ISSN 0022-0930, Journal of Evolutionary Biochemistry and Physiology, 2008, Vol. 44, No. 6, pp. 643—656. © Pleiades Publishing, Ltd., 2008.
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REVIEWS

Structural-Functional Peculiarities of the Wing Apparatus of Insects That Do Not Have and Do Have the Maneuvering Flight

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Received July 23, 2008

Abstract—The work considers character of behavior in flight and discusses peculiarities of structural-functional organization of the wing apparatus of two representatives of insects—the migratory Asian locust *Locusta migratoria* (a low-maneuvering insect) and the dragonfly-darner Aeshna sp. (an insect able to perform complex maneuvers in air). The main principles underlying the insect wing apparatus activity are considered and the mechanisms allowing the dragonflies to perform complex maneuvers in the flight are analyzed in detail.

DOI: 10.1134/S002209300806001X

Key words: locust, dragonfly, maneuvers in flight, activity of wing muscles.

INTRODUCTION

Study of mechanisms of nervous control of the animal and human motor behavior is one of the main tasks of modern neurophysiology. Of particular interest in this aspect are insects—the higher representatives of invertebrates. It is interesting to note that it is in insects (locusts) that Wilson was the first to reveal [1][1] in 1961 and to study subsequently [2–8] the rhythm generators playing an important role also in control of motor behavior in other animals (in locusts—of the flight). Comparative analysis has shown a principal similarity in the structural-functional organization of such generators not only in different motor systems and in different insects (locust, dragonfly, butterfly), but also in the higher representatives of vertebrates—mammals [11, 12, comps. 13–15].

The latter circumstance, while taking into account a relatively small number of neurons providing the insect motor behavior, allows using these animals as sufficiently simple and convenient models at solution of problems not only of comparative, but also of general neurophysiology. At present, study of mechanisms of generation of motor rhythm in insects has being successfully continuing [16–22].

However, the rhythm generators, with all their significance, perform only the function of a motor providing the straightforward movement of the animal. Meanwhile, insects, like other well-organized animals, are able to perform during movement various maneuvers whose control is realized already by other neuronal mechanisms responsible for activity of special “steering” muscles. It is important to note that whereas the generator

[1] In connection with a large volume of the used literature, we will refer in the paper predominantly to the original and summarizing works as well as some reviews.

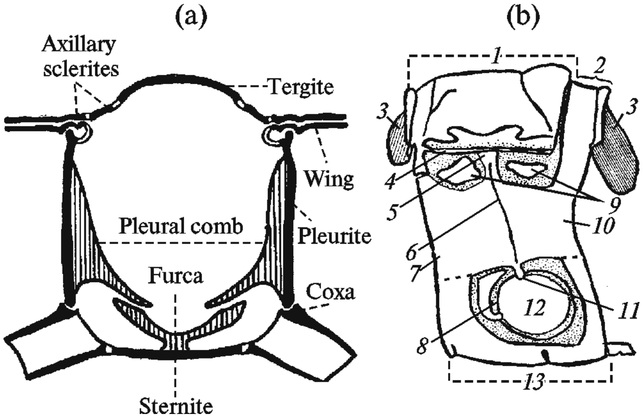

Fig. 1. Scheme of structure of the wing-bearing segment of the insect chest (from [39]). (a) Transverse section, (b) lateral view. (*1*) Notum; (*2*) postnotum; (*3*) fragma; (*4*) base of wing; (*5*) pleural column: (*6*) pleural suture, (*7*) episterna, (*8*) trochantine, (*9*) basalar and subalar sclerites, (*10*) epimera, (*11*) coxal process, (*12*) coxal invagination, (*13*) sternum.

mechanisms are working in thoracic ganglion of the trunkal brain rather autonomously, the steering mechanisms are guided by the command coming into the ganglia from the higher brain centers tracing the situation surrounding the insect. Thus, participating in control of complex forms of the insect motor behavior also are the significantly more complicated neuronal mechanisms. Unfortunately, these mechanisms at present have been studied very little; whereas motor systems of locusts and other insects are studied in hundreds of works, the study of steering systems is published only in several tens of papers (see [23–28], etc.).

Of course, a certain, although indirect, help in understanding the steering mechanisms can be provided by numerous studies of peculiarities of the flight aerodynamics and kinematics of insect wings (see [29–34]). Of interest are experiments on modeling of the insect flying possibilities [35–38]. However, without direct neurophysiologic experiments in this direction the problem hardly can be solved. Therefore, in the present paper, we will be based predominantly on the data obtained by neurophysiologists.

At the same time, study of the corresponding neuronal mechanisms, in turn, is impossible without knowledge of the role and mechanisms of functioning of the steering muscles as well as of morphology of the chest skeleton, to which these muscles are attached. It is these issues that are analyzed in the present paper. We will consider here the available data about peculiarities of the structural-functional organization of the wing apparatus of two insect representatives, in which mechanisms providing the straightforward flight have been studied the most completely: the locust—a relatively low-maneuvering insect, and the dragonfly able to perform exclusively complex maneuvers in the flight. We will start this consideration from description of general principles of structure of the insect thoracic part.

STRUCTURE OF THE INSECT CHEST SKELETON

Skeleton of each insect segment is formed by four main sclerites: the superior—tergite, the inferior—sternite, and lateral—pleurites (Fig. 1a). All segments are covered with a dense, but sufficiently elastic cuticle performing function of the external skeleton—exoskeleton; muscles are attached to certain points inside such skeleton.

