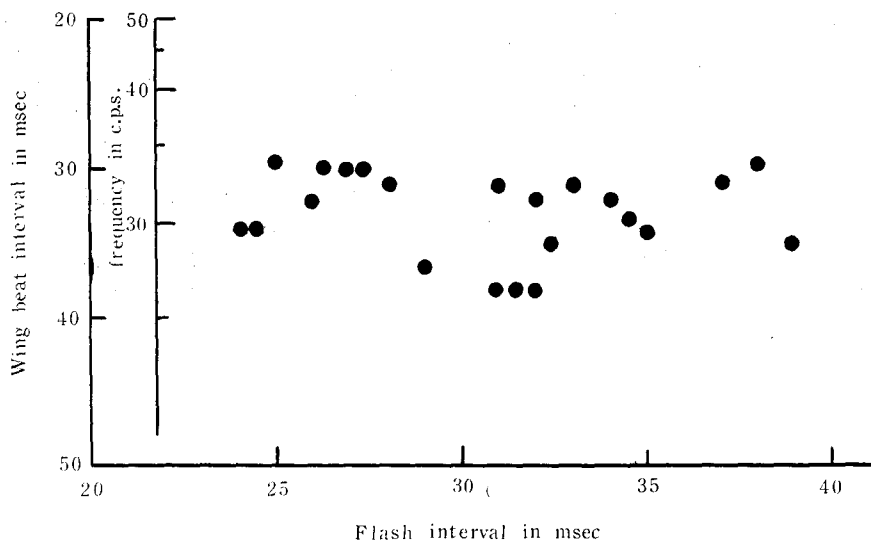


Fig. 4. Wing beat intervals plotted against the flash intervals. Wing beat intervals were measured as an average of 10 beats starting from 10 seconds after the onset of each flight. Data from 22 flights of the same specimen.

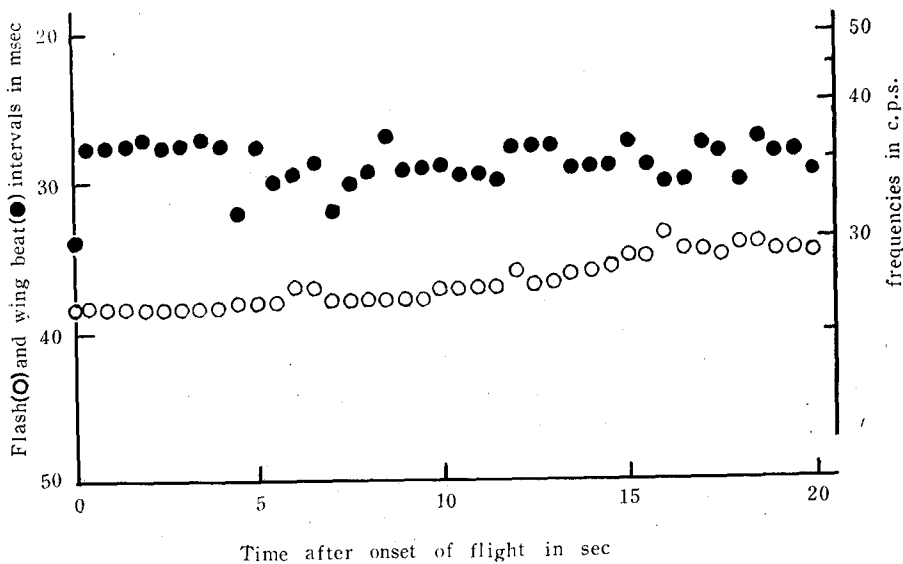


Fig. 5. Intervals of wing beat (●) and flash (○) of every 0.5 second after the onset of flight. Flash frequency was gradually increased during the flight of a specimen. Note the tendency of deviation of the wing beat interval at the time of change in flash interval.

frequency itself was carried out by monitoring the wing frequency through electrical recording of a motor unit activity of the one of the pleural muscle, Ipm_1 , while the stroboscopic flashes of various frequencies were given. When the average frequencies of both flashes and wing beat were taken into consideration, the results seemingly showed no cross-correlation between these two frequencies (Fig. 4). However, there is one feature which should be studied more precisely. If the each interval of the wing beat was plotted against the intervals of the flashes of the same instance, which were varied stepwise in each 3 sec or more, there seems to be a tendency of the fluctuation of the wing frequency corresponding to the moment of shift of the flash frequency, indicating the wing beat frequency becomes less stable at this moment (Fig. 5). Accumulation of a large number of data and subsequent checking of cross-correlation between these two frequencies could be a revealing approach to the visual control of the flight. Though the fluctuation of the wing beat frequency of this extent is not likely to have any significance in flight performance of the insect, and seems to be, at present, of no disturbing nature to interpret the results of present study.

