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Professor Bennett,

With the respectful compliments of
the writer —

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Observations on the Minute Structure and Mode of Contraction of Voluntary Muscular Fibre; being the abstract of a Paper read before the Royal Medical Society, Edinburgh, December 15th, 1848. By W. MURRAY DOBIE, F.B.S.E.

[With a Plate.]

THE structure of cross-striated muscle is a subject which has more or less engaged the attention of minute anatomists, since the first introduction of the microscope as a means of histological research.

There is perhaps no animal texture as to the nature of which more contrary opinions have been held, or more conflicting statements advanced, than that of voluntary muscle, so that even at the present time it must still be considered a question by no means set at rest.

My object in the present communication is to state briefly the opinions which a careful examination of this texture in several animals has led me to adopt, confining my observations to the elementary fibre, independent of its sarcolemmal sheath.

Before proceeding to do so, I shall very shortly notice the opinions of the principal microscopic anatomists who have been employed in this investigation.

Robert Hooke and Leuwenhoek were the first to examine muscular fibre with the microscope. Robert Hooke speaks of the "fibres resembling a necklace of pearl;" it is probable that by fibres he means the ultimate fibrillæ.

Leuwenhoek saw and figured the transverse striæ, which he regarded as only surface-markings produced by the windings of a spiral thread. He considered the fibre to be composed of globules, less in size than the corpuscles of the blood. He made cross-sections of the fibres, and showed them to be polygonal and surrounded by areolar texture.

Malpighi, in an isolated passage of his works, notices the transverse striæ. De Heide also described and figured them.

In the large work of Muys, which appeared in the middle of the last century, the author describes muscle with great care; he was evidently acquainted with the transverse striæ, and figured the fibrillæ, which he terms "fila," and describes as "nonnunquam etiam nodosa" (Pl. VII. fig. *abcd*). The nodose appearance would seem to have perplexed him, and he considered it not universal. Muys was well-aware of the solidity of the elementary fibres, and his drawings of cross-sections of muscle are well-worthy of examination.

Prochaska wrote an excellent treatise on muscle*; he supposed that the markings seen on the surface of a muscular fibre were caused by the lateral pressure of vessels, nerves or fibres. He injected muscle very successfully, and found the vessels so numerous, that he attributed the contraction of muscle to the distension of these vessels throwing the fibre into zigzag flexures.

Fontana, in his treatise "On the Venom of the Viper†," makes some short but excellent observations on muscular fibre; he was the first anatomist who ascribed the transverse striæ to the lateral coaptation of the sarcal elements of the fibrillæ. He thus speaks of the fibrillæ:—

"Les fils charnus primitifs sont des cylindres solides, égaux entr'eux, et marqués visiblement à distances égales de petits signes, comme d'autant de petits diaphragmes, ou rides. Je n'ai pû apercevoir dans ces fils une marche vraiment ondée, et il m'a paru que les petites taches curvilignes du faisceau primitif étoient formées par les petits signes, ou diaphragmes, des fils charnus primitifs." (Pl. VII. fig. 2.)

Sir Everard Home and Mr. Bauer took up the microscopical investigation of muscular fibre in 1818 and again in 1826. Unfortunately for science they fell into remarkable errors. Their observations retarded rather than advanced the microscopic anatomy of muscle, and raised doubts as to the credibility of any conclusions drawn from microscopic observations.

Sir Everard Home and Mr. Bauer ‡, seeing the tendency which blood-corpuscles have to unite in a longitudinal series, fancied it highly probable that the fibrillæ of striated muscle were formed in the same manner. Sir Everard states that the particles of the fibrillæ are of the same diameter as the blood-corpuscles deprived of their colour; he supposes Leuwenhoek's assertion, that muscle is composed of globules of less diameter than the blood-corpuscles, incorrect, and he endeavours to account for this supposed mistake by adducing the fact, that Leuwenhoek never possessed a micrometer.

* De Carne Musculari.

† Sur le Vénin de la Vipère, 1781.

‡ Philosophical Transactions, 1818 and 1826.

Mr. Skey, in a paper in the 'Philosophical Transactions,' sets forth as his opinion, that each muscular fibre is a tube, containing in its interior a semi-transparent amorphous substance; the tube he supposes to be composed of fibrillæ, and the transverse striæ to be depressions on the surface of the fibre.

The views of Müller, Schwann, Lauth and Henle are very similar to those advanced by Fontana.

Schwann considers the fibrillæ to be beaded filaments, presenting under the microscope a succession of dark points separated by light and somewhat narrower portions of the fibril.