The chest carrying locomotor organs consists of three segments: anterior chest (prothorax), middle chest (mesothorax), and posterior chest (metathorax). Skeleton of thoracic segments is more complex than of abdominal ones: tergites, pleurites, and sternites are subdivided here into series of secondary smaller sclerites.

Well developed in winged insects is pleurite. It contains ventrally the coxal process, dorsally—the winged process (the pleural column). From the coxal to the winged process, the inclined suture runs; it divides pleurite into the anterior area—episternum and the posterior one—epimeron (Fig. 1b). Tergite in the thoracic part is called notum, or dorsum, while sternite—sternul, or chest. Accordingly, differentiated are pro-, meso-, and metasternum. In the chest, where particularly powerful muscles are attached to exoskeleton, it is especially firm. A line of supporting folds forms the internal chest skeleton (endoskeleton). Let us consider only the main ones of these folds.

The above-mentioned pleural suture represents the external part of the powerful internal fold of the pleurite cuticle—the pleural comb. Invagination of the sternite cuticle—the V-shaped suture forms furca. The pleural combs and furca in each chest segment form a system of transverse beams (Fig. 1a) providing the necessary rigidity to the thoracic part.

Folds of the tergite cuticles, which also go across the body and serve for attachment of muscles, are called fragma. There are three such fragmae: between pro- and mesothorax, between meso- and metathorax, and between metathorax and abdomen. Also there are two cuneate fold systems (the parapsidal and V-shaped one) increasing the tergite rigidity. These folds divide the tergite into three parts: anterior—prescutum, middle—scutum, and posterior—scutellum.

Rather complex is structure of joint of tergite with pleurite—the area of location of wings. Bases of wing veins do not reach tergite. Between them and tergite there are sclerites playing an important role during the wing movement (Fig. 2). Lying dorsally are several axillary sclerites and associated wing plates. The number and complexity of these structures are different in insects of different genera. In typical cases, three or four axillary sclerites are identified. Located ventrally to the wing are two alar (basillary and subalar) sclerites, while anterior to and above the wing tegula—the sensory organ playing an important role in control of the wing stroke [42, 43].

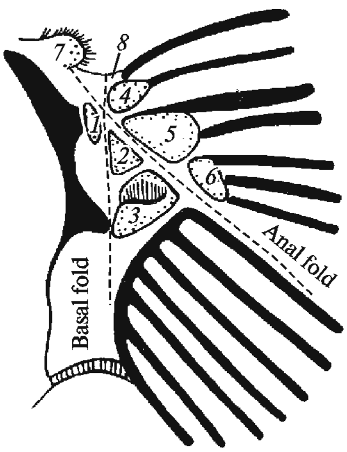

Fig. 2. Axillary sclerites (*1–3*) and their connected plates (*4–6*) in the base of wing (from [40]). (*7*) Tegula, (*8*) costal fold.

Each of three thorax segments carries one pair of feet, while meso- and metathorax in flying forms—additionally the wings. Two posterior, wing-bearing thorax segments are called pterothorax. It is to be emphasized that unlike the majority of other body appendages of these animals (and unlike bird and bat wings) the insect wings do not contain any own internal muscles and are activated with aid of thoracic muscles or directly or indirectly with aid of the corresponding sclerites.

BEHAVIOR OF LOCUSTS IN FLIGHT AND STRUCTURAL-FUNCTIONAL ORGANIZATION OF THEIR WING MUSCLES

Locust belongs to the Neoptera insects able to fold wings along the body at rest, to the order Orthoptera, to the family grass-hoppers (Acrididea). There are identified more than 10000 species of Acrididea, but we will consider here only two of them: the migratory, or Asian, locust *Locusta migratoria* and the desert locust *Schistocerca gregaria*. Insects of both species have absolutely similar total organization as well as organization of the wing apparatus.

Locust is an herbivorous insect able to overcome hundreds of kilometers in the search for food, while during migration—even thousands of kilometers. The locust flight is not distinguished by a great maneuverability, particularly that it usually moves in total flocks; however, this insect is able to perform non-steep turns and some other maneuvers associated with upward flight, landing, provision of stability of its movement.

Locust has two pairs of large wings that reach 5 cm in length. This is the posterior-motor insect. By shape, the surface area, and structure, these wings differ from the more narrow and dense anterior wings. The anterior and posterior wings are closely connected between them in their work (mainly on the basis of nerve–muscle coordination)[2], although function with a delay by phase of duration of several milliseconds. The first to be involved into the wing cycle are the posterior wings. In other words, the phase relation between the

[2] The connection between the anterior and posterior locust wings also is partly due to mechanical causes—peculiarities of articulation in the meso- and metathorax and even due to aerodynamic ones—because of interference of air flows around the wings during their work.