Discussion

The ability of the dragonfly to align their back to the stronger side of illumination was first partly described by von Buddenbrock (1937) who gave the term of 'Lichtrückenreaktion', dorsophotic response, on this phenomenon. The integral action of the dorsophotic response together with the equilibrium sense organs in the swimming posture of some fishes has also been under the study of some investigators (Holst 1935, 1950). Since the flying insects have no equal organs to the statocyst of fishes and still they are generally able to maintain a stable flight posture relative to the ground, the role of the visual organs for orientation should be more important in these animals. In fact, the responses to light of dragonfly (Mittelstaedt 1950) and of locust (Goodman 1965) indicate that the direction of light is a decisive factor of orientation of these insects in flight. In these insects, information about the direction of incident light was first conveyed to the muscles of head rotation existing around the neck, and the resulting compensatory rotation of the head then induced the change in wing parameter through the mediation of the sensory hairs detecting relative position of the head against the rest of the body. When all of the sensory hairs around the neck were destroyed, the locust is known to be no longer able to hold the body in line with the head, thus the animal becomes unable to remain orientated relative to the direction of light, although they responded in the usual manner to the onset of illumination (Goodman 1965). However, this is not true in some insects, for instance, in the honey-bee *Apis mellifera* (Wolf and Zerrahn-Wolf 1936), indicating the visual input alone is sufficient to maintain the orientated flight without the mediation of sensory hairs. Not many studies have been done on the relation between the dorsophotic and the various parameters of wing movement. Mittelstaedt (1950) observed only the tilting as well as the

twisting of resting wings to compensate the rotation of the head to the body axis, and Goodman (1965) reported a change in amplitude in the locust wings as a part of dorsophotic response but did not clarify the detail quantitatively.

Altering the lift between right and left side of the body could be accomplished by various ways, and any one of many parameters of wing is likely to be related to the lift. Possible importance of the modification of the angle of attack as a means to control the lift was favoured by Chadwick and Williams (1949), and Chadwick (1951) in their studies on *Drosophila* and by Weis-Fogh (1956) in locust. Though the present study did not go in detail to analyse the change in angle of attack during the asymmetric illumination, the large increase observed in the wing amplitude of the darker side seems to be sufficient, at least in dragonfly, to explain the required change in lift, and a preliminary observation did not reveal any noticeable variation in this angle. The increase of the lift will cause a rolling of the body and in an insect experimentally fixed, restricting in yaw and pitch but freeing in roll, holding of the body axis relative to the direction of light will be complete.

The apparent incapability of ocelli to produce the dorsophotic response without the compound eye is elucidated but may need further analysis, because a profound 'off' response from the ocelli of dragonfly was reported by Ruck (1960), which seems to indicate a certain role of the ocelli pertaining to the visual control of behaviour.

A possibility still remains that the ocelli might be functioning as an auxiliary receptor for this response though could not function by itself but in combination with the compound eye. Occlusion of the ocelli is reported to have a decreasing effect on the sensitivity of the compound eye (Cornwell 1955, Goodman 1965).

The results of the experiments with asymmetric illumination and with occlusion of the eye can not be interpreted on the same line, though they gave the similar results. In the asymmetric illumination, the optomotor reaction to bring the uppermost ommatidia of the same eye to the direction of incident light will be initiated first, consequently carrying the both eyes into the light field. This results in a binocular orientation. Pertinent quantitative study may reveal a certain difference in the responses obtained by these two methods.

Recording of nerve impulses at the connectives indicated there is an information inflow into the second thoracic ganglion and outflow from it in a form of tonic discharge. Synchronous nature of the flight muscle of dragonfly necessitates phasic output of motoneurons supplying the musculature and the amplitude variation observed can only be achieved by the phasic modification of the minute details of cyclic motor output, demanding the presence of a mechanism which will convert the tonic sensory information into a phasic form. The complicated nature of this mechanism deserves the extensive studies in the future.

Summary

1. Wing beat frequency of the dragonfly *Sympetrum darwinianum* Selys was measured both with stroboscopic and electrophysiological methods. Normal

wing beat frequency was found to be 30 c.p.s. in average.

2. Measurements of the wing positions of fore- and hindwings were made photographically, and average values of wing amplitudes were found to be 85 degrees for the forewing and 65 degrees for the hindwing.

3. Both asymmetrical illumination and unilateral occlusion induced increases of the wing amplitudes in the fore- and hindwings of the darker side producing more lift necessary to attain the dorsophotic position.

4. Nervous activity relating to the asymmetric illumination was recorded at the connective between first and second thoracic ganglia.

5. Stability of the frequency of wing beat against the cyclic visual input was tested by stimulating the eyes with stroboscopic flashes. No apparent correlation was found between these two frequencies.

6. Role of the change in the wing amplitude and the nature of the controlling mechanism were discussed.

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