Review
Mandible movements in ants ☆

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Abstract

Ants use their mandibles for almost any task, including prey-catching, fighting, leaf-cutting, brood care and communication. The key to the versatility of mandible functions is the mandible closer muscle. In ants, this muscle is generally composed of distinct muscle fiber types that differ in morphology and contractile properties. Fast contracting fibers have short sarcomeres (2–3 μm) and attach directly to the closer apodeme, that conveys the muscle power to the mandible joint. Slow but forceful contracting fibers have long sarcomeres (5–6 μm) and attach to the apodeme either directly or via thin thread-like filaments. Volume proportions of the fiber types are species-specific and correlate with feeding habits. Two biomechanical models explain why species that rely on fast mandible strikes, such as predatory ants, have elongated head capsules that accommodate long muscle fibers directly attached to the apodeme at small angles, whereas species that depend on forceful movements, like leaf-cutting ants, have broader heads and many filament-attached fibers. Trap-jaw ants feature highly specialized catapult mechanisms. Their mandible closing is known as one of the fastest movements in the animal kingdom. The relatively large number of motor neurons that control the mandible closer reflects the importance of this muscle for the behavior of ants as well as other insects. © 2001 Elsevier Science Inc. All rights reserved.

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1. Introduction

For the majority of insects, the mouthparts are the most important tools for almost any task. This is particularly true for the mandibles of ants. Ants employ their mandibles for fast or powerful actions like prey-catching, fighting, digging, leaf-cutting, and also for delicate tasks such as grooming, brood care, carrying nestmates, transporting liquids and communication (Hölldobler and Wilson, 1990). Accordingly, ant mandibles have to perform many different kinds of movements in terms of velocity, force output and precision. While some tasks are common among ant species (e.g. brood care), others represent specific adaptations. Predators often have long jaws equipped with piercing teeth and sharp edges, whereas herbivorous ants have more compact mandibles suited for the special task of processing plant material (Gronenberg et al., 1997). In many ant species, however, the mandibles resemble a general type found in many other insect groups: they are sturdy, shovel-like, non-segmented limbs. But mandible specialization is not only based on shape but also

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depends on the speed of movement and on the force the jaws can generate. Catching elusive prey obviously requires different movement characteristics and tactics than cracking seeds.

Force and velocity of a limb movement depend on the muscles and the accessory structures that control the particular limb. In ants, the mandible design is simple. It conforms to the common mandible organization of other hymenopterans (Snodgrass, 1935, 1956): the mandibles are connected to the head capsule by a hinge joint, movable only in a single plane (inwards/outwards), operated by only a single closer and opener muscle on each side of the head. Even though opener–closer muscle co-contraction may occur, the mandible closer muscle is much larger and the key to the versatility of mandible functions (Gronenberg et al., 1998a). All the fast, forceful, or delicate mandible movements are generated by the mandible closer muscle.

Because of its relative simplicity and its great behavioral relevance, this movement system is very well suited for studying adaptive muscle morphology, biomechanics, and motor control. This review gives an overview of the diversity of ant mandible movements and the underlying mechanisms considering an evolutionary context by comparing species adapted to different lifestyles.

2. Muscle fiber types and general morphology of the mandible closer muscle

In ants, as in most other animals, the mandible

closer muscle is much larger than the opener muscle. In large species or in large individuals of polymorphic species (Hölldobler and Wilson, 1990), the mandible closer occupies up to two-thirds of the entire head capsule volume (Fig. 1a). The proportion of the mandible closer muscle volume in relation to the head capsule volume decreases with decreasing size of the ant (Fig. 1a). In small species or small individuals, the mandible closer muscle only fills approximately 25% of the head capsule (Fig. 1a). The reason for this allometric correlation is that other organs and structures within the head take up relatively more space when the head capsule volume decreases (e.g. antennal, labial, and maxillary muscles; Fig. 1b; Paul and Roces, 1999). Most notably, the brain is relatively larger in small ants (Jaffe and Perez, 1989). However, the mandible closer is the largest muscle in any ant worker, even in very small species or individuals.

In almost all ants, the mandible closer muscle is composed of two morphologically distinct types of muscle fibers (Gronenberg et al., 1997; Paul and Gronenberg, 1999): fibers with short sarcomeres (sarcomere length 2–3 μm) and fibers with long sarcomeres (5–6 μm). As a general rule, in long sarcomeres, more myosin–actin cross-bridges act in parallel (Huxley, 1974; Tregear and Marston, 1979; Cooke, 1997). Therefore, fibers with long sarcomeres generate larger forces. In muscle fibers with short sarcomeres many units simultaneously shorten in series, resulting in a high contraction velocity (Jahromi
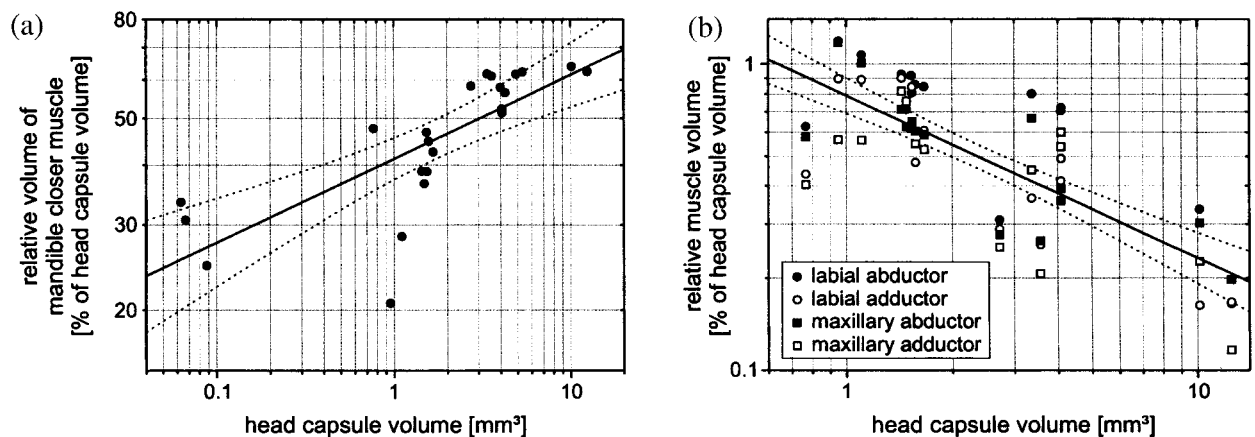