Dr. Martin Barry holds the structure of muscle to be spiral; he says each fibril is composed of two spirals coiling in opposite directions.

From these observers I shall pass to those who in recent times have examined the fibrillæ of muscle, with a view to determining the real constitution of these filaments.

The publication of Mr. Bowman's paper in the 'Philosophical Transactions' was an æra in the microscopy of muscle, though he does not seem to have been able to make out the ultimate constitution of the fibrillæ, which he considered ~~were~~ composed of a series of highly refracting particles of one kind; he thus describes them:—

"Fibrillæ present alternate dark and light points when the part is a little out of focus. The light parts are the centres of highly refracting particles acting as lenses; the dark points the intervals between them. If now the focus be carefully adjusted and the achromatic condenser be used for the purpose of defining the outline with the utmost precision, each dark interspace between the refracting points will be found to be reduced to two very slender straight lines, crossing the fibrillæ in a transverse direction, and giving the light spaces as now seen a rectangular figure." (Fig. 3 *a b*.)

Dr. Sharpey, from an examination of Mr. Lealand's preparations of the muscle of pig, considers the sarcal particles each to be composed of a dark central and clear outer part. Dr. Sharpey mentions that Mr. Lealand himself first pointed out a cross line in the clear interval, and also the bright surrounding areas (fig. 4 *a & b*).

Dr. Carpenter examining the same dissections comes to a similar conclusion (fig. 2 *b*).

Professor Allen Thomson of Glasgow, in his late work on Physiology, describes the structure of the fibrillæ in the same way as Dr. Sharpey: but since the publication of that work he has been led to doubt the existence of any lateral clear edge, as he himself has informed me.

Mr. Erasmus Wilson, from an examination of Mr. Lealand's preparations, which he is pleased to call his "own investigations," describes the fibrillæ very differently; he does not represent any clear lateral edge to the fibril; he considers the clear as well as the dark space to be severally composed of a pair of cells, the dark pair containing a denser "*myoline*" than the clear pair; each of these cells is again subdivided into two, thus giving four square cells of equal size in each dark or light interval (fig. 5 *a* & *b*).

I shall now advert to my own views regarding this structure, which I have deduced from the examination of very numerous demonstrations of the fibrillæ, which I have succeeded in making in several kinds of muscular fibre, generally in the perfectly fresh state.

When a favourable specimen of the muscular fibrillæ of the frog, pig, or ox, is placed under a microscope magnifying about 500 diameters, and the focus is adjusted with great care to the point at which the fibrillæ can be seen with the greatest distinctness, or at what I shall term the *distinct focus*, the appearance presented is the following:—The fibrillæ are seen to be divided equally into a series of quadrangular spaces or areas, which are ~~observed to be~~ of two kinds, the one dark, the other clear or light, regularly alternating with each other. The clear area may be observed in favourable specimens to have a distinct edge, and when the fibril has been in no way distorted or stretched, to be continuous with the edge of the dark area. Crossing the clear space at its centre, and at right angles to the length of the fibril, will be seen a distinct dark line; this line divides the clear area into two equal parts or divisions, which are necessarily quadrangular. The dark space in the same focus presents a shape very similar to the clear one, though generally of a more elongated form; its whole surface is dark, with the exception however of a clear line crossing it in the same manner as the dark transverse line does the clear space, and dividing it equally into two dark particles (fig. 6 *a*).

In some cases I have seen the dark spaces divided into *three* by two clear cross-lines; an appearance I think which cannot be relied on, as the other dark spaces in the same fibrils presented the space as double only, with the single clear transverse line.

When the fibrils are stretched, the dark space often appears as if somewhat elevated above the clear space; I have seen this very distinctly in stretched fibrils from the lobster, examined very shortly after death, the clear space having scalloped edges (fig. 7 *a*).

With regard to the term *dark space*, it must not be supposed

that it is really *opaque*; for under a *superficial* focus it also becomes *clear*, as I shall presently describe. I shall still retain the term as expressive of what is observed when the fibril is seen under the *distinct* focus.

If the focus of the instrument be now adjusted for the more superficial part of the fibril, or a little above it, a remarkable change is observed; the general appearance of the fibril is diminished in distinctness, and what was ~~before~~ the dark space now appears clear (but not so translucent as the clear space in the *distinct focus*), and is then seen to be crossed transversely by a dark line (fig. 6 *b*).

The clear area or space undergoes a similar change of appearance, becoming quite dark, but no line can be observed to cross it. The focus under which this is observed, to avoid confusion I shall call the *superficial focus* (fig. 6 *b*).