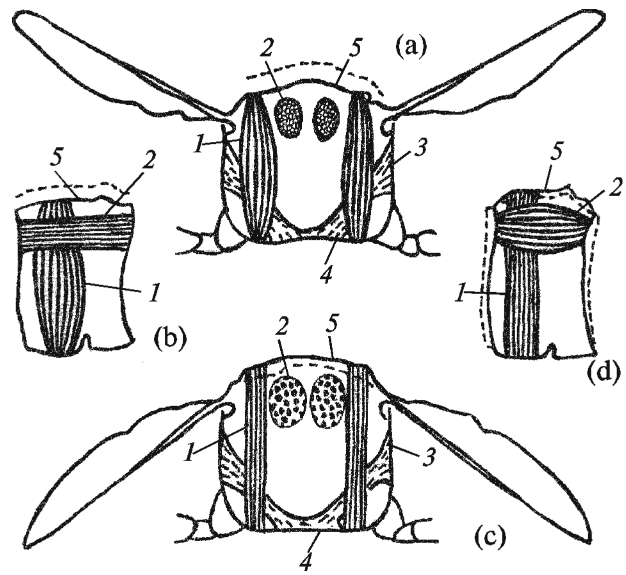

Fig. 3. Schemes of work of wing muscles of indirect action. (a), (c) Contractions of dorsoventral and longitudinal spinal muscles (transverse sections of the thoracic segment); (b), (d) contractions of the same muscles (longitudinal sections of the thoracic segment). (*1*) Dorsoventral; (*2*) longitudinal spinal muscles; (*3*) pleurite; (*4*) sternite; (*5*) tergite. *Broken lines*—position and boundaries of segments, which precede this position or follow it.

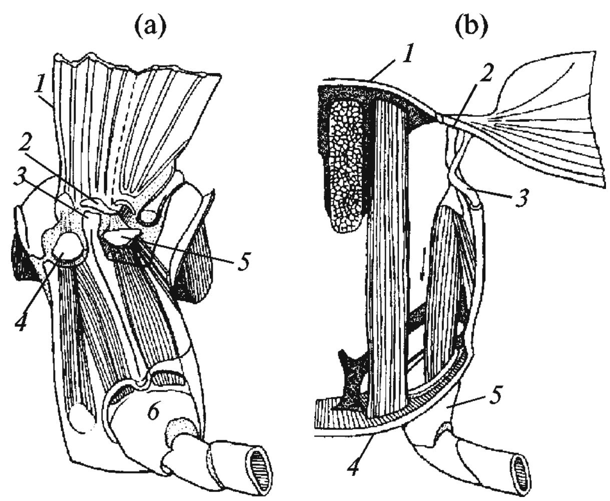

Fig. 4. Wind muscles of the direct action on the wing (from [39]). (a) Sagittal section: (*1*) wing, (*2*) the second axillary sclerite, (*3*) pleural column, (*4*) basalar muscle, (*5*) subalar muscle, (*6*) coxa; (b) transverse section: (*1*) tergite, (*2*) pleural column, (*3*) basalar muscle, (*4*) sternite, (*5*) coxa.

posterior and anterior wings in locust are fixed, which of course does not allow this insect to perform complex maneuvers in the flight [44, 45].

During the established straightforward and horizontal locust flight the main parameters of movement of its wings as well as some effects produced by these movements remain sufficiently constant: the wing stroke frequency (on average) in the desert locust amounts to 17.5 per 1 s, the stroke amplitude to 60–70° for the anterior and 110° for the posterior wings, plate of the wing strokes 30°, the carrying power about 2 g, and the flight rate 3.5 m/s (12.6 km/h) [36]. Maximum of the carrying power in the flight (71%) in locust is provided by posterior wings. This power is provided by anterior wings only during their movement down, while by posterior wings—during movement during the wing movement not only down, but also up [47].

Like in the majority of other insects, the muscles providing the wing strokes during the locust flight are not attached directly to the wings and act on the wings with aid of sclerites of the back– tergites. How this occurs can be seen in Fig. 3.

Reference point of the wing at its movements is the pleural column that is located almost at the wing base; thereby the wing represents a two-arm lever with different arm lengths, the muscles descending the wing—depressors being located the tergite fragmae. These are the longitudinal muscle of back. Muscles ascending the wing—elevators are located between the tergite and sternite. These are dorsoventral (tergosternal) muscles. Both the spinal longitudinal and the dorsoventral muscles are called (and in fact are) muscles of indirect action on the wing or the indirect wing muscles.

When the dorsoventral wing muscles are contracted, the tergite, to which these muscles are attached, slightly descends and its edges pull down the wing base, which leads to elevation of the wing plate (Figs. 3a, 3b). During contraction of the spinal longitudinal muscle the reverse relations take place; fragmae approach each other, while tergite is somewhat bending (Figs. 3c, 3d), which results in the movement of wing down. Although these tergite movements are very small, they, due to the long lever arm, are transformed into the wing plate movements quite sufficient by amplitude.

Apart from the wing muscle not connected with the wing base, locust also has muscles not attached to wing. These are muscles of direct action on wing, or the direct wing actions (Fig. 4). Among the muscle of direct action, the basilar and subalar muscles playing an important role in twisting of the wing plate are to be identified, as well as the third ones—axillary muscles that are their antagonists.