Fig. 1. Allometric correlations between mouthpart muscle and head capsule volumes in ants. Data points represent single individuals of various ant species, respectively (*Atta sexdens, Camponotus rufipes*, $n = 4$; *Diacamma* sp., *Ectatomma ruidum, Harpegnathos saltator, Leptothorax sordidulus*, $n = 3$; *Pachycondyla villosa, Myrmecia* sp., $n = 2$). (a) The relative volume of the mandible closer muscle increases with increasing head capsule volume ($r = 0.76315$; $P < 0.0001$). (b) The relative volumes of the labial adductor, abductor, maxillary adductor, and abductor decrease with increasing head capsule volume ($r = -0.75849$; $P < 0.0001$).

and Atwood, 1969, 1971; Lang et al., 1977). This correlation between sarcomere length and contractile properties of a muscle fiber has been shown in many different studies (O'Connor et al., 1982; Stephens et al., 1984; Günzel et al., 1993; Taylor, 2000). Hence, muscle fibers with short sarcomeres are fast contracting fibers, whereas long sarcomeres indicate slow but forceful muscle fibers. Ultrastructural observations and considerations support this classification of muscle fiber types in ants (proportion and density of myofilaments, mitochondria, sarcoplasmatic reticulum, and thickness of z-discs; van Leeuwen, 1991; Gronenberg et al., 1997). However, absolute values of sarcomere lengths and other structural properties do not always accurately predict physiological performance of muscle fibers in arthropods (Costello and Govind, 1983; Silverman et al., 1987; Günzel et al., 1993). A causal relationship between the characteristics of the mandible movement and the electrical activity of particular muscle fiber types has been established (Paul and Gronenberg, submitted). In conclusion, the mandible closer muscle of ants is composed of two different sets of fibers: slow but forceful muscle fibers (sarcomere length 5–6 μm) and probably less forceful but fast ones (sarcomere length 2–3 μm).

In arthropods, muscle fibers attach to the exoskeleton (e.g. the thorax or head capsule) directly via a deeply serrated area of adhesion between the muscle fiber and the cuticle (Neville, 1975a,b). The opposite end of the muscle fiber connects to a specialized region of the moving body part (e.g. the leg or mandible) referred to as the apodeme, which is the functional analogue of the vertebrate tendon. In some arthropod muscles, including the ant mandible closer, muscle fibers may connect to thin thread-like processes of the apodeme rather than attaching to its main body through the entire cross-sectional area. These fibers are referred to as 'filament-attached' fibers to differentiate them from the more common type of 'directly attached' muscle fibers. Fast contracting fibers of the ant mandible closer always attach directly to the apodeme, whereas slow muscle fibers are either directly or filament-attached fibers (Paul and Gronenberg, 1999).

In all ant species, the mandible closer apodeme follows a basic plan that may be modified to a greater or lesser extent (Paul and Gronenberg,

1999). The main body of the apodeme is a massive sclerotized structure, which funnels the forces of all closer muscle fibers into the mandible. The apodeme base gives rise to apodeme collaterals. Typically, three branches project from the apodeme base posteriorly into the closer muscle: a central principal branch and two accessory branches, a median and a lateral one. The most significant alteration of the basic design is the introduction of apodeme filaments. Bundles of such filaments, each of which connects exclusively to a single muscle fiber, may replace the accessory branches entirely although the basic organization can still be discerned.

The muscle fiber types of the ant mandible closer (fast directly attached, slow directly and filament-attached fibers) are arranged in bundles of like fibers (Gronenberg et al., 1997; Paul and Gronenberg, 1999). In all ants studied, the mandible closer muscle is thus composed of subunits that each comprises only a single muscle fiber type and occupies characteristic positions within the head capsule (Fig. 2). While the relative and absolute size of each muscle fiber group differs across species and in some cases between individuals of different body size, the relative position of the different muscle fiber bundles is very similar in different species (Fig. 2). These typical positions of the muscle fiber types possess functional significance (see below; Paul and Gronenberg, 1999).

In contrast to the mandible closer of ants, other insect muscles are either homogeneous or comprise several morphologically, histochemically, and physiologically different muscle fibers or a continuum of fiber types (Hoyle, 1974, 1978; Rathmayer and Maier, 1987; Müller et al., 1992). Other muscles in ants do not consist of distinct muscle fiber bundles as well. Antennal muscles contain fibers of different properties arranged concentrically (fiber diameter and sarcomere length increase from the center to the periphery of the muscle; Gronenberg and Ehmer, 1995; Ehmer and Gronenberg, 1997). The smaller mandible opener, labial, or maxillary muscles may comprise only a single muscle fiber type.