It will perhaps be considered trivial thus to describe the appearance of the fibrillæ under an indistinct focus: but that it is not so, I hope afterwards to be able to prove; for on the change of appearances thus presented, I believe hangs the true explanation of the cause of the transverse striæ of voluntary muscle.

In some kinds of muscular fibrillæ, it is a matter of great difficulty to perceive any dark transverse line in the clear space: this arises from the extremely small size of this space, especially when the fibril is in a relaxed condition, and is more particularly found in the examination of the muscular fibrils of fish, lobster or crab, in which indeed this line can be *very rarely* seen (fig. 7 *b*). Hence most probably the reason why Mr. Bowman does not represent it. In such cases the only way to obtain a view of it is by stretching the fibril when in a perfectly fresh state; this cross-line of the clear space in the lobster partook more of the nature of a *band*, in the cases where I was enabled to examine it (Pl. VII. fig. 7 *a*). In the fish (salmon) I have only seen it in a few cases, but in these the appearance was so distinct as not to leave the least doubt of its existence.

I am not aware that this cross-line in the lobster, salmon, skate and frog has been seen by any preceding observers. In the pig and human subject it has been seen; I have also distinctly observed it in the muscular fibrillæ of the ox.

The length of the dark and clear spaces is sometimes ~~identical~~ ^{equal}; at other times, and more frequently, the clear space is shorter; and in the lobster and salmon is often so narrow as to be diminished to a somewhat dark line when the fibril is in a perfectly relaxed condition.

I have also frequently observed, in dissections of the muscular fibrillæ of the frog and salmon, an appearance which I consider it

important to mention, the true explanation of which I am at present unable to ~~decide upon~~^{decide}. It is as follows:—At the point where two fibrillæ are separated from each other, extended for a greater or less distance between them, there often exists a beautiful homogeneous membrane, (resembling the web between two of the toes of a duck,) which is stretched by the violence used in the separation of the fibrillæ (fig. 8 a). In some recent observations which I have made on the muscular fibres of the skate when perfectly fresh, this appearance invariably presented itself, with this peculiarity however, that instead of being perfectly homogeneous, it was marked with stripes corresponding to the dark and light spaces of the fibrillæ between which it was stretched (fig. 8 b).

I was at first inclined to regard this membrane as a shred of the sarcolemma accidentally stretched out between two fibrillæ; but from its being of a decidedly more delicate nature than that membrane, and from its being present in nearly every part of some preparations, I am inclined to consider it ~~as being caused by~~ some homogeneous connecting medium spread among the fibrillæ.

The striæ in this membrane in the skate I am at a loss to account for; perhaps ~~from~~^{by} the tearing of the membrane over the fibrillæ, the surface of the membrane may have been thrown into delicate rugæ by the elevation of the dark spaces above the clear ones, as may be often seen in stretched fibrils.

I have seen appearances in the skate that would almost lead to the belief that this membrane was a fibril spread out laterally into a membrane; this would quite account for the striæ on its surface. The subject requires more investigation.

The form of the fibrillæ I consider to be somewhat flattened or ribbon-shaped; this can be easily seen when an isolated fibril becomes accidentally twisted.

The conclusions ~~which I would draw~~ with regard to the structure of muscular fibre from what I have myself observed, I shall now endeavour to give.

1. That (excluding the sarcolemma) an ultimate fibre of voluntary muscle is composed of two kinds of sarcolemmal matter, arranged in a definite manner, having a tendency under certain circumstances to split up into fibrillæ (Pl. VII. fig. 9), very rarely into discs, and then generally after prolonged maceration in spirit. The fibrillæ are divided into *dark* and *light* spaces.

2. That the dark sarcolemmal element or space has some peculiarity in its molecular arrangement, differing from the clear sarcolemmal element or space, which causes it to refract light in a different way. ~~But~~ ^{But} That we are not entitled to say that it is composed of cells *containing a fluid* of greater density than that contained in the con-

tiguous clear space ; in fact, ~~that~~ we are not able to say with any degree of certainty, that any portion of a muscular fibril in the mature state is a cell containing fluid, as Mr. Erasmus Wilson believes.

3. That the clear space can be distinctly seen to have a dark line crossing it transversely and dividing it into two equal parts, and that the dark space also presents a similar division caused by a line which is generally seen of a lighter shade than the other parts of the same space, and not a broad black band as is erroneously represented by Mr. Erasmus Wilson (fig. 6 *a* & fig. 5 *a*).

