ELECTROMYOGRAPHY OF HETEROGENEOUS DARK AND PALE MUSCLE

by

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INTRODUCTION

The physiological significance of muscle coloration has long been a topic of much discussion. Upon gross observation, muscle is generally classified as being either red (dark) or white (pale). The literature describing the structure of such muscle is both vast and controversial, probably due to species differences. However, there does seem to be some agreement on the following characteristics: White muscle is predominantly composed of fibers which have small myofibrils of equal size and spaced in a regular lattice (*Fibrillenstruktur*) (26, 32, 35) single, discrete innervation (*en plaque type*) (26, 27, 32), large cross sectional area, poor vascularity, little myoglobin, few mitochondria and a low lipid content (1, 2, 3, 9, 14, 37). Red muscle fibers have myofibrils which are larger and irregular in size and spacing (*Felderstruktur*) (26, 32, 35), multiple, diffuse innervation (*en grappe type*) (26, 27, 32), small cross sectional area, rich vascularity, high myoglobin content, many mitochondria and a high lipid content. (1, 2, 3, 9, 14, 37).

The physiological significance of these structural differences was probably first recognized by Ranvier (39) when he associated white muscle with fast contraction and easy fatigability, as compared to red muscle. This, again, is controversial, but many investigators have found it to be basically correct (10, 13, 25, 27, 32, 36). Thus, the concept that white muscle contracts rapidly or *phasically* and that red muscle contracts slowly or *tonically* is generally accepted today. However, cross innervation experiments (6, 11, 39) tend to minimize the role which structure plays in contraction rate and emphasize that of innervation. It has been found that slow (red) muscle can be made to contract phasically when innervated by nerves normally innervating fast muscle and that fast (pale) muscle can be made to contract tonically when innervated by nerves normally innervating slow muscle. Closer observation has also revealed that some of the long-considered red and white muscles are actually heterogeneous; i.e., they are composed of red, white and intermediate (having transitional characteristics) fibers (38, 42). The relationship between structure and function then becomes more complicated as additional data are reported.

An expiratory muscle of the chicken, the m. transversus abdominis (transversus abdominis) was found to be an ideal muscle for studying the correlation between structure and electrophysiological function. de Wet (14) observed this muscle to be a heterogeneous pale muscle in the adult bird with a fiber population of about 50% pale, 30% intermediate and 20% dark. He classified the fibers by differences in diameter, innervation, vascularity and affinity for Sudan Black B, a lipid stain. Sudanophilia has also been observed by Chinoy and George (9) and Gauthier (19) as being a property of red fibers. In the one-day-old chick, de Wet found the fibers of this muscle to be predominantly dark with less than 10% being pale, as observed with Sudan Black B stain. He suggested that dark fibers are the stem fibers from which intermediate and light fibers differentiate. This suggestion is in agreement with the findings of Germino et al. (2) and of Close (10) who found that fast muscle differentiated from muscle that was initially slow.

The purpose of the present investigation was to electromyographically study the transversus abdominis in both its dark and pale states. Extracellular recordings were taken from single muscle fibers to compare the shape and amplitude of the action potentials. The patterns of motor unit recruitment in response to changes in tension exerted by the muscle in these two anatomical states were also studied. The goal was to correlate electrophysiological phenomena with structural changes.

METHODS AND MATERIALS

Bird Preparation and Artificial Respiration

Seventeen mature (9-12 months) and 20 one-day-old (18-36 hours) White leghorn male chickens served as experimental animals. Mature birds were anaesthetized with sodium pentobarbital injected intravenously via a cannulated cutaneous ulnar vein. The comb pinch reflex was used to determine the level of anaesthesia. Slight head movement resulting from pinch of the leading edge of the comb indicated surgical anaesthesia. An intraperitoneal injection of 0.04 ml of sodium pentobarbital was sufficient to bring the one-day birds to surgical anaesthesia and to maintain light anaesthesia throughout the experiment. Since the anaesthetic depresses the respiratory centers, it was necessary to maintain the bird under light anaesthesia during the recording period. Deeper anaesthesia resulted in a decrease in motoneuronal output to the transversus abdominis and a decrease in electromyographic activity in this muscle in response to increased CO_2 stimulation (18).

