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Motor unit properties affecting the excitation-force relation of a muscle: a simulation study

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Contents

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Abstract
Muscles consists of multiple motor units (MUs) that produce the force required for our movements. Motor unit properties are responsible for the relation between neural excitation and muscle force (excitation-force relation). The force of the muscle is dictated by the recruitment and the force output of the different motor units. The recruitment is physiologically determined by the recruitment thresholds of the motor units, where motor units with a higher force output are thought to have a higher recruitment threshold, conform Henneman's orderly recruitment principle. The goal of this study was to predict the effects of the MU-threshold and MU-force output distributions on the excitation-force relation of a muscle. Assuming that a muscle's excitation-force relation depends on the values of the motor unit properties present in the muscle, the recruitment threshold and maximum force distributions among the motor units can be derived from muscle force recordings. To achieve the goal a computer model was build to simulate motor unit recruitment and force production of a group of MUs with different (combinations) of MU-threshold and maximum MU-force output distributions. Both MU-threshold distribution and maximum MU-force output distribution of the muscle were mathematically varied between linear and exponential curves. Input of the muscle model was a linear increasing neural activation profile and the force output profile of the muscle was simulated. The resultant MU-activation and force patterns were compared with published results of simultaneous MU-recruitment and force recordings obtained from literature. The simulation results showed that the excitation-force profile does not show characteristics that can be linked to either the MU-threshold distribution or the MU-force output. As a consequence, force recordings alone are not sufficient to estimate the recruitment threshold and maximum force distributions. However, the use of a computer model in combination with additional recorded data such as (surface) electromygraphy (EMG) is expected to show results from which estimating MU properties is possible.

Keywords: motor unit, recruitment, force, distribution, excitation

1 Introduction

Walking, controlling our posture or brushing our teeth are daily tasks that all have something in common. Each of these tasks require forces produced by (skeletal) muscles. A muscle can produce different forces that can range in magnitude, accuracy and precision allowing us to perform a diversity of tasks. If a muscle is simplified as a device with an input and output then the input is a signal sent from the brain or spinal cord called the (neural) excitation and the output is the force. The relation between input and output, hence the excitation-force relation, determines the dynamics of the muscle. The excitation-force relation is not the same for every muscle and between persons the excitation-force relations of the muscles vary as well. Which is why not everyone has the same maximum weight they can lift, has the same maximum speed they can run or has the same hand dexterity.

The excitation-force relation of a muscle is not permanently set, but is affected by various factors. One of those factors is repeated exercise. The idea is that different exercises can lead to different changes in the excitation-force relation of a muscle. If for certain (competitive) sport disciplines a specific excitation-force relation of the muscle(s) is preferred than for the practitioners of those sport disciplines knowing which exercises help to achieve the desired excitation-force relation can mean the difference between winning and losing. Another factor that can alter or influence the excitation-force relation of a muscle is a disease or condition, such as multiple sclerosis (MS), Amyotrophic lateral sclerosis (ALS) or cerebral palsy (CP) to name a few. For physicians knowing the excitation-force relation and recognising abnormalities or changes corresponding to muscle disorders can give further insight and improve the diagnosis procedure. For example, there is room to improve the diagnosis of ALS as the current method to diagnose ALS is based on exclusion of other diseases (with similar symptoms) which can take months to complete [1, 2, 3]. The idea is that the excitation-force relation reveals information about the properties of a muscle as the excitation-force relation is dictated by those muscle properties. Two motor unit properties are of particular interest.

1. The maximum force of the motor units (MU-force) as the maximum forces determine the force range of a muscle.
2. The MU-threshold of the motor units (MU-threshold) as the MU-threshold is important for coupling (the recruitment of) a motor unit to a certain level of excitation.

The goal of this study is to predict how the distribution of the recruitment threshold (MU-threshold) and maximum force (MU-force) among the motor units of a muscle affect the excitation-force relation.

Some anatomic knowledge is required to understand the reason for the focus on the distribution of the MU-threshold and MU-force among the motor units of a muscle. In the below subsections, introductory explanations are given of the role of motor units, recruitment, force production and motor unit properties. At the end of the introduction the research question and specific goals of this study are outlined.

1.1 Motor units

Muscles consist of groups of muscle fibers that are able to contract and as a result produce a force. To have a group of muscle fibers contract they need to be activated by an Action Potential (AP) from a (lower alpha) motor neuron that for most skeletal muscles is positioned in the anterior horn of the spinal cord. An AP is an electro-chemical signal used by neurons for communication. The motor neuron (main body) and the group of muscle fibers are connected by a nerve fiber (the anterior or ventral root) along which an AP is conducted. See figure 1.1 for a graphical illustration.