3. Muscle fiber composition reflects adaptive differences among species

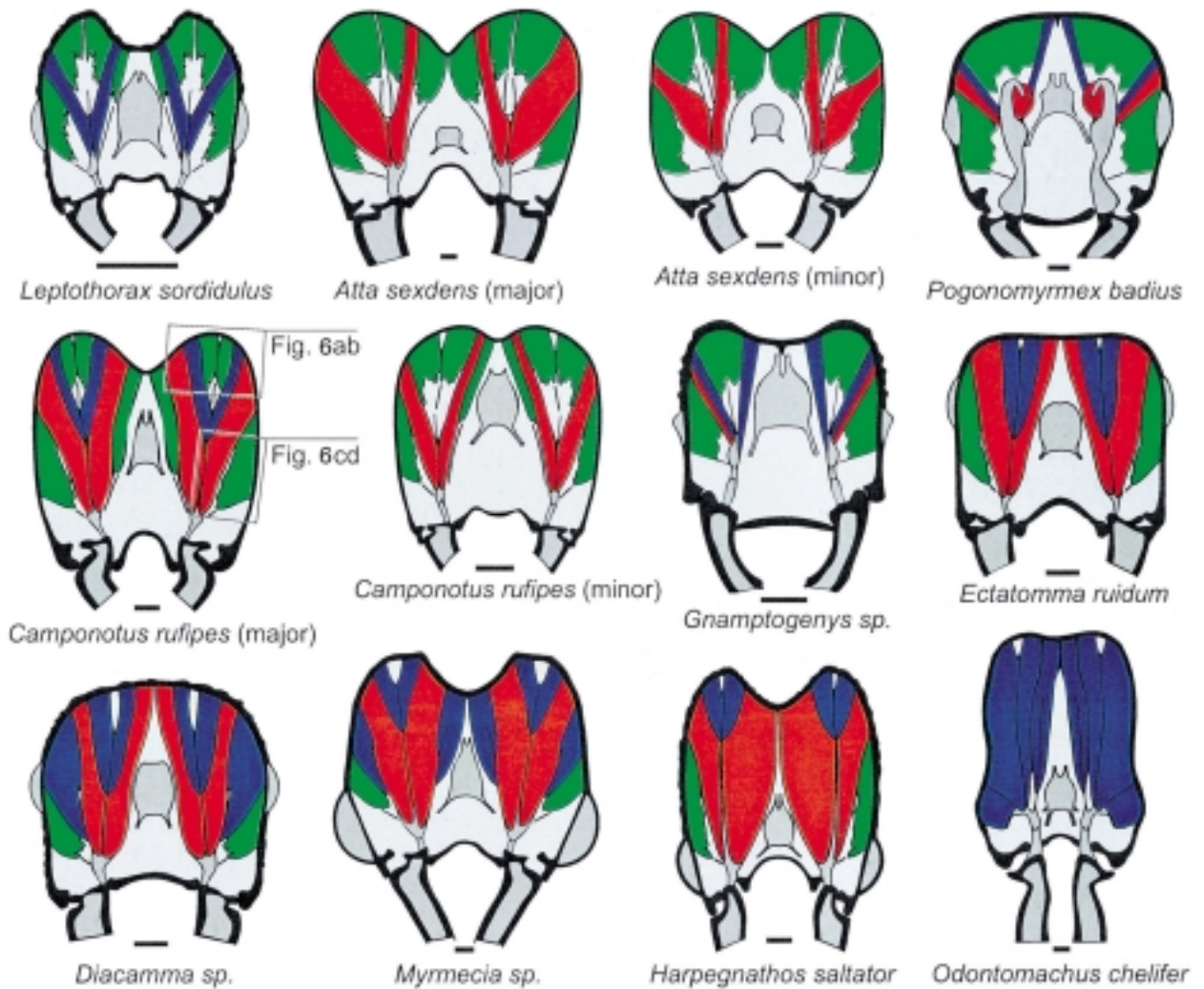The fiber composition of the mandible closer

Fig. 2. Schematic drawings of mandible closer muscle fiber groups of selected ant species. Each drawing represents the fiber composition of several mid-frontal sections at the level of the suboesophageal ganglion, but does not reflect the amount of fibers located more frontally or more caudally in the head. Arrangement of ant species reflects the decreasing amount of filament-attached muscle fibers. *Solid black*: cuticle; *dark grey*: mandibles, eyes, closer apodemes, suboesophageal ganglion; *green*: filament-attached slow muscle fibers (long sarcomeres); *black lines* indicate filaments; *red*: directly attached fast fibers (short sarcomeres); *blue*: directly attached slow fibers (long sarcomeres); *scale bar*: 250 μm.

muscle is species-specific (Gronenberg et al., 1997; Paul and Gronenberg, 1999). The drawings in Fig. 2 illustrate the variation in fiber composition among species. Most ants have both fiber types (fast and slow) and both types of fiber attachment (direct and via filaments) in their closer muscle. In the small *Leptothorax sordidulus*, no fast fibers were found. In *Atta sexdens* and small individuals of some *Camponotus* species, all slow muscle fibers are filament-attached. In the ponerine genera *Odontomachus* and *Anochetus* (Gronenberg and Ehmer, 1996), almost all fibers are of the

directly attached type with long sarcomeres. The drawings in Fig. 2 represent sections in the mid-frontal plain, and roughly reflect the distribution of the muscle fiber types. However, since the distribution is not homogeneous throughout the entire head, these drawings are not a quantitative rendering of the fiber composition.

Fig. 3 shows the actual volume ratios of the muscle fiber types in different ant species. The species are arranged according to their proportion of fast fibers. *Camponotus rufipes* is an example for a species that is not specialized on particu-
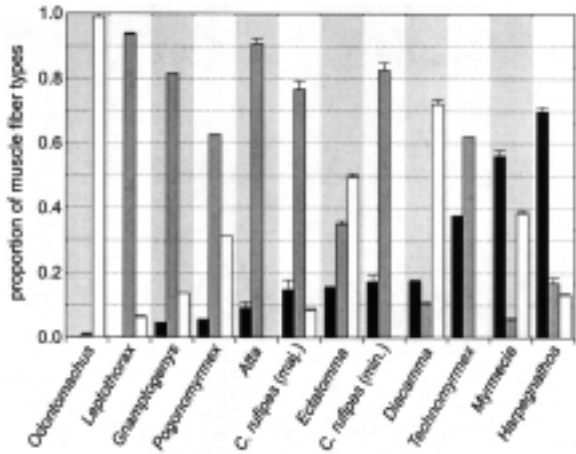
Fig. 3. Ratio of the three mandible closer muscle fiber types in different ant species. *Black bars*: directly attached fast muscle fibers (short sarcomeres); *open bars*: directly attached slow fibers (long sarcomeres); *grey bars*: filament-attached slow fibers (long sarcomeres). Mean ± S.D. (3 animals); bars without standard deviation (1 or 2 animals); *Atta*: 2 majors and 2 minors; *Camponotus rufipes*: 3 majors and 2 minors. The organization of ant species on the *abscissa* reflects the increasing proportion of fast fibers.