Artificial respiration, whereby the CO_2 concentration in the ventilating gas could be varied, permitted strict control of respiratory movements and hence strict control of muscle tension produced by the transversus abdominis. The birds were prepared for artificial respiration by exposing the trachea, opening the thoracic and abdominal cavities and the thoracic and abdominal air sacs. The trachea cannula was then inserted and the ventilating gas was forced in a unidirectional manner through the respiratory system. The time interval between opening of the body cavities and cannulation of the trachea did not exceed one minute in order to prevent hypoxic injury to the respiratory centers. The respirator consisted of a unidirectional gas flow system described by Burger & Lorenz (7) and a gas heater-humidifier described by Fedde and Burger (17). This apparatus controlled the volume of O_2, N_2 and CO_2 ventilating the birds as well as the gas temperature, which is important in regulating the bird's body temperature, and the gas humidity. Body temperature, measured with a rectal thermometer inserted 5 centimeters in the mature bird, was held at about 40° C. This was accomplished by maintaining the gas temperature at 46° C. at the trachea cannula and by loosely covering the opened body cavity with Saran wrap. Mature birds were ventilated at a rate of 4,000 ml of gas per minute and the day-old birds at about 200 ml of gas per minute. Oxygen concentration was maintained at 20% while N_2 concentration varied inversely with CO_2 concentration. The transversus abdominis was either left in its natural position, in which case the recordings were taken from the mid-dorsal area of the medial surface or, separated from the *m. obliquus abdominis internus* and suspended via threads through its ventral aponeurosis. In this case, the recordings were taken from the mid-dorsal area of the lateral surface.

Electrode Preparation and Recording

The metal microelectrodes (50 μ tungsten wire) were electropolished to a tip diameter of 1 μ by applying a 3 volt a.c. current to the wire in a 2 M. NaOH solution. The electrodes were insulated with insl-x, E-33 clear[1] which had been allowed to evaporate to the consistency of honey

[1] insl-x, E-33 clear. Insl-x Products Corporation, Yonkers, New York.

at room temperature. This was accomplished by bending the electrodes into the shape of a fish hook and dipping them into the insl-x, then removing them slowly, tip first. It was important to closely observe the removal process and stop for approximately 30 seconds when the tip broke the surface. This allowed the insl-x to dry around the tip, thereby preventing the surface tension from pulling the insulation back from the tip and leaving an unduly large exposed area. The direct current resistance, with the electrode negative, was between 10 and 50 megohms when measured in physiological saline. The electrode wire was bent into a Z shape to help it float with the muscle. It was then clamped into a coil spring that was soldered to the distal end of the preamplifier lead-in wire.

The bipolar EMG electrode used for recording motor unit activity consisted of two teflon coated stainless steel wires, 150 μ in diameter, insulated except for the last 1 mm and sharpened to a 30 μ point. The tips were held 1 mm apart by a drop of dental acrylic. The wires were twisted together and coiled 10 turns to allow the electrode tip to move freely with the muscle.

Five of the mature birds were prepared for simultaneous recording of efferent electrical activity in a ramus of one of the nerves which innervated the transversus abdominis, electrical activity in the transversus abdominis, and tension produced by this muscle. Fig. 1 illustrates the recording system. The suspended muscle was attached to an isometric strain gauge transducer[2] which was connected to a strain

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[2] Stratham strain gauge transducer, Model GI-16-350. Stratham Laboratories, Inc., Hato Rey, Puerto Rico.

