Timed essay answering the unseen question:

Describe what is meant by a “motor unit”. Why are there different types of unit and in what order are they recruited in a voluntary contraction?

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Introduction

A muscle is made of many muscle fibres. Each fibre is formed by the fusion of many individual cells during development, hence a mature muscle fibre is one large multinucleated cell. Muscles are innervated by motor neurons. When a motor neuron fires an action potential, the action potential will travel to the nerve terminal and release acetylcholine. The acetylcholine binds to receptors in the motor end plate of the muscle, opening sodium channels, leading to an influx of sodium ions and generating a depolarising current – the end plate potential. This depolarisation can spread throughout the muscle along T-tubules and cause the release of calcium from the sarcoplasmic reticulum of the muscle. The released calcium ions can bind to troponin, a regulatory protein found within muscles, changing its conformation. This conformational change facilitates the binding of actin microfilaments and myosin motor proteins. ATP found within the head of myosin can be hydrolysed, causing a conformational change in which the actin and myosin strands slide past each other, generating the force of muscle contraction. These muscle fibres are organised into motor units, and during a voluntary contraction these units are recruited to contract in a particular order. This essay will describe the basic structure of motor units and their intrinsic properties that lead to a specific order of recruitment.

Motor units and their differential properties

The motor neurons that innervate muscles originate from the ventral horn of the spinal cord and can branch at the motor point of a muscle to innervate a large number of muscle fibres. The combination of a motor neuron and all the muscle fibres it innervates is called a motor unit. Motor units can be large or small. Large motor units, containing a large number of muscle fibres, are innervated by motorneurons with large diameter axons. Small motor units, containing a small number of muscle fibres, are innervated by small diameter axons. Motorneurons that innervate the same muscle group are clustered together in the ventral horn of the spinal cord. All the muscle fibres of a motor unit fire synchronously, and all the fibres of a unit are of the same type. This can be slow (type I), fast fatigue resistant (type IIa), or fast fatigable (type IIb). Slow muscle fibres tend to make up smaller motor units, and fast fatigable muscle fibres tend to make up the largest motor units. The slow muscle fibres are said to be slow oxidative. They contain a large number of mitochondria allowing them to generate lots of ATP via aerobic metabolism, utilising oxidative phosphorylation. The force of their contraction is moderate, but it is sustained for a very long time. The energy to maintain this sustained contraction is dependent on their large number of mitochondria. Fast fatigable fibres are also known as fast glycolytic fibres. This is because they produce most of their energy via anaerobic metabolism, termed glycolysis. The force of their contraction is powerful, and this force is generated very quickly, but the fibres also fatigue very rapidly. The fast fatigue resistant fibres, or fast-oxidative glycolytic fibres, are intermediate between the slow oxidative and fast glycolytic fibres. Therefore, the different types of motor fibres innervated by a motor neuron lead to motor units with different properties. The properties of these motor units change in a graded fashion from the smallest units to the largest units.

Motor unit recruitment order

Our muscles are therefore made up of: small motor units, with small axons, that produce a moderate but sustained contraction force; large motor units, with large axons, that produce a rapid and powerful contraction that fatigues rapidly; and intermediate motor units with intermediate properties. However, the brain must be able to control muscle contraction to recruit a small number of muscle fibres when only a weak force is needed, and a large number of muscle fibres when a large force is needed. The intrinsic properties of motor units facilitates this requirement. Small motor units contain small diameter axons. Small diameter axons have a smaller membrane capacitance, hence it takes less current to charge small axons to the threshold voltage required to initiate an action potential. Large motor units have large diameter axons with higher capacitance, and hence take much larger currents to charge the axon to the threshold potential. These intrinsic properties of motor units mean that small motor units with their small axons will be activated first, by weak descending signals; and large motor units with their large axons will only be activated by strong descending signals, and hence will be activated last. Intermediate motor units with their intermediate sized axons will be recruited somewhere between small and large motor units. This particular recruitment order of muscles is termed the size principle of muscle contraction, as the order of recruitment is determined by the size of the motor unit. This allows the motor system to produce a graded response of muscle contractions by simply altering the strength of the input signal. If the motor system wants to perform a delicate movement, such as threading a needle, a weak descending signal will be sent. This weak signal will only be strong enough to charge small motor neurons to threshold. They will fire action potentials, activate the small number of muscle fibres they innervate, leading to a weak contraction. If a strong contraction is needed, such as kicking a football, a large signal will be sent that will lead to the firing of both small, intermediate, and large motor units. This will produce a large contraction to produce a short but powerful kick.

Motor unit fusion and signal dependent noise

As the motor fibres of small motor units are slow to generate tension, to produce a constant contraction in which the firing of small fibres fuse, the motor system only needs to send a low frequency signal. In contrast, as large motor units generate a twitch force that is large but brief, to get a sustained contraction from large motor fibres the motor units must fire at a much higher frequency. Therefore, a steady, low force contraction requires a low frequency descending signal, and a steady high force contraction requires a high frequency descending signal. As a result, during the activation of a muscle, the small fatigue-resistant slow fibres are activated first. At first they will be unfused, leading to force fluctuation, or noise. As the strength of activation rises, the firing of smaller motor fibres will fuse leading to a sustained contraction, and larger motor units will be recruited. These larger motor units will at first be unfused, and hence add a proportional fluctuation in force – this pattern will continue throughout muscle contraction and is responsible for the signal dependent noise of muscle contraction.

Why do we have different motor unit types and a particular recruitment order?

There are two important physiological advantages of this size principle of recruitment order. Firstly, it acts to minimise the fatigue that an organism experiences when carrying out motor movements. This is because the organism will always recruit the fatigue-resistant fibres first, and only recruit the fatigable fibres when it is necessary to produce a force of greater magnitude. Secondly, it ensures that as more fibres are recruited to contract, they add an increase in force that is proportional to the current force. This ensures that relative increases in force remain somewhat constant as more and more motor units are recruited. For example, if there was no difference in force between motor units, then recruiting another motor unit when 5 are already active would increase force by 20%, but if 50 units were active, it would increase force by just 2%. This would result in needing to recruit exponentially more motor units to produce a proportional increase in force.

There is also a computational advantage to the size principle of recruitment order, in that the brain does not need to put in work to decide what order to recruit the muscles. The recruitment of motor units of the appropriate type and size is built into the design of the motor units. The brain is only required to send the appropriate level of excitatory input, and motor units will be recruited in the most suitable order.

Conclusion

To summarise, a motor unit consists of a motor neuron and all the muscle fibres it innervates. There are different types of motor units due to the fact they are made up of muscle fibres and motor neurons with different physiological and anatomical properties. Neurons of small units synapse onto weakly contracting slow oxidative fibres, and have smaller axons that are easy to charge and hence are recruited first. Neurons of larger units synapse onto more powerfully contracting fast oxidative-glycolytic and fast glycolytic fibres, and have larger axons that require more current to charge and hence are recruited last. This recruitment order minimises muscle fatigue, ensures proportional increases in force upon additional muscle fibre recruitment, and limits the computational demands on the motor system.