4. That no clear area exists at the edge of the fibrillæ extending transversely outwards from the dark spaces, giving the fibrillæ the appearance of a chain of nucleated cells, as is represented by Dr. Sharpey and Dr. Carpenter (fig. 4). ~~To~~ This conclusion I have been irresistibly led ~~to~~ by the following considerations :—

a. The fact that when two fibrillæ lie side by side, the edges of the black spaces are in accurate apposition.

b. That if this lateral clear area really existed, the fibre would be spotted, or at least marked with longitudinal striæ quite as distinct as the transverse ones, which in this case would not be well-marked (fig. 4 *a*).

c. That the edges of the clear space can be seen under a fine instrument not to extend farther laterally than the edges of the dark space (fig. 6 *a*).

[I perceive Mr. Quekett in ^{has} one of the plates to his recent work on the Microscope ~~has~~ distinctly represented this, though he gives an incorrect diagram to explain an appearance which he represents quite correctly.]

d. That the cross-line in the clear space measures exactly the same as the breadth of the dark space, and that it can be distinctly seen in favourable cases to touch the edges of the clear space (fig. 6 *a*).

5. That it seems probable that there exists a homogeneous connecting medium among the fibrillæ (fig. 8 *a* & *b*).

6. That the structure of cross-striated muscular fibre is essentially the same in all the members of the animal kingdom.

7. That from all I have seen of the structure of voluntary muscle, I am perfectly certain that the appearances presented are quite inconsistent with any palpable spiral arrangement, either in the fibre or fibrillæ, as is still the opinion of Dr. Martin Barry. Mr. Bowman's observations ought to have set this point at rest.

8. That the dark spaces become clear, and clear spaces dark, during a change in the focus of the instrument, causing a peculiar appearance of movement on the fibrillæ (fig. 6 *a* & *b*).

9. That the clear spaces are generally narrower in the fish and lobster than in the frog and mammalia (fig. 6 a).

10. That the fibrillæ are somewhat flattened bands.

11. That the dark spaces in some cases appear as if slightly elevated above the clear spaces of a fibril (fig. 7 a).

The transverse striæ.

The transverse striæ, when observed with great care and during rapid though slight alterations of the focus, are seen to undergo some change in appearance; a kind of shifting a short space backwards and forwards. This appearance I explain in the following manner.

The muscular fibrils being composed of a series of clear and dark particles, which under change of focus alter from dark to clear and from clear to dark, this change also takes place under the same circumstances in the complete fibre, so that the dark transverse striæ are at one time formed by the lateral coaptation of the dark spaces, at another time by a like coaptation of the clear spaces.

I see no other way of ^{rationaly} explaining this peculiar appearance of movement on the surface of the fibre during alterations of focus in a rational manner, and I believe that Mr. Erasmus Wilson is wrong in stating that the dark transverse striæ are always formed by the lateral union of the *light* spaces.

This appearance of movement cannot be caused by dark spaces of fibrillæ lying immediately below the *clear* spaces of a set of fibres which are *superficial* to them. As the movement can be seen in a perfectly fresh and undisturbed fibre, it can also be seen on the individual fibrillæ, as I have already stated.

The contraction of voluntary muscle.

Hales, Prevost and Dumas, from observations made on the abdominal muscles of the frog, considered the contraction of muscle to be due to zigzag flexures taking place in each fibre. Prevost and Dumas imagined it to be an electrical effect of the passage of nervous cords across the fibre at the angles of flexure.

Professor Allen Thomson repeated the experiments of Hales, Prevost and Dumas, and was led from the observations he then made to consider that the zigzag plicæ were not produced until the contraction had ceased in the fibres which were the subjects of it; he observed single fibres continuing in contraction, being simply shortened and not falling into the zigzag flexures. Professor Owen was also led to doubt the accuracy of the statements of Prevost and Dumas from noticing that during the contraction

of unstriated muscles in some Filarias and in a Vesicularia, a swelling took place in the centre of the fibre which thus became shorter and thicker.

Dr. A. Farre observed a similar fact in the unstriated muscles of the Polypifera.

The admirable researches of Mr. Bowman have left us little to wish for with regard to the nature of the contraction; I refer to his observations published in the 'Philosophical Transactions' for 1842. All his observations were made on muscular fibres of animals shortly *after death*.

I shall briefly allude to some observations made with reference to this subject on the living and uninjured tadpole.

In April this year (1848), when observing the circulation in the tail of a tadpole after the disappearance of the gills, I was surprised on noticing that the cross-striated muscular fibres were distinctly visible through the external tegument; the contractions after the animal was somewhat exhausted were slow and beautiful, not uniform throughout, as is the case when the tail is observed immediately after the death of the animal and stripped of its integument: the former is the active, living and voluntary, the latter the passive contraction.