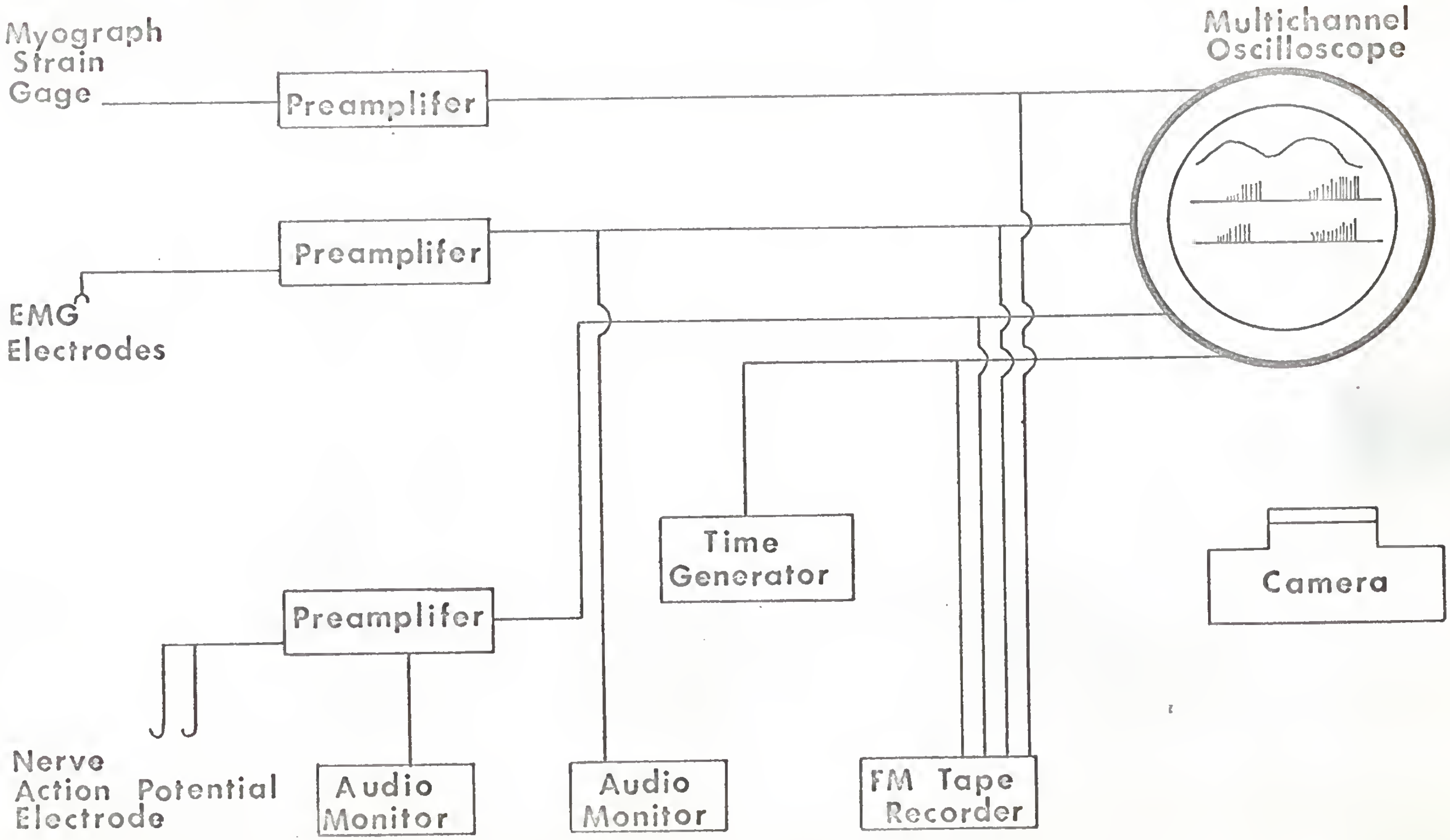

Fig. 1 -- Recording system for the simultaneous recording of muscle and nerve electrical activity with the tension produced by the muscle.

gauge preamplifier.[3] The n. intercostalis internus 6 (14) was carefully dissected from the lateral surface of the transversus abdominis, cut, and the central end draped over a bipolar silver electrode. Both nerve and muscle electrodes were connected to Grass a.c. preamplifiers[4] which were set at the maximum high frequency cut-off of 30 kilocycles. A time mark generator[5] was also used to accurately note time. The above phenomena were simultaneously observed on a multichannel oscilloscope[6] and recorded on a multichannel tape recorder.[7] Film strips were obtained by replay of the tapes and photographing with a Grass Camera.[8] Single cell and motor unit recordings required the use of only one preamplifier. The single cell recordings were photographed directly from the oscilloscope since the tape recorder's frequency response of 2.5 kilocycles was too slow for the accurate recording of the fast action potentials. A storage oscilloscope[9] (not shown in Fig. 1) was used to monitor the multichannel oscilloscope. This enabled the observation of superimposed multiple sweeps of potentials from single cells for the determination of the

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[3] Tektronix type Q plug-in unit. Tektronix, Inc., P.O. Box 500, Beaverton, Oregon.

[4] Grass model P5 low level a.c. preamplifier. Grass Instrument Co., 101 Old Colony Ave., Quincy, Massachusetts.

[5] Tektronix time-mark generator, Type 180A. Tektronix, Inc., P.O. Box 500, Beaverton, Oregon.

[6] Tektronix oscilloscope, Type RM 565 with 2 four-trace plug-in amplifiers, Type 3A74. Tektronix, Inc., P.O. Box 500, Beaverton, Oregon.

[7] Dacord tape recorder, Model 144 with Model 110 voice commentary unit. Cambridge Instrument Co., Inc., Ossing, New York.

