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Muscle insertions do not incur mechanical advantage

Sprawność mechaniczna nie wynika z miejsca przyczepu mięśnia

Abstract. In any particular array of an equivalently contracting muscle, each sarcomere makes an equivalent contribution to the moment generated. This suggests that the concept of mechanical advantage is inappropriate for analysis of muscle attachment patterns. The differences of insertion along lever arms are due to other factors. Mechanical advantage does remain an important topic in analyses of outward forces directed by skeletal elements against the next component in a chain or against portions of the external environment.

I. INTRODUCTION

Introductory physics has long discussed the application of forces to solid bodies through the rules of levers. The basic concept derives from an equivalence of moments, i. e. forces applied further from a fulcrum generate proportionally greater moments than those applied near to it; hence they have a mechanical advantage. Thus the differences among levers of the first, second and third class continue to be memorized by students, although they represent only minor permutations of the ways three forces may be applied to a rotatable body.

Biologists utilize the rules of lever systems as a convenient shorthand for characterizing the effects of the forces that act or once acted on skeletal elements. For instance, HILDEBRAND (1972) characterizes limb and jaw bones by referring to the moment arms of the in-(ward) forces imposed by muscles and to the out-(ward) forces the element imposes upon the environment, in terms of the distances (moment arms) from the fulcrum. He then uses the ratio of moment arms to characterize a "gear-ratio", again utilizing the implicit idea of a potential mechanical advantage.

Such concepts as "mechanical advantage of a muscle" and "gear ratio" are appealing as they immediately identify major architectural differences, for instance among sprinters and diggers (HILDEBRAND et al., 1985), and thus

have superficial didactic value. However, the approach tends to confuse cause and effect because the magnitude of the two lever arms is affected by quite distinct factors. Furthermore, the simple comparison of lever arms does not separate the critically distinct demands and tasks of force production from those for the generation of displacement and velocity. The most important fallacy derives from the demonstration that shifts in muscle placement do not affect the mechanical advantage (GANS et al., 1985; GANS and de VREE, 1987). Hence, the use of muscle mechanical advantage is misleading in models of musculo--skeletal systems.

I begin this essay by documenting why muscle placement does not affect the mechanical advantage. I then offer a reinterpretation of some of the observations that seem in the past to have led myself and others to this erroneous concept. Next I review the factors important in the analysis of biological lever systems and develop a simple theory for their consideration in the structure of Recent and extinct animals. Throughout I use examples from limbs and jaws; however, the model will hopefully apply to other skeletal elements as well. Much of what follows was stimulated by a recent analysis of the meaning of packing factors in muscle architecture (GANS and de VREE, 1987).

It is a pleasure to dedicate this brief analysis to Dr. M. MŁYNARSKI in recognition of his studies on the structure of fossil reptiles.

II. MOMENT ARM AND MUSCLE PLACEMENT

The forces generated by a muscle reflect the behavior of its component sarcomeres (cf. BURKE, 1978; LOEB and GANS, 1986). The force generated by a stimulated sarcomere is not constant over time but reflects (1) the length of the sarcomeres at the time the muscle is stimulated, and (2) the velocity at which the sarcomere can shorten. Hence the placement of the sarcomeres relative to the potential movement of the lever becomes important.

A shorthand approach permits statement of some simple rules. The first is that the closer the sarcomere (muscle) to a median (resting or plateau) length, the greater the force it produces whenever stimulated. To the extent that the sarcomeres (fibers) are stimulated while positioned (by the action of other muscles or whatever) at a lengt longer or shorter than plateau, they generate less force. Finally, the faster a muscle fiber (sarcomere) is allowed to shorten, the less force it produces. (This relation is hyperbolic rather than rectilinear, so that the force-velocity curve mainly contains two zones, one of high-force/low--velocity and the other with low-force/high-velocity). As the work performed and hence the energetic cost of any contractile twitch is roughly equivalent,

whatever the force or velocity thereby achieved, it is necessary to match the muscular design to the functional demand.