lar food (Hölldobler and Wilson, 1990). It features an average ratio of fast to slow muscle fibers (Fig. 3). Accordingly, its morphology is suited to illustrate the 'generalized' ant mandible muscle

design (Paul and Gronenberg, 1999). *Odontomachus*, *Pogonomyrmex*, and *Atta* have only few fast muscle fibers, whereas in *Myrmecia* and *Harpegnathos*, the majority of mandible closer muscle fibers are fast ones (Fig. 3). The proportion of fast fibers correlates positively with mandible closing velocity (Fig. 4). The fastest closing movements were measured in species that feature a high proportion of fast fibers (e.g. mandible closing velocity of *Harpegnathos saltator*: 1.25°/ms; relative proportion of fast fibers: 69.9%; Fig. 4; Gronenberg et al., 1997). *Myrmecia* and *Harpegnathos* are predators. *Myrmecia* is known as a predator with particular rapid mandible closing movements (Gray, 1971a,b). *Harpegnathos* species display jumping behavior and are able to catch flying prey in mid air (Ali et al., 1992; Baroni Urbani et al., 1994; Tautz et al., 1994). Hence, the mandible closer muscle of species that depend on fast mandible actions such as predatory ants consists of many fast muscle fibers.

Ants of the genera *Odontomachus*, *Pogonomyrmex*, and *Atta* have many slow but forceful muscle fibers, whereas the mandible closer of the predatory ants *Myrmecia* and *Harpegnathos* contains only few of such particularly forceful muscle
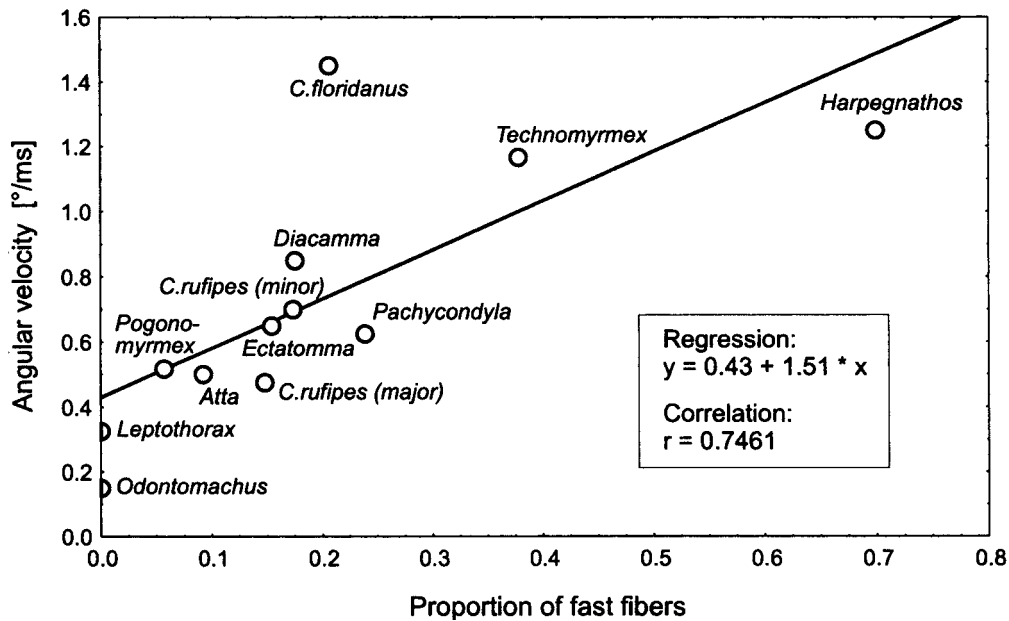

Fig. 4. Correlation between the angular velocity of mandible closing movement (*ordinate*) and the proportion of fast fibers in the mandible closer muscle (*abszissa*) of different ant species. Angular velocities were measured using a high frequency video system. For detailed interpretation see Gronenberg et al. (1997) (e.g. the data point for *C. floridanus*).

fibers (Fig. 3). *Pogonomyrmex* and *Atta* are herbivorous ants. As a harvesting ant, *Pogonomyrmex* needs very forceful mandible closing movements to crack dry seeds (Hölldobler and Wilson, 1990). The leaf-cutting ant *Atta* relies on a powerful mandible closer muscle to cut through tough leaves (Hölldobler and Wilson, 1990). In *Atta sexdens*, the mandible closer has a very high metabolic rate approaching that of insect flight muscle, and cutting leaves consumes almost 30 times as much energy as inactivity does (Roces and Lighton, 1995). Although *Odontomachus* is a predator (Hölldobler and Wilson, 1990), its mandible closer features slow muscle characteristics (e.g. it exclusively consists of slow muscle fibers; Fig. 3). This finding in *Odontomachus* and other 'trap-jaw' ants may seem puzzling, but we will see the reason for this combination of fast movement and slow muscle characteristics later.

To conclude, lifestyle variables such as feeding habits determine the species-specific volume ratios of mandible closer muscle fibers. Predators like *Harpegnathos saltator* depend on very fast mandible strikes to catch their prey, corresponding to a high proportion of fast fibers (Fig. 3). Herbivorous ants like *Atta sexdens* need a forceful mandible closer muscle for processing plant material, corresponding to a high proportion of slow but forceful muscle fibers (Fig. 3).