[8] Grass oscilloscope recording camera, Model C-4. Grass Instrument Co., 101 Old Colony Ave., Quincy, Massachusetts.

[9] Tektronix, Type 564, Storage oscilloscope.

presence or absence of the jitter phenomenom which has been described by Ekstedt (16) as a method of defining single fiber extracellular activity. Ekstedt described the jitter phenomenon as the variation in the shape of successive action potentials due to the variability in the time intervals between potentials arriving from two or more fibers.

RESULTS

The action potentials recorded with microelectrodes from single fibers of the transversus abdominis of the mature and one-day-old chickens were almost identical, except for amplitude (Fig. 2). They meet Ekstedt's (16) criteria for unicellular action potentials; i.e., they are smooth and biphasic and consecutive action potentials were identical in shape (absent of the jitter phenomenon). Amplitude of the spikes, from peak to peak, varied from 4-7 millivolts in the mature birds and from 0.5-1.0 millivolts in the one-day-old chicks. The smaller potentials in the young birds required increasing the gain of the amplifier, thereby increasing the noise and not producing as smooth an action potential as found in the mature bird. The rise times, 90% of the full change from peak to peak, varied from 50-100 microseconds in both mature and one-day birds. Though the transversus abdominis in the mature bird is a heterogeneous muscle structurally, action potentials similar to that in Fig. 2a were the only type that could be found and identified with certainty as action potentials from single fibers by Ekstedt's criteria.

Motor unit potentials were also recorded with metal microelectrodes. Fig. 3a depicts a complex potential which was about 4.5 milliseconds in duration. Two or more similar, successive traces indicated that the indi-

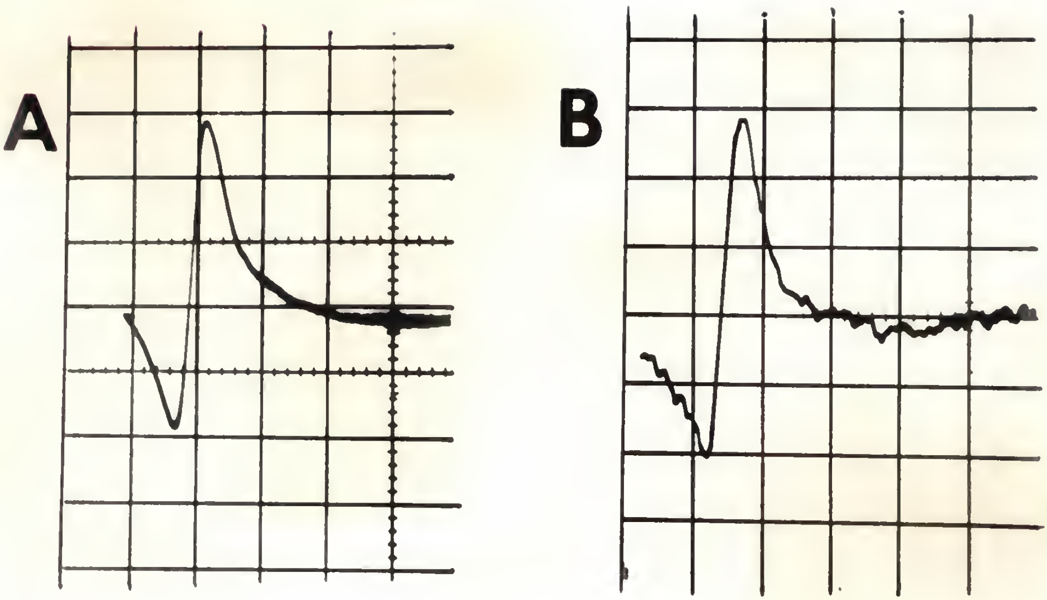

Fig. 2 -- Action potentials, recorded with metal microelectrodes, from single fibers of the transversus abdominis of the mature (A) and one-day-old chicken (B). Sweep speed: 0.2 milliseconds per major division. Calibration: 1.0 millivolt per major division (A) and 130 microvolts per major division (B).