Assuming that under equivalent conditions each standard sarcomere is likely to produce equivalent force, power and work, there are simple rules for understanding the combined actions of multiple sarcomeres: A string of x sarcomeres arranged in series will produce the force equivalent to that generated by a single sarcomere and x-times the unit sarcomere excursion, leading in a twitch to x-times the velocity. An array of y sarcomeres arranged in parallel will produce y times the force, but only the excursion and velocity equivalent to that of a single sarcomere. Hence the force involved cannot be constant throughout the range of movement, but must reflect the initial position and rate of length change at time of activation of a muscle.

The greater the distance from the fulcrum to the attachment site of a muscle, the greater the absolute distance through which the muscle must shorten as the lever rotates through a particular angular excursion. If the rotational velocity of the lever is constant the velocity of muscular shortening has to increase as well. This set of relations generates the seeming paradox that all sarcomeres of a particular type in a parallel-fibered muscle shortening at an equal rate from an equivalent starting position will generate a constant per--sarcomere moment (GANS and de VREE, 1987). The reason for the constancy is that an increase in the moment arm of a muscle also increases the absolute displacement through which it must shorten. This amplification of displacement increases the fraction of sarcomeres that must be placed in series, and this increase will be directly proportional to the increased moment arm. Hence (for a given angulation, sarcomere property and shortening range) it is the mass of a muscle rather than the distance from the fulcrum that determines the moment.

III. WHY DO THE INSERTIONS OF SOME MUSCLES SUGGEST THAT THEY HAVE LONGER MOMENT ARMS?

The hypothesis that muscle placements do affect moment arm (in contrast to above and GANS and de VREE, 1987) has often been adduced to explain cases cited in the literature. For instance, one obtains the impression that species which chew their food or crush objects between their jaws have increased the moment arm of the muscle insertion. Similarly, diggers seem to have the centroid of the insertion area placed outward along the limb.

Setting aside a couple of reasons (cited below) independent of moment arm, the "outward" shift often appears to be due to two distinct factors. The first is that the cases generally involve animals in which the site of force application has also shifted inward, hence the comment that the gear-ratio has changed. However, comparison with other and independent dimensions of the animal shows that the relative shift of muscle insertion is minor. A second factor that seems to be much more common reflects the observation that greater

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work output requires a greater mass of muscle. This muscle has to be placed somewhere; thus, one notes that the centroid of the insertion area will shift outward, even if the mass of muscle is placed immediately adjacent to the fulcrum. The visual effect is often exacerbated due to the general increase in the robustness of bones transmitting the increased moments. Other examples are referred to below.

IV. DESIGN FACTORS FOR LEVERS

General

Most vertebrates propel themselves and effect functions that to them have biological meaning by exerting forces onto specific aspects of the environment. The structural elements that transmit these actions will be simple or compound levers and what follows is a series of statements reminding of the several influences on such systems. To the extent that the bodies of animals are optimized to perform particular sets of roles, we may expect that the costs and effects here tabulated will be matched to some compromise level that is reflected in the multiple aspects determining the phenotype of any organism.

(1) The laws of motion indicate that moving part of an animal incurs a cost that reflects the mass moved and the change of its velocity (acceleration). This cost is independent of and hence additive to the mass-related and tissue-specific cost of metabolic maintenance, for instance of the supportive parts of the limb and of the muscles that move it.

(2) The places onto which an animal may advantageously apply forces are not randomly positioned in space; they may lie some distance away from the current position of its head and trunk. Appendages that induce the action (thus reducing the fraction of mass that is subject to acceleration) may have to perform other actions, for instance postural maintenance, as well.

(3) Also there is a potential conflict between the need slowly to exert high forces and rapidly to exert smaller ones. Contrast snapping at prey with crushing it, and sprinting with climbing, but remember that pairs of such tasks often have to be performed by a single system.