4. Force and velocity require different angles of attachment

In addition to the physiological properties of the muscle fibers, speed and force of a whole movement system depend strongly on the musculo-skeletal design such as joint characteristics and on the geometrical arrangement of the muscle fibers (Full et al., 1991; Full and Ahn, 1995). The muscle fiber's angle of attachment with respect to the muscle's overall direction of pull is a particularly important determinant of the force a single fiber contributes (Paul and Gronenberg, 1999). Different muscle fiber types attach to the apodeme at different angles. On average, fast fibers attach at smaller angles than directly attached slow muscle fibers do. Variation in attachment angle is largest in filament-attached fibers (Paul and Gronenberg, 1999). What determines the angle of attachment and why is it different in different muscle fiber types?

The optimal angle of attachment for any individual (!) muscle fiber in terms of both speed and force would be 0°, which is parallel to the principal direction of pull. Such a fiber arrangement is shown on the left of Fig. 5a, where all muscle fibers act in that optimal direction. However, this pattern is not found in any arthropod for two main reasons. (1) The apodeme is composed of cuticle (Neville, 1975a,b; Snodgrass, 1935) which, even if sclerotized, is most stable in the direction parallel to the fibrils (Alexander, 1988; Neville, 1975a,b). A thin sheet-like apodeme as shown on the left of Fig. 5a would become bent upon contraction of the muscle rather than transmitting the force into the mandible. To function, a muscle fiber arrangement of this kind would require an extremely thick apodeme, taking up space and representing an additional load which would reduce the advantage given by the muscle fiber's optimal angle of attack (Paul and Gronenberg, 1999). (2) During contraction, such a muscle would swell considerably perpendicular to the direction of contraction because muscle volume remains almost constant while it shortens (Alexander, 1983; Baskin and Paolini, 1966). This, however, is not possible in the restricted space of the inflexible head capsule, which would either prevent the muscle from shortening or crack. In contrast, a pennate muscle of the design shown on the right of Fig. 5a will not swell during contraction (Alexander, 1988).

The angle of attachment at the apodeme is crucial to the overall force generation of the entire muscle because the apodeme surface area is limited (the number of muscle fibers that can attach directly to the apodeme depends on the attachment angle). The significance of the attachment angle can best be explained using a simple model for directly attached muscle fibers (Fig. 5; Paul and Gronenberg, 1999). The optimal angle of attack for maximum force output depends on the ratio of an apodeme's horizontal (x) and longitudinal (y) components. Fig. 5b shows the standardized force produced by five different apodeme designs; the optimal angle of fiber attachment is that which gives maximum force production. For real apodemes, all of which have a small x component ($x/y < 0.3$), the optimum fiber attachment angle is between 41° and 45° for maximum force output (shaded region in Fig. 5b).

However, in order to maximize the shortening velocity, the angle of attachment should approach
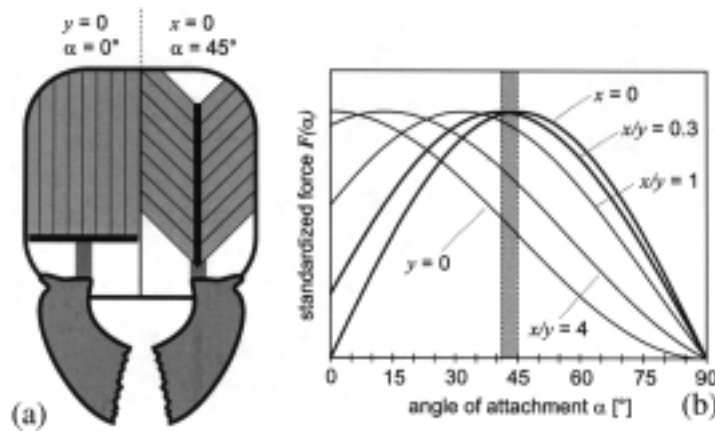
Fig. 5. The effects of apodeme design and muscle fiber attachment angle on force production. (a) Diagrammatic representation of the head showing attachment angles $\alpha = 0°$ and $45°$; real apodemes have both horizontal (x) and longitudinal (y) components. (b) Force output ($F(\alpha)$; normalized to the maximum of the curve for $x = 0$) for apodemes with varying x/y composition. The range of x/y ratios found in most ants lies between the two thick black lines; the shaded area ($x/y = 0–0.3$) shows the corresponding range of optimal angles of attachment for maximum force output. The equation for the graphs is $F(\alpha) = (f_i/d)(\cos \alpha)[2y(\sin \alpha) + x(\cos \alpha)]$; for derivation see Paul and Gronenberg (1999); α: angle of attachment; f_i: individual force of a single muscle fiber; d: fiber diameter.

$0°$. A muscle will be fast if it consists of particularly long fibers composed of short sarcomeres (see above) that attach to the apodeme at small angles; the absolute amount by which the muscle shortens is thus maximized. At acute angles, fewer fibers can attach directly to the apodeme. Hence, small mean attachment angles indicate fast muscle characteristics because the attachment angle is minimized at the expense of overall force output (Paul and Gronenberg, 1999).

5. Why apodeme filaments?

The presence of filament-attached muscle fibers in ants and some aspects of their development have been known for a long time (Janet, 1905, 1907a,b) and have become textbook knowledge for insects in general (Snodgrass, 1935; Gullan and Cranston, 1994). However, the first concepts regarding their functional significance have been published by Paul and Gronenberg (1999).

The apodeme filaments are composed of unsclerotized cuticular material and thus are flexible and can easily follow movements of the apodeme. This is of particular importance for fibers such as the lateral fibers that attach at large angles (Fig. 2). Such fibers are subjected to larger angular changes when the apodeme moves during mandible closing. This explains why filament-

attached fibers are found in this location in all ant species (Fig. 2).