When the contraction was comparatively slow, the approach of the transverse striæ could be seen with extreme distinctness; the relaxation was as instantaneous as the contraction in that part of the fibre which was the subject of it.

The circulation of the blood was visibly accelerated after a rapid series of contractions; the blood seemed to be pressed out of the vessels of the part undergoing contraction; on relaxation taking place the afflux was immediate.

These observations were made at a time when I was much engaged with other matters, and are consequently very imperfect. I hope to be able to resume the inquiry during the ensuing spring, when these interesting animals can be obtained in a proper state for ~~the~~ examination. I believe this is the first observation of the contraction of a cross-striated muscle, so high in the scale of being as the Batrachia. I may mention that Dr. Allen Thomson repeated my experiments on the tadpole about the same time and with similar results.

Among the Rotifera I have observed very beautiful examples of cross-striated muscle, more especially in the *Euchlanis triquetra* and in the *Euchlanis Hornemanni*, which are not uncommon species; the approach of the transverse striæ is very marked. The relaxed fibres are subject to a degree of zigzag flexure when other muscles of the animal are in action.

In conclusion, one word on the mode of displaying or separating fibrillæ from the mass of a fibre, which is unquestionably a

very difficult operation. Mr. Lealand the optician seems to have almost completely monopolized this branch of minute dissection, as nearly the whole of the best preparations extant are from his hands. I am not aware that he has yet made known his mode of procedure to the public.

If a muscular fibre of the salmon be used, it is in general not very difficult to separate the fibrillæ in water. ~~By~~ ~~allowing~~ it to remain in moderately strong spirit for a short time, not only removes the oil-globules from around the fibre, but greatly facilitates the dissection; it may then be mounted in the usual way, in spirit, or what perhaps answers better, in glycerine diluted with about three times its bulk of water.

The most characteristic specimens are obtained with greatest ease from the frog, the size of the fibres rendering them very easy to manipulate. Allow the leg of a frog stripped of integument to remain in moderately strong spirit for about two hours, then commence the dissection with extremely fine needles set in long handles. The largest fibres should be selected. After a few trials the rudest operator can scarcely fail to separate the fibrillæ.

The muscular fibres of the skate, treated in the same manner, afford easily-dissected and most characteristic examples of muscular fibrillæ.

EXPLANATION OF PLATE VII.

Fig. 1. a b c d, four figures of fibrillæ after Muys.

- 2. "A fibre covered with cellular membrane at the upper part," cross-striated and splitting up into fibrillæ at one end: after Fontana.
- 3. Diagram of fibrillæ after Bowman.
- 4. Diagram to illustrate the views of Sharpey, Lealand and Carpenter: *a*, two fibrils united; *b*, single fibril, with each sarcal particle having a dark central and clear outer part.
- 5. Diagram of two fibrillæ to illustrate the views of Mr. Erasmus Wilson: *a*, usual appearance of fibrillæ; *b*, a very much stretched fibril to show the dark and clear spaces, each divided into four.
- 6. Diagram to show the fibrillæ in the distinct and superficial focus: *a*, fibrils in distinct focus; *b*, fibrils in superficial focus from the frog.
- 7. Diagram of two fibrils from the lobster: *a*, fresh fibril much stretched, showing scalloped edges of clear space; *b*, similar fibril unstretched, showing clear space apparently dark from its narrowness.
- 8. Diagram to illustrate a membrane observed among the fibrillæ: *a*, membrane as seen in frog and salmon; *b*, similar membrane observed among fibrillæ of the muscle of skate, perfectly fresh.
- 9. General appearance of a dissection of muscular fibre from the frog, magnified about 500 diameters.

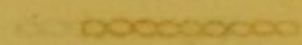
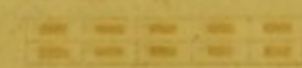
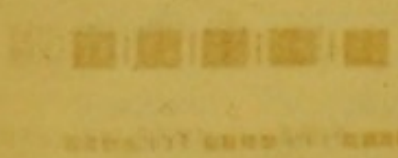
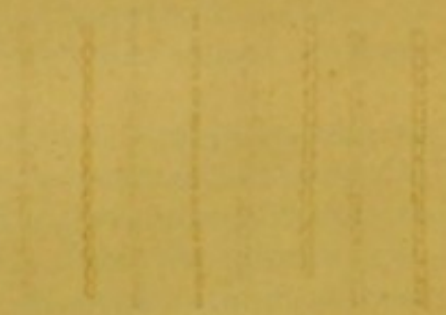
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