Location of the main wing muscles in meso- and metathorax of the desert locust is presented in Fig. 5. The mode of action of these muscles is as follows. The wing stroke down is provided predominantly by the spinal longitudinal muscles (81 and 112) hat are simple depressors. However, during the intensive flight, the basilar and subalar muscles also participate in the wing movement down. The wing flap is provided mainly by the dorsoventral muscles (83 and 113, as well as 84). They are also assisted by other muscles—85 and 114, 89 and 118, 90 and 119, 91 and 120, 103 and 133. Thereby, all these muscles are involved (or can be involved) in work of the"wing motor". During the movement down, the wing is pronated. Pronation is an active process, it is provided by the basalar muscles: the first one—97 and 127 (the main pronators) and the second one—98 and 128 (the auxiliary pronators) as well as by the subalar muscles 99 and 129. Effort of these muscles is directed against the supinating action of the third axillary muscle (85 and 114) that begins supination only at the end of stroke in each chest segment and thereby prepares wing to the movement upward. And although wing moves upward in the supinated position, supination in this phase of the wing cycle is realized not by action of some wing muscles: here it is the passive process. The supination is provided by elastic properties of the chest skeleton as well of the base of the wings themselves.[3]

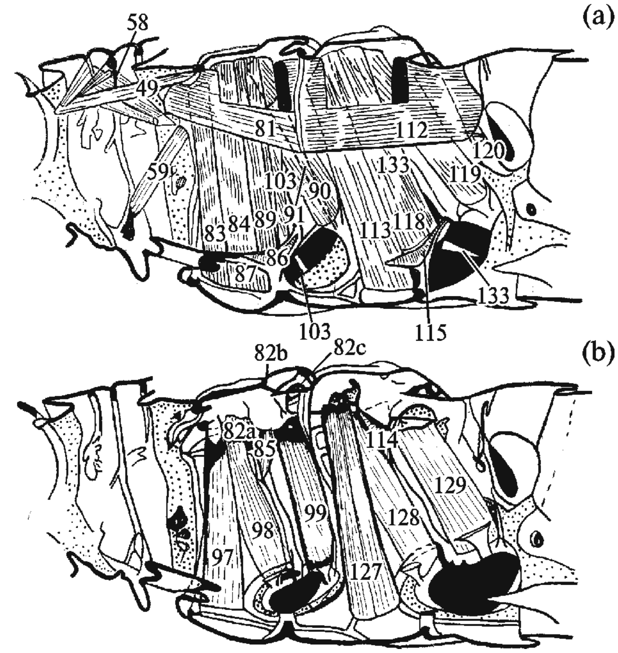

Fig. 5. Position of wing muscles in the locust meso- and metathorax. View from inside (from [2]). (a) Medial, (b) lateral groups. Explanations in the text.

Muscles regulating the degree of twisting of wings during the locust flight regulate thereby the degree of the lifting force and of the tractive force evolved by wings. With aid of the asymmetrical on the right and on the left) work of these muscles, locust can perform turns as well as some other maneuvers. However, these possibilities in locust are quite restricted. The point is that locust is an insect-stayer, and during the flight (especially for a long distance) it is important for the insect not to maneuver, but, on the contrary, to preserve stability of its flight in spite of a possibility of the appearance of external disturbing actions, for instance, of gust of wind. This function in locust is also performed by muscles of the direct action on the wing, although the body position in this insect is corrected, when necessary, by involvement of the corresponding movements of abdomen, feet, and head (for details, see [6]). However, since such situations during the locust flight seem to appear not too often (to save energy, locust strives for fly with the wind), its systems of the "first reacting" in the flight did not get significant development. It is not by chance that even the muscles of the direct action on the wind (the basalar and subalar ones) in locust are "pluralists"—additional depressors, while independent work of all four wings in this insect to perform complex maneuvers is simply impossible.

The number of motor units composing the locust wing muscles is not high (Table 1). Accordingly, the number of axons innervating wing muscles of this insect also is rather low.

As a result of performed studies on the locus flying with a string, Wilson [52] recorded the whole

[3] It is to be reminded that pronation represents rotation (twisting) of the wing plate relative to the longitudinal axis, at which the anterior wing edge goes down, whereas supination is the twisting, at which the anterior wing edge goes up.

Table 1. The main wing muscles in locust mesothorax: function and he number of motor units (from [2, 48–51])

Muscles	Design-ation of muscles	Function of muscles	Way of action on wing	The number of motor units
The 1st tergosternal	83	elevator	indirect	1
The 2nd tergosternal	84	"	"	1
Anterior tergocoxal	89	"	"	1
Posterior tergocoxal	90	"	"	3
Tergotrachant-eral	103	"	"	3
Spinal longitudinal	81	depressor	"	5
The 1st basalar	97	depressor + pronator	direct	1
The 2nd basalar	98	"	"	2
Subalar	99	"	"	2

pattern of commands sent by motoneurons to the wing muscle during flight of different intensity in a wind tunnel. He showed that if the locus was flying with "a half a strength," some motor units if the wing muscles simply were not involved into the work. Thus, both motor units of the second basalar muscles could be inactive, as well as some motor units of spinal longitudinal muscles of posterior wings. At a more energetic flight all these units also were involved in the work (the phenomenon of recruiting also known for muscles of vertebrate animals).

Wilson revealed in locust another way of an increase of strength of wing strokes—owing to different number of nerve impulses sent to motor units in each wing cycle. At the non-intensive flight, one nerve impulse came to the working units in each cycle, at a more intensive flight—2, at the most intensive one—3 and sometimes even 4. Meanwhile, for the usual "cruise" flight, as a rule, 1–2 nerve impulses were sufficient in each cycle.

Unfortunately, all these interesting observation were related by Wilson with the locust straightforward horizontal flight. In his experiments, even the steering muscles were working as additional depressors. As to the possible control of locust maneuvers with aid of asymmetrical involvement (at the right and at the left) in work of steering muscles of different number of motor units, for instance, during turns, this problem has remained unstudied. However, even if such mechanism in the locust steering muscles acting according to their direct assignament does function, it cannot (because of the small amount of units) produce any significant effect on the capability of this insect for maneuvering.