Ant heads, and elongated ones in particular, contain regions in which the apodeme surface area and the head capsule area are approximately equal (regions a_1 and h_1 in Fig. 6c,d). In these regions, muscle fibers preferentially attach directly to the apodeme because directly attached fibers do not waste space for filaments, which do not develop any force. However, filament-attached fibers minimize the apodeme surface area required. Accordingly, muscle fibers are filament-attached where the ratio of apodeme-to-head capsule surface area is small (regions a_2 and h_2 in Fig. 6c,d). Such an arrangement is often found at the muscle periphery and where the curvature of the head capsule is large (most notably at the posterior end of the head; Fig. 6a,b). Filament-attached fibers help to fill the head capsule with muscle fibers in regions that would otherwise remain unused because too little apodeme surface area would be available for the muscle fibers to attach directly (Fig. 6c,d; Paul and Gronenberg, 1999).

The distribution of filament-attached and directly attached muscle fibers with respect to the ratio of apodeme-to-head capsule surface area (a/h) is depicted by the graphs in Fig. 7. The equation underlying these curves is derived from calculations describing the geometrical situations shown in Fig. 6c,d (Paul and Gronenberg, 1999).
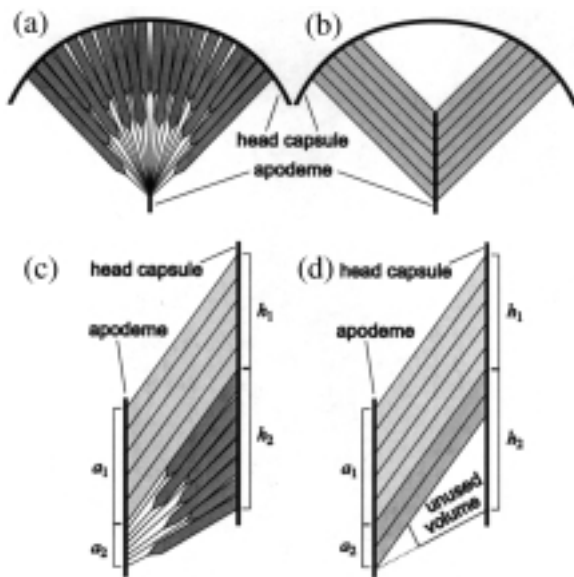
Fig. 6. Diagrams illustrating the advantages of filament-attached muscle fibers in the regions marked by rectangles in Fig. 2. Filament-attached fibers make a better use of the available head capsule volume and attachment surface in head regions where the apodeme attachment surface is limited (see text for further details). The unused space in b is needed for backwards moving of the apodeme that is compensated by flexible filaments and shortening of fibers in a.

For directly attached muscle fibers (relative length of filaments $f = 0$) the proportion of the head volume utilized may reach 100% if a/h is 1 (Fig. 7). For $a/h < 0.5$, filament attachment becomes necessary in order to maximize the utilized volume (Fig. 7). The smaller the a/h ratio, the longer the filaments have to be to fill the space most efficiently with muscle fibers (Fig. 7). This is the reason why the filaments vary in length within and between species. More efficient use of head volume means a larger overall force output or that the required muscular power can be generated within a smaller head capsule. An efficiently designed (hence smaller) head means that less energy has to be spent to move the body mass around, and a smaller head may also be more easy to manoeuvre.

Filament-attached fibers can make better use of the available head capsule surface area, resulting in a higher absolute number of muscle fibers (compare Fig. 6a,c with b,d, respectively). Moreover, filament-attached fibers may insert at a more efficient angle at the apodeme ($\alpha < 45°$; Fig. 6a,b) because there is no additional 'cost' in terms of apodeme surface area as is the case in directly

attaching fibers (their optimum angle for maximum force output is 45°; see above). Due to the steeper attachment angles and the higher absolute number of muscle fibers acting in parallel, the filament-attached fibers in the schematic example of Fig. 6a would generate more than twice as much force as the directly attached fibers in Fig. 6b (Paul and Gronenberg, 1999). Of course, on average the filament-attached fibers are shorter, meaning that fewer sarcomeres shorten in series and the resulting movement in Fig. 6a would not be as fast as the one in Fig. 6b.

It seems that the conditions under which filament-attached or directly attached fibers are advantageous can be clearly defined. One might thus expect a single optimal ratio of the two fiber types to be expressed in all ant species. Why, then, do we find divergent designs and varying proportions of filament-attached fibers among different species (Fig. 3)? The ratio of directly attached and filament-attached fibers varies with the behavior and the living conditions of a given species (Paul and Gronenberg, 1999), just as is the case for the proportions of fast and slow muscle fibers (see above). Species that perform fast mandible movements generally have long
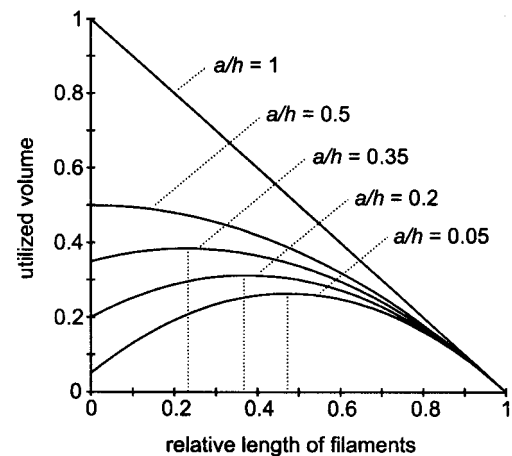

Fig. 7. The relationship between head capsule volume that can be used by muscle fibers (*y*-axis; utilized volume η) and the relative length of filaments f (*x*-axis), for areas differing in the ratio of apodeme to head capsule surface area (a/h). The relationships were using the equation: $\eta = (a/h - 1) f^2 + (1 - 2 a/h) f + a/h$ (for derivation see Paul and Gronenberg, 1999). Directly attached fibers ($f = 0$) can use 100% of the head volume if $a/h = 1$. For $a/h < 0.5$, filament-attached fibers ($f > 0$) make better use of the available head capsule volume, hence more force can be generated. *Vertical dotted lines* indicate the maxima of the three lower curves. See text for further details.