(4) Limbs and jaws should not only be able to exert forces, but must transmit energy and do work. In short, the force must be exerted throughout a distance and within a defined unit of time.

(5) The out-force that may be exerted at any point of a lever is a function of the available moment. For a given moment, we know that the longer the moment arm along the lever, the less the force that can be exerted at its tip. Exertion of a given force requires an increased moment as the moment arm increases.

(6) However, for a given angular movement a longer limb also produces a greater linear excursion of its tip. With this it becomes important to know the time during which the swing can take place and still perform the role.

(7) A moving lever incurs rotational inertia. Proximal placement of its

mass is advantageous as it reduces the inertia and with this the cost of oscillating the lever. Inertial relations appear to explain the general observation that limbs tend to become more slender with distance from the trunk (HILDEBRAND and HURLEY, 1985; STEUDEL and MYERS, 1986). The distal-most aspects of some limbs sometimes do not fit this generalization, apparently because specialization for various kinds of force transmission to particular kinds of substrates imposes independent effects. Also, the demonstration of such a benefit to slenderization should not be assumed to explain all cases of distally slender limbs.

(8) The muscular force applied to the lever will be influenced by the relative stiffness and compliance of the connecting elements. These values vary with magnitude and frequency of loading.

(9) The muscular force applied to the lever must be sufficient both (i) to generate (and maintain) the moment needed for force production at the distal site and (ii) to overcome the intrinsic rotational resistance so that the distal part may achieve the needed rotational velocity.

The considerations change the way we should contrast different types of levers, for instance stout with slender limbs. Presumably, there is an advantage to subdividing the animal into differentially moving parts, so that the maximal accelerations involve only a small fraction of the animal's mass. The key determinants are, first of all, the sites to which forces must be applied and then the rates at which it is desirable to apply them. Also ecology may impose a number of geometric constraints. For instance, the length of giraffe limbs probably tells more about the feeding habits of the animal than about its motor needs. Similarly, there are aspects of the substrate and of the climate which transcend locomotor demands, but constrain overall shape and architecture. These several factors may be conflicting; stout limbs of equivalent length reduce heat-loss in cool climates but swinging them requires more energy both because of their greater inertia and because they incur greater environmental resistance during the forward swing.

Such issues must not be treated in a single-valued fashion. Shift from short and stout to long and slender theoretically increases the rotational inertia of limbs with equivalent mass. However, many runners reduce the inertia of their limbs by folding them during the recovery stroke. Also, there is the contrast between absolute velocity and velocity in terms of body lengths per unit time. A relatively longer limb may achieve an equivalent velocity with relatively fewer strides, or may reduce the angular excursion if the cycling frequency is maintained. In all of these systems one must ask whether the animal has the capacity to produce the necessary force and to generate the needed work.

The supportive elements

The supportive tissues of an animal must maintain the shape of the lever, keeping the lever from deforming under the moments that it must transmit. Limb bones must neither buckle, nor bend significantly. Similarly the mandible

must be kept from deflecting during the bite against prey. Naturally, the direction of force application will be a critical determinant of the stresses actually generated. Some animals avoid or reduce the lever problem by loading the bone differently. Thus, a standing or pronking mammal will load many of its long bones in axial compression. It imposes mainly axial compressive loads, the magnitude of which will not be affected by lever length as long as buckling is avoided.

In contrast, transverse loads such as those during walking, scratching and biting, require that the lever must transmit moments. The stresses that these moments generate increase with the cantilevered length of the lever and must presumably be maintained at a tolerable level by repositioning of material (e. g., local thickening of bones at the cost of increasing the rotational inertia). However, application of the muscular forces further out along a limb, perhaps via tendons, changes the force distribution by limiting the distance of cantilevering (CURREY, 1984). This allows reduction of the distally-placed mass of supportive tissue.

