

developed by P (40 to 60 kPa). SC peak force occurred 45% through upstroke, whereas pectoralis peaked at 40% of downstroke. Thus, elastic recovery of inertial work by the SC tendon is small compared with muscle work to elevate the wing. Both muscles contracted over a large range of length (SC: 35 to 54% and P: 26 to 47%). Whereas the SC mainly shortened relative to rest length, the pectoralis mainly lengthened. SC produced 1.6 W during level flight, 31% of the power generated by the pectoralis (5.1 W). Both muscles generated greater (22-30%) power during ascending and less during descent (-61% to -65%). (NSF IBN-9723699)

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Mechanics of rattlesnake tailshaker muscle.

MOON, B.R.* and K.E. CONLEY. Univ. of Washington Medical Center, Seattle.

Rattlesnake tailshaker muscle is specialized for high speed, low force contractions. Each muscle is a single motor unit, whose temperature-dependent contractions range from 20-90 Hz over 10-35° C. As body temperature and rattling frequency increase in western diamondback rattlesnakes (*Crotalus atrox*), the mechanical work and twitch force of rattling increase, whereas twitch duration decreases. Two factors may account for the discrepancy between these results and the constant metabolic cost per twitch reported previously: (1) Twitch force and duration tradeoff to produce a constant force-time integral, and hence constant cost per twitch. This appears to be the case for mid-frequency twitches. (2) An energy saving mechanism may allow increased mechanical work at some frequencies without increased metabolic cost. The mechanism of energy savings is currently under study. Therefore, in contrast to the constant metabolic cost per twitch, shaker muscle mechanics and energy savings are frequency-dependent. These unique physiological and mechanical properties of rattlesnake shaker muscle allow sustained high speed, low force contractions at very low metabolic cost.

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Twisting and bending: The role of hypaxial musculature during locomotion in a salamander *Ambystoma tigrinum*.

BENNETT, W.O. Univ. of Massachusetts, Amherst.

When salamanders locomote through aquatic and terrestrial habitats, their pattern of axial muscle activity changes. Carrier (1993) found that all four layers of lateral hypaxial musculature in *Dicamptodon ensatus* fire synchronously during swimming, but asynchronously during walking. This study concluded that hypaxial muscles contribute primarily to lateral bending during swimming, whereas they function primarily to counteract torsional forces caused by diagonal limb support during walking. This 'torsional hypothesis' has been controversial, and data from walking lizards indicate that these muscles function primarily to produce lateral bending. The goal of this work was to test whether Carrier's findings from *D. ensatus* hold for another salamander, *Ambystoma tigrinum*. In agreement with Carrier's results, all hypaxial muscles were found to fire synchronously during swimming in *A. tigrinum*. Data from *A. tigrinum* also support the torsional hypothesis: during walking, the external obliques were active on the side towards which the trunk was bending, while the internal oblique and transverse abdominus were active on the opposite side. However, during some walking trials, a biphasic muscle activity pattern that is correlated with both lateral bending and torsion control was evident. This work was supported by a Sigma Xi Grant in Aid to WOB.

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Function of the oblique hypaxial muscles in trotting dogs.

FIFE, M. M.* and D. R. CARRIER. Univ. of Utah, Salt Lake City.

When dogs trot the timing of activity in the obliquely oriented hypaxial muscles is consistent with the functions of stabilization against vertical accelerations that cause the trunk to bounce in the sagittal plane and stabilization against horizontal accelerations that tend to shear the trunk in the sagittal plane. To test these hypotheses we compared the intensity of muscle activity 1) when dogs carried weights (4 -10 % of body weight) supported over the limb girdles versus supported mid-trunk

(sagittal bounce), and 2) when dogs trotted up versus down a 12o slope (sagittal shear). The loading experiment had a variable effect on the intensity of muscle activity. In contrast, the hill experiment produced dramatic results. Relative to level running, muscles with a craniodorsal orientation (external layers) showed an increase in activity when the dogs ran uphill and a decrease when they ran down. Muscles with a cranioventral orientation (internal layers) exhibited the opposite pattern; increased activity when the dogs ran down and decreased activity when they ran up. Thus, the obliquely oriented hypaxial muscles of dogs appear to help stabilize the trunk in the sagittal plane against cranial and caudal directed accelerations.

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Mechanics of fast contracting squid muscle: Mechanisms of specialization.

KIER, W.M.* and N.A. CURTIN. Univ. of North Carolina at Chapel Hill, and Imperial College of Medicine, London, United Kingdom.

Comparison of striated muscle from diverse animals reveals a remarkable range of performance and specialization. In contrast to work on vertebrate muscle, recent research shows that specialization of the fast-contracting tentacle muscle of squid occurred by dramatic changes in the arrangement and dimensions of fiber components, rather than by changes in chemical composition. To explore the physiological implications of these changes, the mechanical performance of the cross-striated cells of the prey capture tentacles of *Loligo pealei* was analyzed and compared with that of the obliquely striated cells of the arms, which are the evolutionary and developmental precursors. Length-tension, frequency response, and force-velocity data have been obtained from fiber bundle preparations. The unloaded shortening velocity of greater than 13 l/s (19 ° C) of the tentacle cells is an order of magnitude higher than that of the arm cells. The tentacle cells also show dramatic changes in excitation. The ratio of twitch force to tetanic force of the tentacle fibers was measured to be approximately 0.65, compared with 0.05 in the arm. Supported by NSF IBN972707 & NATO CRG 971179.

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Stabilizing properties of invertebrate skeletal muscle.

MEIJER, K.* and R.J. FULL. Univ. of California, Berkeley.

Muscle can serve a role in stabilization to rapid perturbations. Intrinsic muscle properties may result in a stabilizing response acting before reflexes, hence termed a preflex (Loeb and Brown, 1996). To investigate the stabilizing properties of muscle, we measured mechanical impedance of two leg muscles used by the cockroach, *Blaberus discoidalis*. Experiments consisted of ramp stretches (0.5-4%; 0.1-5 l/sec) and sinusoidal length oscillations (5-150 Hz; 0.5% strain; muscle length 90-130% l₀) that were imposed on active as well as relaxed muscles. The force response to perturbations in relaxed muscle was a significant fraction (10-50%) of that observed in active muscle. Impedance (delta force/ delta length) of relaxed muscle doubled over the range of frequencies, whereas it increased 5-fold with a 40% increase in muscle length. The tangent of phase angle ranged from 0.2-0.6, indicating significant damping. The contribution of leg muscles toward rejecting perturbations could be substantial and in part due to passive mechanisms. The relative importance of active and passive preflexes to stability will require a multiple muscle model which includes moment arms to yield apparent joint stiffness and damping. ONR N00014-98-1-0669.

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Muscles stimulated by the same motor neuron function differently in running roaches.

AHN, A.N.* and R.J. FULL. Univ. of California, Berkeley.

Studies of neural control often infer muscle function from electromyography (EMG) and kinematics. Muscles within the same anatomical group innervated by the same motor neuron are assumed to function similarly. We examined the in vivo function of two leg muscles in the cockroach, *Blaberus discoidalis*. Both muscles are innervated by the same, single excitatory motor neuron and extend a single degree-of-freedom