head capsules to accommodate long muscle fibers which attach directly at small angles at the apodeme (e.g. the predatory *Harpegnathos saltator*; Fig. 2). An apodeme filament would shorten the contractile part of the muscle fiber and thus diminish its fast properties. For this reason, fast fibers are never filament-attached. In contrast, species depending on particularly forceful mandible movements, such as seed-cracking harvesting ants or leaf-cutting ants, generally have broad heads (compare *Atta sexdens* and *Harpegnathos saltator* in Fig. 2) in order to have more muscle fibers acting in parallel in the optimal direction of pull. However, broad heads feature relatively less apodeme surface area for the muscle fibers to attach to (larger regions with small a/h ratio). For this reason, more muscle fibers are filament-attached in these species. Moreover, in posterior head regions, filament-attached fibers have a force advantage over directly attached fibers (see above).

6. Trap-jaw mechanism yields maximum velocity

Some ant genera (the so-called trap-jaw ants) feature a particular catapult mechanism to over-come the temporal limitations inherent to muscular contraction (Alexander, 1988). Such spring-loaded systems are widely employed by insects (e.g. the jumps of fleas, Bennet-Clark and Lucey, 1967; springtails, Christian, 1979; click beetles, Evans, 1973; flea beetles, Furth et al., 1983; locusts, Bennet-Clark, 1975). Trap-jaw mechanisms have evolved convergently in the ponerine ant tribe Odontomachini and in two other unrelated ant tribes, the formicine Myrmoteratini and the myrmicine Dacetini. These ants possess large mandibles that can be closed extremely rapidly to trap prey between them (Wheeler, 1900; Wilson, 1962; Dejean and Bashingwa, 1985; Dejean, 1986; Moffett, 1986; Carlin and Gladstein, 1989; Hölldobler and Wilson, 1990). In some ant genera this mechanism also serves a defensive function (Jaffe and Marcuse, 1983; Carlin and Gladstein, 1989). When the mandible strike is used against a large solid object, the ant will bounce off that object (retrosalience; Wheeler, 1900, 1922).

Mandible closing of trap-jaw ants is known as one of the fastest movements in the animal kingdom. Photoelectric scanning has revealed that these trap-jaws can be closed in less than 0.5 ms (Gronenberg, 1995a). In all trap-jaw ants, however, the mandible closer muscle features slow muscle characteristics. It is solely composed of

Table 1
Major features underlying and determining the trap-jaw mechanisms (modified from Gronenberg, 1996)

	Ponerinae		Myrmicinae			Formicinae
	Odontomachus sp.	*Anochetus* sp.	*Acanthognathus* sp.	*Daceton armigerum*	*Strumigenys* sp.	*Myrmoteras* sp.
Catch mechanism formed by	Mandible joint	Mandible joint	Accessory mandibular processes	Labrum	Labrum	?
Sarcomere length [μm] of mandible closer muscle	9.8	11.4	8.4	7.2	4.9	?
Trigger muscle derived from, sarcomere length [μm]	Mandible closer, 2.7	Mandible closer, 2.9	Mandible closer, 3.0	Labral adductor, 1.8	labral adductor, 1.8	?
Number of trigger hairs and sensory neurons	4 large	2 large, 2 slightly smaller	2 large	2 large	2 large, 2 small	None (visual)
Number of trigger motor neurons	4	4	4	2	2	?
References	a,b,f	a,d	e	c	c	g

[a] Brown (1978).
[b] Gronenberg (1995a,b).
[c] Gronenberg (1996).
[d] Gronenberg and Ehmer (1996).
[e] Gronenberg et al. (1998a).
[f] Just and Gronenberg (1999).
[g] Moffett (1986).

muscle fibers with particular long sarcomeres (up to 11.4 μm, Table 1). Fast muscle fibers with short sarcomeres are completely absent within the mandible closer (e.g. *Odontomachus* in Figs. 2 and 3). The slow muscle fibers directly attach to the apodeme at the optimum angle for maximum force output (approx. 45°, Paul and Gronenberg, 1999; see above). In some trap-jaw ants (*Strumigenys*), the majority of mandible closer muscle fibers are filament-attached (Gronenberg, 1996). Hence, the mandible closer of trap-jaw ants is specialized to generate large forces.

The high velocity of trap-jaw closing is based on a specific catch mechanism that keeps the extended mandibles open during contraction of the powerful mandible closer muscle. This catch mechanism allows the potential energy the mandible closer muscle produces to be stored within cuticular elements, the head capsule, apodemes, and the closer muscle itself (Gronenberg, 1995a; Gronenberg et al., 1998a). The mandible strike is released in a reflex-like action when particular trigger hairs are touched. During a strike a relatively small and highly specialized trigger muscle unlocks the catch, instantaneously releasing the stored energy to accelerate the mandible.

The catch mechanism differs among species. In ponerine species, it is formed by specific adaptations of the mandible joint, whereas in myrmicine species, the mandibles are locked in the open position by the labrum, which functions as a latch, or by opposing accessory mandibular processes (Table 1). The trigger hairs can be located on the mandible surface or on the labrum, respectively. The trigger muscle of ponerine species is probably evolutionary derived from the fast muscle fibers of the mandible closer muscle (Table 1). In ponerine ants, upon contraction of the trigger muscle, the hump at the ventral tip of the mandible base slightly moves which serves to unlock the mandible catch (Table 1). In *Acanthognathus*, mandibles are unlocked by contraction of fast mandible closer muscle fibers that rapidly rotate the closer apodeme and the mandible around its long axis (Table 1). In the other two myrmicine genera, the labral adductor muscle serves as trigger muscle as the mandibles are blocked by the labrum (Table 1). Comparison of trap-jaw mechanisms among species reveals a remarkable example of convergent evolution.