Finally, there are the special demands of compound or segmented levers. A chain of mechanical links, such as an entire limb, may be treated as a single lever; if the joints can be stabilized, so that they do not deform significantly during the loading cycle. Limb stabilization may, for instance, occur in the limb of a scratch burrower. The key will then be the mechanism of interlocking the distal elements, either mechanically (reducing the metabolic cost) or by muscular arrangements. Major design components seen are locking devices, that keep the chain from collapse if loaded in the direction of main force application (cf. the flexor bone of *Amblysomus* PUTTICK and JARVIS, 1977; accessory plate of the forelimb of *Bipes*, ZANGERL, 1944).

The difference between a single lever and one composed of articulated links capable of interlocking is likely established by extraneous factors occurring during another part of the motor cycle. Thus the joints of knee and even ankle may involve the retraction stroke, during which reduction of the rotational inertia and clearance of the ground are the most critical factors. Other joint adaptations increase stiffness, blocking the degrees of freedom, as do the lands and grooves in the ankle of goats. Commonly one sees limitations of the control pattern, such as devices that cause two or more elements to move in unison (see discussion of two-joint muscles below).

The muscular elements

Most of the forces transmitted within the body of a moving animal are ultimately generated by muscular contraction. Muscles must generate the moments required to derive distal forces and move the lever at the desired velocity. The amount of muscle required is a function of the maximum forces ever required. However, the forces and moments at any instant observed within the body of a moving animal need derive only in part from current muscular contraction, because animals supplement contraction with the momentum

conserved in the mass of their moving parts (kinetic energy) and elastic storage in skeletal and connective tissue parts (potential energy). The energy thus conserved will blunt the peak requirements for muscular force that would otherwise have to be generated coincident with some critical activities. This implies that at any instant the level of useful force likely differs from that generated by the simultaneously contracting muscles. (The reference to current or "simultaneous" contraction sets aside the general effect of excitation-contraction coupling, i. e. that contractile force will lag the electrical events observed during muscular contraction.)

Conservation of energy is stressed because peak forces may be only one of the determinants for muscle design. Forces that must be exterted repeatedly for prolonged periods may be as important adaptively. For that matter, we now know that some muscles are divided into "task groups", i. e. are subdivided functionally into suites of motor units that perform different functions, generally not simultaneously. Consequently, experiments on living animals are required to determine whether all or part of the fibers of a muscle participate in the activity peak observed for a particular behavior.

The consideration that sarcomeres produce moments, and that this capacity changes with factors such as relative shortening, documents one fundamental difference between the loadings on the out-lever and the in-lever. The load on the out-lever (action onto the environment) is behaviorally determined and often represents a single value, determined for instance by the need to impose a load on ground of prey. There is no intrinsic reason why the out-force should change as the lever rotates. In contrast, the force generated by the muscle is affected by the relative shortening.

The literature would suggest that the shift of insertion site distally along the limb would increase the moment generated by the muscle; hence, such more distally placed muscles should be more powerful. However, as each sarcomere contributes equal moment this consideration makes mass distribution irrelevant for a particular muscle pattern (fiber angle relative to the line from insertion to fulcrum). Naturally, this simple relation is complicated slightly if the muscles are pinnate (GANS and de VREE, 1987); however, the general relation holds (for instance if the angle of pinnation is constant for the entire muscle).

The placement of muscles incurs particular rules. As the distance from the fulcrum does not matter as long as equivalent sarcomeres may be placed in parallel, placement of the muscular mass closer to the fulcrum will establish selective advantage by reduction of rotational inertia. Hence we see that most muscles lie proximal to the joints they activate. A variant is seen whenever sarcomeres are placed in positions of shallow insertion which allows all of the fibers to have closely equivalent moment arms. In many cases, such muscles exert their forces by elongate tendons that are sufficiently stiff so that there is limited compliance in response to sudden loads. Another variant involves a subdivision of tasks, with arrays of muscles involved in positioning the joint by producing excursion and velocity, whereas a second set generates high

forces for low excursion. Such sets are possible by arrangement of two joint muscles that bridge more than a single joint. As these are often placed so that the two rotations are opposed, the muscle incurs little excursion (velocity), and its force production remains in the high-force/low-velocity range.