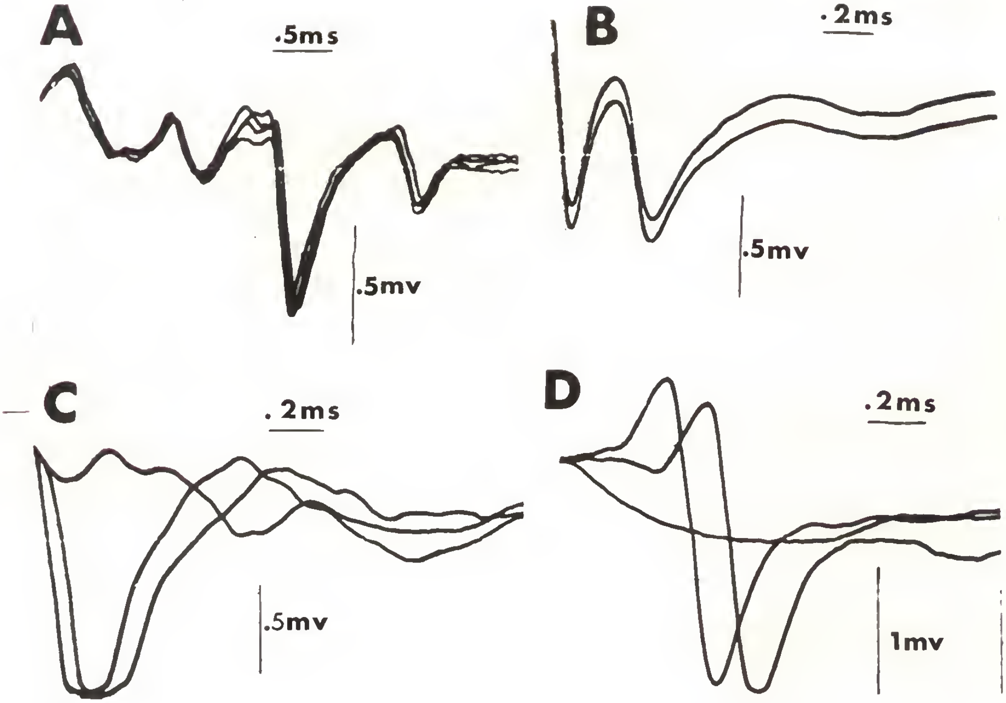

Fig. 3 -- Motor unit potentials, recorded from the transversus abdominis of the mature bird, with a metal microelectrode, range from a slow, low amplitude, complex potential (A) to fast, high amplitude potential (D). The jitter phenomenon is present in D, indicating a unit rather than a single action potential. In A four consecutive sweeps are superimposed. In B, C and D the second sweep was lowered to allow for more detail of the individual potentials.

vidual potentials were generated by a single motor unit. Figs. 3b and 3c are examples of other types of motor unit potentials which were less complex and shorter in duration. Though some potentials were smooth and biphasic, successive traces showed a slight variation in shape and amplitude (presence of the jitter phenomenon), indicative of a motor unit potential (Fig. 3d). Potentials of the preceding nature have also been recorded with the bipolar EMG electrode. This electrode, because of its relatively large, uninsulated surface area, generally detected only motor unit activity.

The electrical activity in the transversus abdominis of the mature bird and in efferent neurons to the muscle was recorded simultaneously with the tension it produced (Fig. 4). The nerve potentials, observed with a fast sweep speed on the oscilloscope, were smooth and fast, indicative of single action potentials. Even when the bird was in apnea (0% CO_2 in the respirator gas), there was electrical activity in the nerve and muscle (Fig. 4a). The amplitude of potentials in both nerve and muscle was generally small with a few intermediate potentials found at random. This activity was associated with a maintained tension produced by the muscle, which was about 20% of the maximum tension produced during 12% CO_2 stimulation. Maximum tension fluctuated between 50 and 100 grams, depending upon the bird and preparation. At 6% CO_2 stimulation (equivalent to an air capillary PCO_2 of about 41 mm Hg.), there was a much higher incidence of intermediate potentials in both the muscle and nerve, particularly near the end of expiration (Fig. 4b). At 12% CO_2 the bird was in hypernea (Fig. 4c). There was a marked increase in the occurrence of intermediate potentials in both muscle and nerve and the advent of large motor unit potentials in the muscle and large action potentials in