Nevertheless, the concept about the locust as an inert clumsy animal seems to need revision. As early as in 1992, Robertson and Reye [53] paid attention that during flight in flocks, locust can respond sufficiently rapidly (also see [54] to translocation of its neighbors and avoid collisions. In special experiments, the locust "flying" with a string in the wind tunnel was exposed in front of it with objects (cardboard squares with the side of 7 cm) threatening to collide with the insect; the authors used a high-rate movie and video shooting to fix all the ways by which the locust strived to avoid collisions. There were three such ways: the locust tried to fly either above the oncoming object or fly under it or, lastly, to bend around it. As the authors note, the locust strategy depended on the position of the obstacle relative to the insect as well as on time that the insect had to prevent collision.

In an attempt at flying above the obstacle, all four wings of the locust increased amplitude of the wing strokes as well as their intensity; this, naturally, increased the lifting force developed by wings of this insect. In an attempt at flying beneath the obstacle, reverse relations were observed, the locust flight rate decreasing.

Since the locust lift above the object and the flight both above and below it is to a degree similar to the locust behavior at lift and landing (when the right and left wings of the insect work symmetrically and the "steering" as such does not occur), we will consider below in detail only the part of the Robertson and Reye's work, in which the locust behavior during the bending around the object was studied. Interestingly, it was easy to judge about the start of the turn to some particular side by position of the locust abdomen that bent to the side of the turn. Functional significance of such bending is not precisely known, but it is believed that the abdomen somewhat increases inhibition of movement on the side of turn and functions as a peculiar steer by shifting the insect gravity center and facilitating thereby the work of wings.

Peculiarities of the locust wing work during its turns are as follows. If the locust makes the right turn and its wings at this moment are located in the upper position and are ready for depression, the right anterior wing can be seen to begin pronation much earlier and greater than the left wing. This decreases the attack angle of the right wing and accordingly the lifting force at this side. In this position, wings descend and in the middle of the cycle the angle asymmetry also appears in the anterior wing position: the left wing ascends higher than the right one and shifts from the left posterior wing. It is to add that during depression, amplitude of wing strokes on the left always remains higher than that on the right. At the upward lift, elevation, the symmetry in the wing positions is restored.

It is to be reminded that the muscles controlling wing pronation are the basalar and subalar muscles that in locust serve as muscles-pluralists (apart from the steering function, they can perform function of auxiliary depressors). Therefore, in spite of efficiency of work in emergency situations and taking into account peculiarities of functional morphology of the locust wing apparatus, these muscles cannot provide to this insect a high maneuverability (which, however, he locust does not need).

In conclusion, it is to be noted that the locus wing muscles are the synchronous ones (the muscle responds by one contraction to each coming nerve impulse) and belong histologically to the densely packed type.

BEHAVIOR OF DRAGONFLIES IN FLIGHT AND STRUCTURAL-FUNCTIONAL ORGANIZATION OF THEIR WING MUSCLES

Dragonflies are ancient winged insects (Paleoptera) unable to fold wings along the body at rest. They belong to the dragonfly order (Odonata) that is subdivided into three suborders: the equal winged (Zygoptera), different winged (Anisoptera), and Anizozygoptera, with the only genus inhabiting India and Japan and combining signs of the former two suborders. In total, there are about 5500 species of dragonflies. In this work, we will be interested in the largest and highly maneuvering dragonflies-darners (Aeschna) belonging to the blue darner family (Aeschnidae) as well as in some dragonflies of closely related genera. These dragonflies are different-winged (their posterior wings in the bases are somewhat larger than the anterior ones), and at rest, they hold both wing pairs stretched aside. The length of wings reaches 9 cm.

Unlike locusts, dragonflies are predators hunting in the flight for such insects as midges, mosquitoes, flies, horseflies. Dragonflies simply swallow small insects in the flight, while catch the larger ones with their extremities supplied for this purpose with peculiar pins. On catching prey, dragonflies sometimes eat it by sitting on some plant, but most often they eat the prey in the flight. Being rather voracious, dragonflies-darners are able to spend many hours in air by hunting for prey.

Dragonflies usually live near water reservoirs and although darners can sometimes go away from them for several kilometers, they are typical sprinters behaving an active and mobile mode of life. In all fairness, it is to be noted that there are dragonflies, predominantly in hot countries, for instance, watchers or spotted dragonflies, that perform annual migrations for hundreds of kilometers. But there not more than 20–25 such species, and "our" dragonflies do not belong to this category.

Many interesting observations have been accumulated about behavior of dragonflies in the flight (see [55, 56]). These insects are able to start by jerk or, on the contrary, to decelerate sharply its flight and hang in the air. They are able to rapidly shoot upward by increasing height of their flight, to glide smoothly, to fly sideways, with abdomen forward. It is curious that dragonflies even can turn in the flight by two different ways: the first—by an arc, like this is done by other flying insects as well as birds; this way is used by dragonflies during fast fly; the second way—when they are flying very slowly or "hang" over a certain place. By using as few as two wing strokes, dragonflies are able to turn their body at more than 90°!