Some factors still require extension of the insertion sites outward along limbs. Claims have been made that the reduction of bending moments is one of these. Another requirement for outward shift may be the demand for particular muscle packing, i. e., the placement of sarcomeres at sites that will not interfere with movement of the limb or of other muscles. A more important aspect of packing has been discussed above, it is the need to place the required sarcomeres into a space near the joint; as the absolute movement of sites near the joint is relatively low, the sarcomeres will lie in parallel to each other and the centroid of the insertion area must shift outward along the lever. Another factor that leads to a seemingly greater moment arm is seen in joints that allow more than purely rotational movements.

Overview

The preceding statements are provided on a purely functional basis. Which placements are most advantageous from the viewpoint of performance and how can a particular performance be generated? Indeed, how much muscle is necessary relatively and absolutely to perform a particular action, to occupy a particular niche? In generating answers to such questions, we have considered implicit the likely compromises presumably imposed by developmental and comparative factors.

Development has preprogrammed and more labile components. Some groups of vertebrates can modify the fiber type of their muscles as a result of training, the muscles of others, such as man, also show major volumetric changes with increased activity. However, in other species the environmental component is less critical than the genetic one. Also we see that different organisms use distinct muscle arrangements to generate equivalent movements. Analysis suggests that each arrangement is sufficient for performing most of the roles; apparently the developmentally most convenient pathway will be utilized as adequacy is the major determinant. However, the above considerations do not affect the functional interpretations; they need only differentiate the mechanisms by which the phenotypes were initially produced.

The basic position of this essay has been that muscle moment is independent of lever arm. Consequently, the factors required by force application and those influencing muscle placement likely proceed independently, and the two effects must be separated in analysis. Take for instance, the difference between long--snouted and short-snouted crocodilians, or better yet long and short muzzled dogs. In both cases, only the out-lever, but not the in-lever, has become modified. Many mammals have shifted their molars posteriorly, so that they come to lie between the attachment sites of the adductor muscles thus reducing the demand for increased moments; exertion of greater crushing forces does not require

additional musculature. In contrast, the shortening of the femoral component of the limb system of cursors may represent a device for attaching more muscle mass to the in-lever thus generating greater moments and potentially greater out-forces.

The analysis then permits the major conclusion that the position of the in-lever and the out-lever are determined by quite different factors. The out--lever reflects truly functional aspects; it is determined by the adaptive demands of the system. The length of the lever determines the moment demanded to generate the outwardly directed forces required by biological demands; it also influences the absolute distance through which the force can be exerted. In contrast, the magnitude of the in-lever arm only reflects a series of incidental factors, such as the maximum stress level along the lever and the potential for packing an adequate number of sarcomeres close to the fulcrum. As each sarcomere of a parallel array for equivalent per sarcomere shortening contributes an equivalent moment, the mass of muscle rather than the insertion distance establishes the potential contribution of the muscle of the system. (This may explain why muscle-weight tabulations, such as those of SCHUMACHER, 1961, have the potential of correlating well with the functional bases of masticatory demands). Also the moment to be generated by the in-lever system is not only that demanded by the out-force, but also that required to overcome inertia and move the lever at the required velocity. Consequently, the concept of mechanical advantage applies only to the out-forces and the so-called gear-ratio compares two disparate values that are only partially associated and only one of which really reflects the functional design of the organism.

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STRESZCZENIE

W kurczącym się mięśniu każdy sarkomer w jednakowym stopniu przyczynia się do powstania momentu siły. Koncepcja ,,sprawności mechanicznej" (mechanical advantage) jest zatem nieodpowiednia w rozważaniach nad wzorcami przyczepów mięśniowych, gdyż zależą one od innych czynników. Pojęcie sprawności mechanicznej ma oczywiście znaczenie w rozpatrywaniu sił pozamięśniowych, wywoływanych przez elementy szkieletowe.

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