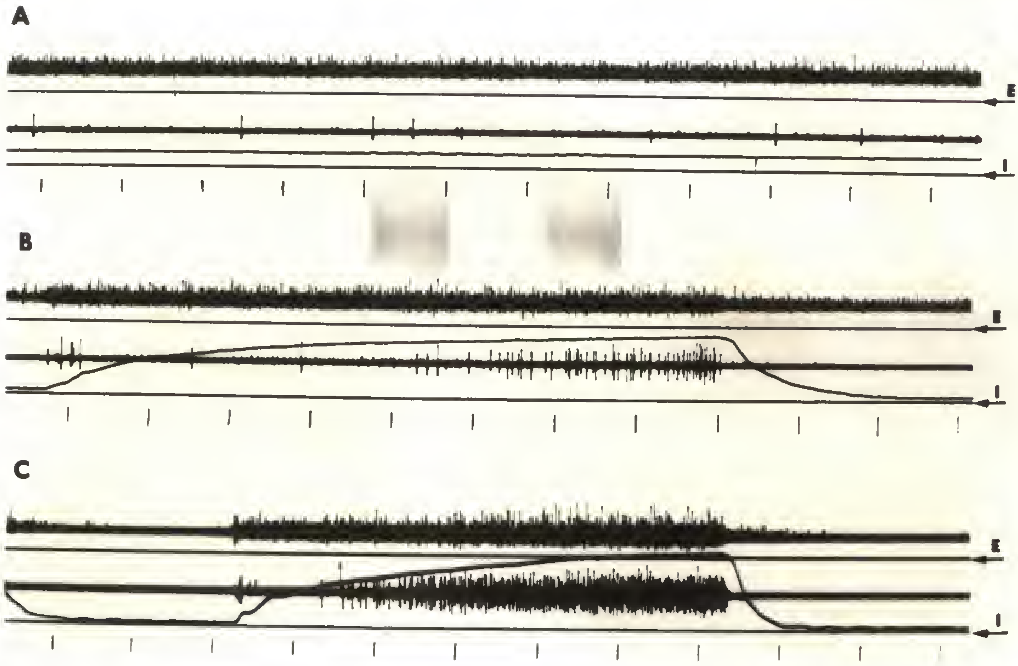

Fig. 4 -- Simultaneous recordings of the tension and electrical activity of the transversus abdominis of the mature bird and of one of its efferent nerves are shown. In A, the bird is receiving 0% CO_2 in the respiratory gas, while in B and C, the bird is receiving 6% and 12% CO_2, respectively. The nerve tracing is on the top, muscle the middle and tension on the bottom. E denotes the maximum tension developed during expiration and I the minimum tension produced during inspiration. Time marks are every 0.5 seconds.

the nerve, primarily near the end of expiration. Twelve per cent CO_2 stimulation also resulted in the complete cessation of nerve and muscle electrical activity during inspiration, which was correlated with the minimum tension produced by the muscle.

Recordings taken with a bipolar EMG electrode of motor unit activity in response to 15% CO_2 stimulation were almost identical in one-day-old and mature birds, except for amplitude and duration of the expiratory phase of the respiratory cycle (Fig. 5). The small potentials appeared at the beginning of expiration and the larger potentials did not appear until near the end of contraction when tension had increased.

DISCUSSION

The results of the electromyographic study of the transversus abdominis in its two anatomical states, with metal microelectrodes, revealed no significant differences in the shape of single action potentials. There was no evidence to indicate any dissimilarity in the electrophysiological properties of individual fibers. The marked difference in amplitude of the action potentials of the two muscles can be attributed to fiber radius. Ruch (40) stated that the size of the action potential at a given point is proportional to the apparent size of the cross sectional area of the cylindrical cell. de Wet (14) noted that the average diameter of the muscle fibers of the transversus abdominis in the one-day-old chick was about 19 μ and from his photomicrographs it appears that the average diameter of the fibers of this muscle in mature birds is about 60 μ. Thus, one would expect the action potentials from the large fibers to be about 9 times larger than those from the small fibers, which is approximately what was observed.