Ants of the genus *Mystrium* employ a peculiar defensive 'snap-jaw' mechanism in which the closed mandibles cross-over to deliver a stunning blow to an adversary (Gronenberg et al., 1998b). The strike is initiated by contact of the adversary with mechanosensory hairs at the side of the mandible, and is powered by slow closer muscles whose energy is stored by a spring mechanism. Recording of closer muscle activity indicates that the mandibles are not triggered by any fast muscle. Instead, it is supposed that activity differences between the left and right mandible muscles imbalance a pivot at the mandible tip and release the strike (Gronenberg et al., 1998b).

In order to generate fast mandible closing movements ants have adapted in two different ways: In predatory ants such as *Harpegnathos* or *Myrmecia*, the mandible closer muscle is mainly composed of particular long muscle fibers with short sarcomeres directly attached to the apodeme at small angles, combining characteristics that result in high mandible closing velocities. Alternatively, trap-jaw ants developed highly specialized catapult mechanisms which rely on slow mandible closer muscles to produce large forces. Their mandibles close even faster.

7. Motor control

Unlike vertebrates, each arthropod muscle is controlled by only a relatively small number of motor neurons, yet individual muscle fibers are often supplied by more than one motor neuron (polyneuronal innervation; Hoyle, 1974) some of which may be inhibitory. Insect muscles may be controlled by a single motor neuron (Strausfeld et al., 1987; Rathmayer, 1996). The classical insect muscle paradigm, the locust jump muscle (extensor tibiae) is controlled by three motor neurons, a fast and a slow excitatory and a common inhibitory neuron (Hoyle, 1974; Rathmayer, 1996).

Relatively little is known about motor control of mandible movements in insects in general, although the mandible closer is a prominent muscle in all biting and chewing insect taxa. The innervation pattern of mandible muscles has been studied in locusts (Baines et al., 1990), caterpillars of the hawk moth *Manduca sexta* (Griss, 1990), and the honey bee (Masuko, 1986; Rehder, 1989). Six to eight motor neurons control the mandible closer muscle in the honeybee *Apis mellifera*

(Rehder, 1989) and 12 motor neurons have been described in the tobacco hornworm larva *Manduca sexta* (Griss, 1990).

Previous work on mandible control in ants focused on the specialized trap-jaw ants. Eight mandible closer motor neurons have been found in *Odontomachus* (Just and Gronenberg, 1999). The trap-jaw reflex takes 4–10 ms and is one of the fastest reflexes yet described for any animal (Gronenberg, 1995a). In *Odontomachus*, it is controlled by a system composed of two giant sensory neurons (trigger hairs) and two giant motor neurons (trigger muscle) on either side (Fig. 8; Gronenberg, 1995b). The giant neurons are most likely monosynaptically coupled (Fig. 8). The large axon diameter and the synaptic coupling result in high conduction velocity which underlies the very fast mandible reflex (Gronenberg et al., 1993; Gronenberg, 1995b). The trigger motor neurons are dye-coupled and receive input from both sides of the body without delay, which ensures the synchronous release of both mandibles (Just and Gronenberg, 1999). Reflex activity is modulated by antennal and other sensory input probably converging onto the large dendritic trees of the trigger motor neurons (Fig. 8; Gronenberg, 1995b).

Much less is known about the control of muscles in other ants. A preliminary study shows that the mandible closer muscle of less specialized ants (genera *Camponotus* and *Pogonomyrmex*) is innervated by at least 10 motor neurons (Paul and Roces, 2000; Paul and Gronenberg, submitted). This set of motor neurons allows the animal to independently activate different types of muscle fibers or locally distinct fiber bundles, resulting in a great variety of possible movements. The large number of mandible closer motor neurons in all insect taxa examined reflects the importance of this muscle for the behavior of insects.

8. Conclusions

Ant mandibles and their accessory structures form a simple system able to generate a wide range of movements. Comparison of the underlying mechanisms across differently specialized ant species reveals common design principles for the efficient generation and control of movements in nature. This review explains the significance of muscle fibers and their attachment in terms of force and speed adaptations (e.g. muscle fiber length, sarcomere length, mode and angle of attachment at the apodeme, ratio of physiologically different muscle fiber types, shape of head capsule, specialized mechanisms). Studies on the control of mandible movements advance our understanding of how a large repertoire of finely tuned movements can be generated by a relatively parsimonious system that comprises only a few muscles and muscle fiber types.
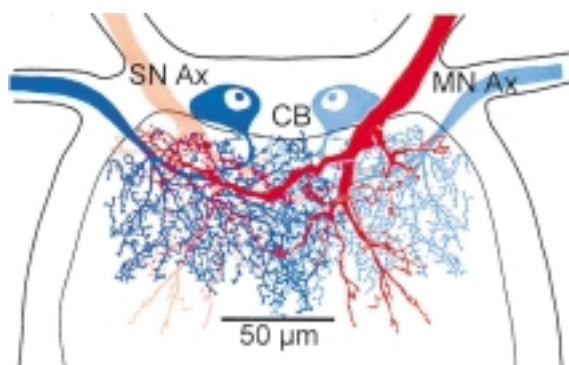
Fig. 8. Schematic drawing (by Wulfila Gronenberg) of the suboesophageal ganglion of *Odontomachus* showing the overlap of a giant mandibular sensory neuron's axon terminal *SN Ax* (*red*) and a trigger motor neuron's dendritic tree *MN Ax* (*blue*). Light colors indicate the respective contralateral neuron to reveal the bilateral overlap. *CB*: motor neuron cell body. Two similar sets of neurons exist on either side, only one of which is shown here. Sensory and motor neurons are connected by highly efficient chemical synapses, motor neurons are mutually coupled by electrical synapses.

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