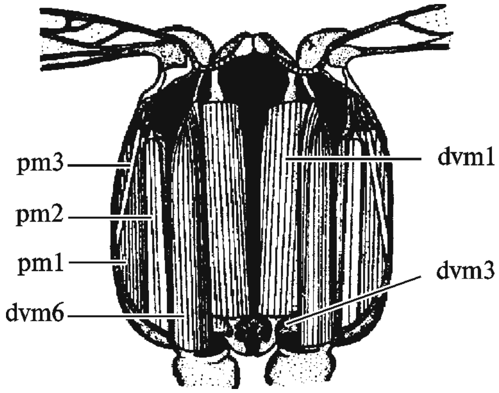

Fig. 6. Wing muscles of the dragonfly mesothorax. Transverse section (from [62]). Explanations in the text.

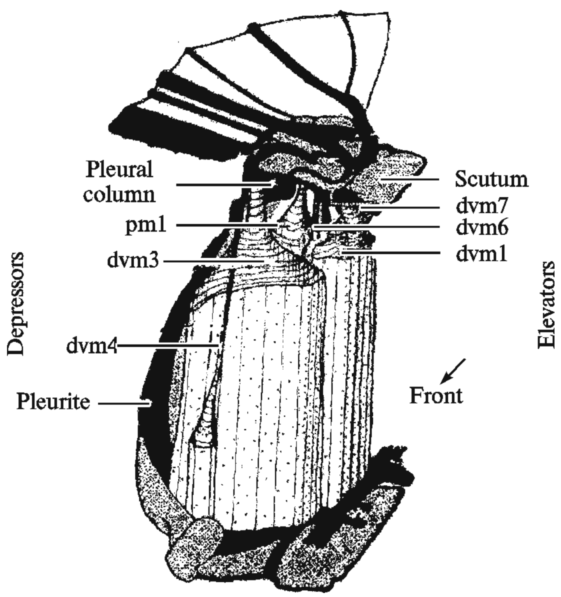

Fig. 7. Wing muscles of the dragonfly anterior wing. Transverse section (from [63]). Explanations in the text.

An example of efficient coordination of movements, especially of two dragonflies simultaneously, can be the process of mating that occurs in these insects in the flight. The dragonflies form a peculiar tandem (in the form of a ring) able not simply to be kept in the air, but also to change the flight rate, direction, and height and to perform turns. It is not by chance that many researchers consider dragonflies the most maneuvering animals on Earth.

Dragonflies belong to biomotor insects; when performing maneuvers, all four their wings can work independently of each other: with different frequency, amplitude, and attack angle. At movement down the wings create the lifting force and tractive force, at movement up—the tractive force. The "inconstancy" and even unpredictability of behavior in the air makes it impossible to identify some stable parameters characterizing the dragonfly flight. The flight rate of these insects varies from 0 (during hanging) to 70 km/h and more (by some data, even up to 96 km/h). Frequency of wing strokes fluctuates from 30 tom40 per 1 s; the wing strike amplitude also changes depending on the performed actions.

However, even at such fantastic possibilities of maneuvering, dragonflies not always can easily catch in the flight some insects, for instance, flies able, like dragonflies, to perform the "aerobatics." However, dragonflies have on this point an astonishing strategy called the "masked translocation" [57, 58]. Maneuvers at such strategy are based on that all insects respond actively only to the objects whose images on their eye retina move. Even there are known special "movement detectors" signaling into the insect central nervous system about such objects [59]. Therefore, dragonflies, when pursuing prey, do not try to overtake it by the shortest way, but to stay initially at some distance and then approach it gradually by the sidewise gliding, thriving their image in the prey eye to remain practically immobile (an increase the image sizes is not that important, as it is perceived by the prey as a component of the background). And only on approaching the prey, dragonfly performs a swift rush so the prey already doe not time to respond with a counter-maneuver.

What are the structural-functional peculiarities in the wing muscle organization, which allow dragonflies to perform such complicated maneuvers? Unlike most other insects, the majority of dragonfly muscles moving wings are muscles of direct action on the wing and are attached to its base [39, 60–63]. In this connection, structure of the wing-carrying segments here has characteristic peculiarities. Since the muscles of indirect action in the work of the dragonfly wing apparatus are not determining (except for the first tergosternal muscle), the chest tergites and sternites in these insects did not get significant development. On the contrary, pleurites are very powerful, the pleural suture going obliquely in them and its lower end laying ahead the superior one. Episternum and epimeron are sloped like a parallelogram, therefore the wing bases are shifted backwards, while the foot bases forwards. As a result, the anterior feet are approached to mouth, which allows these predators, on catching the prey, to eat it "with convenience" in the flight.

Since the muscles of the direct action on wing are attached to its base proximally, while to the pleural column distally (elevators and depressors, respectively), it is more convenient to observe mutual disposition of such muscles in sagittal chest sections (Figs. 6 and 7). Work of each of four dragonfly wings is provided by nine main muscles. All muscles descending wing (depressors) in dragonflies are direct wing muscles (there are five of them). The most powerful of them is the 2nd basalar muscle (dvm3). Another important muscle depressor is the 1st subalar one (pm1). Simmons [63] ascribes these both muscles to the main depressors. The group of auxiliary depressors consists of the 1st basalar (dvm4), 2nd subalar (pm2), and 3rd subalar (pm3) muscles. Owing to the 2nd basalar muscle, wing is pronated during the movement down. However, the final character of the wing twisting is determined by the combined action of this muscle and two subalar muscles able to produce the wing supination [63].