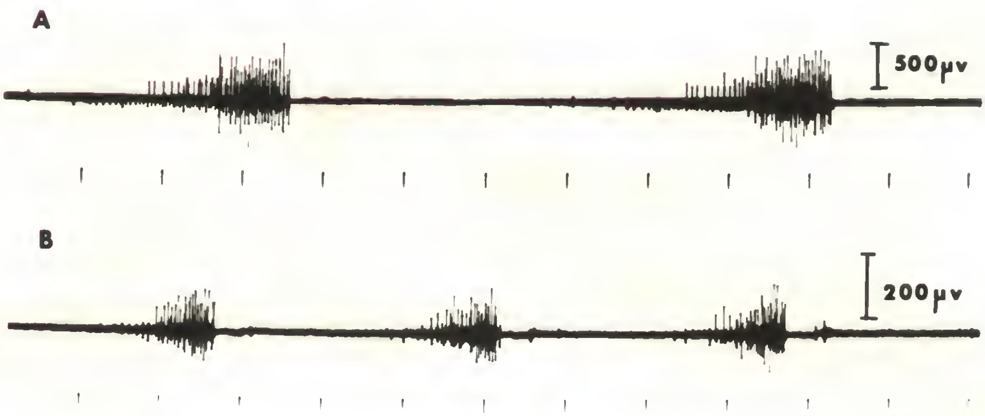

Fig. 5 -- Motor unit activity recorded from the transversus abdominis of the mature cock (A) and one-day-old chick (B). Calibration given in microvolts. Time marks are every 0.5 seconds. The pattern of motor unit recruitment was very similar in the histologically dissimilar muscles from the two age groups.

The patterns of motor unit recruitment, investigated with a bipolar EMG electrode, in this muscle's dark and pale state again failed to display any notable differences. The increase in the amplitude of the potentials in large birds has already been discussed and the longer duration and slower build-up of electrical activity during the expiratory phase in the mature bird is a function of its slower respiratory rate, (24). Therefore, electromyographically, these two structurally dissimilar muscles were not discernible. Thus, from de Wet's observation that the transversus abdominis is a heterogeneous dark muscle in one-day-old chicks and a heterogeneous pale muscle in adults, the results of this study indicate that the histological properties of these fibers do not dictate their electrophysiological activity.

The gradation (increase in frequency and amplitude) of electrical activity in muscle and motor nerves in response to increased tension demands has often been observed (4, 12, 21, 22, 23, 33). However, the significance of the amplitude of the electrical potentials in the nerves is controversial. Gesell et al. (23) believed that an increase in the size of the potentials is due to an increasing coincidence of potentials augmenting each other as a result of increased frequency. However, Henneman et al. (29, 30) found that small motoneurons had small axons (small action potentials) and that the excitability of a motoneuron is an inverse function of its size. He thus hypothesized that motoneurons were recruited in accordance to their size, the largest firing only under maximum stimulation. Corda et al. (12) also noted that the alpha motor fibers to the diaphram of the cat were recruited in order of their impulse amplitude; the smallest appearing first and the biggest toward the peak of the total discharge. The data from the present study also supports

Henneman's hypothesis; the large nerve action potentials being found only under maximum (12% CO_2 stimulation.

Wuerher et al. (42) found that stimulation of the large motor axons innervating the heterogeneous, pale m. gastrocnemius of the cat produced greater twitch tensions than stimulation of smaller axons. He also noted that the greater the twitch tension, the faster the speed of contraction and the more quickly fatigue occurred. Henneman and Olson (31) correlated this with earlier data (29, 30) and hypothesized that the size of a motor unit (the number of fibers it contains) is a function of motoneuron size; i.e., the larger the motor axon, the larger the number of fibers innervated. They further suggested that the excitability of a motor unit is an inverse function of its size; i.e., large motor units respond only to maximum stimulation. The present data would appear to support their hypothesis (Fig. 4). Large motor unit potentials are seldom found without accompanying large nerve action potentials and vice versa, indicating that they are linked together, and as previously mentioned, large nerve and muscle potentials are generally found only when tension is maximum. Henneman and Olson (31) suggested that small motor units are composed of dark fibers, because of their continuous activity, and that the large units are composed of pale fibers. They based this interpretation upon the structural characteristics of dark fiber which indicate that they are more suitable for prolonged activity than pale fibers. Their histological investigation (31) also led to the suggestion that small units consist of diffusely scattered fibers, while large units are more compact.

Henneman and Olson, however, offered no explanation as to the reason the small units contracted more slowly than the large units other than to suggest that they are composed of dark fibers which are generally referred to as slow fibers. Therefore, if there is a relationship between the action potential and the contractile properties of the fiber, as has been noted in the fast and slow fibers of the frog (8), the present investigation would suggest no significant differences in the contractile properties of the individual fibers of the transversus abdominis in its dark and pale state. Thus, there may be a reason other than fiber structure for the longer twitch duration of certain motor units in a muscle. It is very likely that the extent to which the fibers of the motor unit are spread out would radically affect the duration and magnitude of contraction. Krnjevic and Miledi (33) found the fibers of motor units to be irregularly scattered over half the total area of the rat diaphram, while Buchthal _et al_. (5) found the innervation zone of a motor axon to the human biceps to be about 40 mm. The conduction velocity of the terminal axon branches of a motoneuron is undoubtedly much slower than that of the axon prior to branching because of the reduction in size and loss of myelin; Eccles (15) estimated it to be about 0.2 meters per second. Thus, if we assume that the radius of the area innervated by the motor axon is 20 millimeters, a fiber located near the point of axon branching would receive its stimulus about 100 milliseconds sooner than a fiber at the periphery of the unit. This degree of asynchronous fiber stimulation is quite reasonable when Fig. 3a is considered. The duration of the motor unit activity in this recording is approximately 4.5 milliseconds. Since metal microelectrodes detect electrical activity in only a small area (calculated from the formula (41) $E = Em\,\Omega \div 4\pi$ where E = the recorded potential, EM = the transmembrane potential, and Ω = the solid angle subtended from electrode tip to the fiber cross section). Therefore, if