The muscles lifting wing (elevators; there are four of them) also comprise two groups—the main and auxiliary elevators. Unlike muscles-depressors, the muscles-elevators are mixed: the 1st tergosternal muscle (dvm1), as seen from its name, belongs to indirect wing muscles (this is the main elevator muscle); also indirect is the 2nd tergosternal muscle (dvm2) belonging to auxiliary elevators. But two elevator muscles—the anterior (dvm6) and the posterior (dvm6) coxoalar ones are muscles of the direct action on wing. The wing is elevated in the state of supination controlled by the anterior coxoalar muscle (dvm6).

It is curious that the dragonfly wing apparatus also has the spinal longitudinal muscle (dlm) that serves the main wing depressor in the majority of other insects. However, in dragonflies it is reduced to very small size, and its function as a depressor does not even discussed by researchers. This muscle, together with other small muscles located in the wing base (pm4a, pm4b, and pm5), is believed to be able to affect trajectory of its movement owing to changes of geometric relations between small sclerites located in the place of attachment of wing to chest [63].

Table 2. The main wing muscles in dragonflies in mesothorax: function and number of motor units (from [63])

Muscles	Designation of muscles	Function of muscles	Way of action on wing	The number of motor units
The 1st tergosternal	dvm1	elevator	indirect	3
The 2nd tergosternal	dvm2	"	"	?
Anterior coxoalar	dvm6	elevator + supinator	direct	3
Posterior coxoalar	dvm7	elevator	"	5
The 2nd basalar	dvm3	depressor + pronator	"	10
The 1st basalar	dvm4	depressor	"	4
The 1st subalar	pm1	"	"	4
The 2nd subalar	pm2	depressor + supinator	"	2
The 3rd subalar	pm3	"	"	1

It is known from muscle physiology that the maximal strength developed by muscle is determined by its cross-section (by the number of the working in parallel actomyosin transverse bridges), and since the shape of most muscles is identical, also by the muscle mass. The dragonfly muscle are of "different caliber" (Fig. 7) and accordingly have different mass. For instance, the wing muscle-depressor dvm4 is quite miniature as compared with the other muscle-depressor—pm1. In other words, the set of wing muscles in dragonflies is sufficient diverse, which allows these insects to finely graduate the wing stroke strength. However, this graduation in reality can be even finer, as the number of motor units forming the dragonfly wing muscles is relatively not high (Tables 1 and 2)[4]. Since practically all dragonfly wing muscles can be involved in control of maneuvers of this insect, the high number of motor units opens to dragonflies additional possibilities in this direction, too. The record number (10) of motor units in the main wing depressor (muscle dvm3) seems to allow to dragonflies perform sharp accelerations characteristic of their flight.

And finally it is quite probable that in dragonflies, like in locusts, there exists another way of fine regulation of the wing stroke strength by an increase or a decrease of the number of nerve impulses sent to motor units in each wing cycle. However, experiments in this direction on dragonflies have not been carried out.

DISCUSSION

Thus, let us summarize the differences that exist in the structural-functional organization of the wing apparatus of dragonflies and locusts and allow the dragonflies to perform very complex maneuvers.

Both insects are four-winged, each wing being controlled by the equal number (9) of the main muscles. However, whereas phase relations between the anterior and posterior wings of locusts are fixed and the right and left wings in each thoracic segment work synchronously by frequency, in dragonflies (which is the main thing!) all four wings can function independently of each other by the phase, frequency, and amplitude of beatings. The possibility of independent work of the dragonfly wings is provided by peculiarities of their articulation and structure of the wing base as well as by the character of functioning of muscles initiating wing movements. All muscles descending wing in dragonflies are muscles of the direct action (in locusts the main wing depressor—the spinal longitudinal muscle belongs to muscle of indirect action on wing). In dragonflies at the wing movement down, not only pronation can be realized (regulated!), like in locusts, but also supination can, and the total effect of the wing depression depends on the "game" of the muscle-pronator and muscle-supinator.

Like in locusts, at the upward movement, like in dragonflies, the wing is supinated. However, whereas in locusts this process is passive and is provided by elastic properties of the chest skeleton and by articulation peculiarities of the wing themselves, in dragonflies the supination at wing flaps is the active process and is regulated by the peculiar muscle (dvm6).

Both in dragonflies and in locusts, the lifting force and tractive force performed by wings is regulated by changes of twisting of the wing plate—its rotation around the long wing axis. In this process in both insects, four muscles participate: in locusts—the 1st and 2nd basalar, subalar, and the 3rd axillar, in dragonflies—the anterior coxoalar, the 2nd basalar, 2nd subalar, and the 3rd subalar muscles. In dragonflies all four wings can provide for tractive force at movement both down and up, whereas in locusts this can be done only by the posterior wings (the anterior ones provide for tractive force only at movement down). However (which is a very important circumstance), the steering movements in dragonflies can also be performed by the wing motor muscles able to work independently of each other by phase and organize various frequency, amplitude, and strength of wing strokes.

The number of motor units forming wing muscles in dragonflies exceeds more than 1.5 times that in locusts, while the number of motor units in muscles, which are able to create pronation and supination,—even 4 times! (compare Tables 1 and 2). Thus, here the dragonflies also have an advantage: they are able to regulate more finely (and even to adjust) the strength of their strokes.