Em = 130 mv and E = 0.1 mv, the maximum distance from the fiber that 0.1 mv can be detected is about 300 μ, which is in agreement with the empirical findings of Krnjevic (33). This illustrates that there is a relatively long delay in the arrival of neural impulses to the various fibers of the unit even in this small area. A delay of this magnitude would cause a marked asynchronous firing of individual fibers within the whole unit, resulting in a slow, relatively weak contraction and a small, slow motor unit potential.

The fibers of a compact motor unit, on the other hand, would receive an impulse in a much shorter period of time, since the conduction velocity of their terminal axon branches is probably much faster than that to the so-called smaller units and the distance traversed is much smaller. Thus, the fibers of a motor unit of this configuration would contract in a much shorter period of time, reinforcing each other and resulting in a fast twitch of high tension. The associated motor unit potential would also be much larger in amplitude and faster in duration than in the diffuse units (Fig. 3d).

This suggests that one does not have to hypothesize small and large motor units organized for the production of various magnitudes of contraction or motor unit potentials. The various degrees of synchronicity of fiber stimulation within a motor unit could account for the different twitch tensions and durations, as well as for the differences in magnitudes of motor unit potentials as the muscle contracts. Thus, it is possible that the contractile properties of some muscle may depend more upon the degree of synchronicity of contraction of the fibers within its motor units than upon the apparent structure of its fibers.

SUMMARY

The electromyographic study of the heterogeneous, dark transversus abdominis of the one-day-old chick and of the heterogeneous pale transversus abdominis of the mature bird revealed the following:

1. The action potentials from single fibers within these two structurally dissimilar muscles were similar except for amplitude.
2. The amplitude of a single action potential was a function of the fiber's cross sectional area.
3. The patterns of motor unit recruitment within these two muscles were also similar. Large motor unit potentials occurred in conjunction with large efferent nerve action potentials, both appearing only when the muscle is at maximum tension.
4. The long duration of some motor unit potentials within a small area of the muscle indicated marked differences in the arrival time of nerve impulses to the fibers within the motor unit, and thus, asynchronous contraction of its fibers.
5. The degree of synchronicity of fiber contraction within a motor unit was suggested as being the determining factor for the rate and amplitude of motor unit contraction and thus the muscle as a whole, rather than the apparent structure of its fibers.

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ELECTROMYOGRAPHY OF HETEROGENEOUS DARK AND PALE MUSCLE

by

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The *m. transversus abdominis*, an expiratory muscle in the chicken, was found to be an excellent muscle for studying the correlation between structure and electrophysiological function of the muscle fibers. This muscle, in the mature bird, is a heterogeneous, pale muscle, while in day-old chicks it is primarily dark, having yet to differentiate. *In vivo* recordings, using both metal microelectrodes and gross bipolar EMG electrodes, were performed on 20 one-day-old and 17 mature birds. Extracellular recordings from single muscle fibers were found to be almost identical in the two age groups except for spike amplitude, which was much smaller in the young chicks. Spike amplitude appeared to be a function of the fiber's cross sectional area. Motor unit potentials of a given muscle were, however, observed to differ markedly in shape and amplitude; i.e., some were long in duration and small in amplitude, while others were short in duration and of high amplitude. The patterns of motor unit recruitment in response to increased tension demands were also found to be similar in these morphological dissimilar muscles. It was noted that large motor unit potentials were found only during periods of high tension production, while small motor unit potentials occurred throughout the contraction period. The results indicated that the histological characteristics of this muscle do not dictate its electrophysiological activity. It was suggested that the rate and amplitude of contraction of some muscle may depend more upon the degree of synchronicity of contraction of the fibers within its motor units rather than upon the apparent structure of its fibers.