Lastly, the dragonflies are able to move their wings not only up, down, to their attack angle, etc., but also to shift wings (independently of each other) along the horizontal plane forward or backward. The wing can converge with each other or, on the contrary, diverge by continuing their "main" work.

The above enumerated additional possibilities able to be realized in dragonflies in various combinations and to various "degree of expression" are what makes these insects real virtuosos of flying.

From the evolutionary point of view, it is im-

[4] Motor units in different wing muscles have different "power" (the already mentioned muscles-depressors dvm4 and pm1) are composed of the equal number (four) of motor units).

portant to note that it is the dragonflies that were the first animals on Earth which conquer the air environment. As early as at the Carboniferous Period, more than 300 million years ago, the prodragonflies (Protodonata) had emerged and gave origin to the modern species whose history numbers more than 200 million years; thereby, for about 100 million years the dragonflies "were sharpening" their flying skill. As a result, the structural-functional organization of the dragonfly wing apparatus turned out to become so "worked-out" that it preserved practically unchanged till our time. However, this does not mean that this organization that is "ideal" for large dragonflies (and the ancient dragonflies had the wing-spread longer than 70 cm!) has become a standard for other insects. The smaller forms of the flying insects that appeared afterwards have found other ways of development of their flying apparatus.

First of all, these insects belonging to newly-winged ones (Neoptera) have learned to fold wings along the body and thereby have acquired a huge advantage in the fight for survival. Because by making their body compact, they could live in new places inaccessible to Paleoptera: in clefts, under stones, in the depth of grass, etc. And of course they got additional possibilities of hiding from enemies. Dragonflies practically did not need it, as there were no flying enemies of them for hundred million years (the first birds emerged later than dragonflies by 200 million years!), while among other insects they have been completely dominating in the air up to now. However, to be successfully maintained and to move in the air environment, the smallest Neoptera forms had to develop an exclusively high frequency of wing flaps: the house fly (Diptera)—more than 300 per 1 s, honeybee (Hymenoptera)—more than 200 per 1 s. A quite miniature midge (Diptera) is working with its wings with frequency more than 1000 (!) per 1 s, etc. [64]. Such high frequencies of work of the muscle apparatus cannot be provided by the nervous system. Therefore, in all these insects in evolution there were developed resonance wing systems with peculiar (fibrillary) structure of asynchronous muscles evoking movements of wings and able to increase their contraction in response to incoming nerve impulses nerve impulses by development of elastic properties of the chest skeleton as well as of the muscles themselves. However, these interesting problems of creation of very high rhythms of motor activity are beyond the scope of the present paper (see [6])[5].

Large Neoptera—Hymenoptera do not need such "recourses" (the wing stroke frequency, for instance, in sphinx-moths amounts to "as few" as 80 per 1 s), and the wing apparatus of these insects works by principles similar to those in locusts.

It is interesting that many Diptera and Hymenoptera, by going by their own pathways, could achieve great success in flying skills. Thus, some flies can compete with dragonflies in the flight maneuverability, but are significantly inferior in the rate (the maximal flight rate of the house fly, for example, amounts to somewhat more than 7 km/h). On the contrary, large Hymenoptera (sphinx-moths) are able to reach in flight rather high rates (exceeding 50 km/h), but cannot compete with dragonflies in maneuverability.

Of course, such situation quite suits both Diptera and Hymenoptera at their mode of life (otherwise these animals simply would have become extinct), but the dragonfly maneuvering flight that has absorbed the best modes of aerobatics is unique in the animal kingdom.

Unfortunately, in spite of a great progress in understanding of mechanisms providing the insect flying possibilities, some aerodynamic effects produced by wings of these animals still have remained non-elucidated [65, 66]. Also unstudied are the mechanisms responsible for the corresponding wing movements. Peculiarities of wing articulations in various insects are poorly studied [67]. We only begin to understand the functional role played by different sites of the wing surface during strokes, significance of changes of wing shape during the wing movements in the air medium, etc., i.e., all what creates the complex cinematic pattern of the flapping flight [26, 68–70).

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[5] It is to be noted, however, that creation of superhigh frequencies of the work of wing apparatus (and of the corresponding frequencies of muscle contraction) needs for small insects only for their straightforward movement (the work of muscles o the wing motor). For the work of steering muscles of such insects, the high contraction frequencies are not required, and these muscles, like in dragonflies, belong to the synchronous, tubular type.

We emphasized the dragonfly wings to be able to function independently of each other, which creates for these insects good predispositions for performance of complex maneuvers. At the same time, for the motor behavior of the flying insects (for instance, of the dragonflies) also no less important are situations when wings act strictly and mutually coordinatively by creating, for instance, the aerodynamic forces similar to the reactive ones [29]. At present, the peculiarities of interaction of insect wings during their work have been quite intensively [71–75].

CONCLUSION

This work compares capabilities for maneuvering in flight of two representatives of insects—the migratory locust (an herbivorous insect) and the dragonfly of the darner family (an active predator). Structural-functional organization of the wing apparatus of these insects is considered in detail; important peculiarities of this organization, which allow the dragonflies to perform exclusively complex maneuvers in flight, are discussed. The work throws a bridge for the subsequent study and analysis of mechanisms of monitoring of maneuvering of locusts and dragonflies at the level of their central nervous system.

ACKNOWLEDGMENTS

The work is supported by the grant of the Program of the Division of Biological Sciences of the Russian Academy of Sciences, 2008.

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