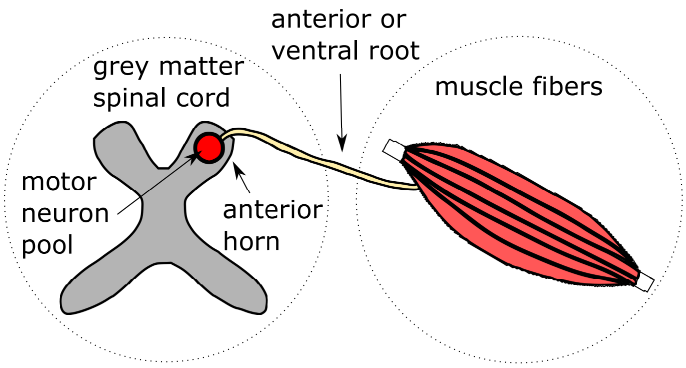

Figure 1.1: Graphical representation of a muscle and the innervating nerve containing the motor neurons. The butterfly shape is a cross-section of the grey matter in the spinal cord. The red filled circle is where the cell bodies (somas) of the motor neurons are located. The anterior or ventral root contains the motor neuron axons that innervate the muscle fibers.

The combination of a motor neuron and the group of muscle fibers that the motor neuron innervates is called a motor unit (MU). The number of muscle fibers in a motor unit can vary per motor unit and is important for the maximum force the motor unit can produce. In turn the number of motor units varies per muscle from fifty up to more than a thousand depending on the muscle, although exact numbers are still unknown [4]. The number of motor units is equal to the number of motor neurons (in healthy humans) and therefor to the number of nerve fibers that innervate the (groups of) muscle fibers.

1.2 Recruitment

To activate or recruit a motor unit, the motor neuron of that motor unit has to be excited to the point that the motor neuron will send an action potential to the muscle fibers that the motor neuron innervates. The muscle fibers contract as a result of the action potential received from the motor neuron. The excitation to the motor neuron comes in the form of other action potentials from (a combination of) higher motor neurons, inter neurons or sensory neurons. Action potentials can be observed using electromyography (EMG) for which several techniques have been developed to be able to distinguish action potentials of individual motor units (see figure 1.2).

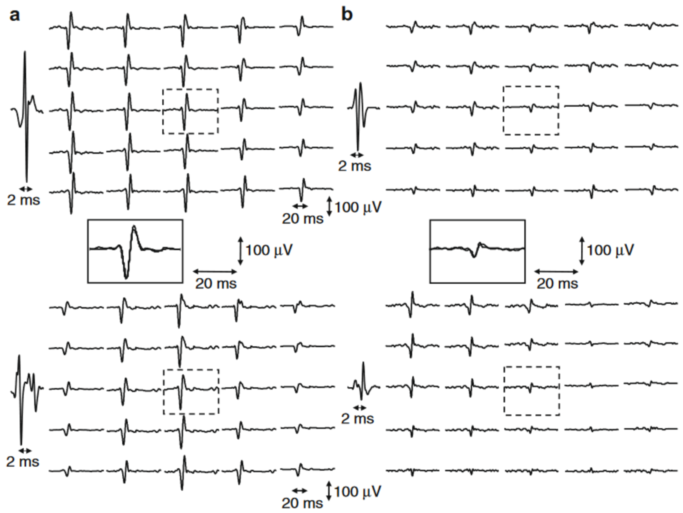

Figure 1.2: Multi-channel surface EMG recordings of four motor units from Merletti et al. [5]. Multi-channel EMG is used to distinguish between action potentials of individual motor units as this is not possible with single-channel EMG (see enclosed square in the middle). (a) The action potentials of two motor units. The action potentials of each motor unit is recorded by five channels. (b) The same as in (a) for a different pair of motor units.

When the excitation level equals the threshold of a motor neuron, that motor neuron will discharge and the AP is being send to the muscle fibers. In case the excitation further increases in strength the discharge frequency of that same motor neuron will also increase [6]. That means that two things happen when excitation reaching the motor neuron pool is increased. 1) More motor units are recruited (until all the available units are active). 2) The discharge frequency of motor neurons of already recruited motor units increases (until the maximum firing rate is reached).

According to the 'size principle theory' [7] the recruitment of the motor units takes place at the motor neuron pool where all the motor neurons for a single muscle are located. The size principle suggests that the larger the motor neuron the higher the MU-threshold of that motor neuron and thus of the motor unit. In turn, the higher the threshold, the stronger the excitation that is required before the motor neuron discharges. The threshold of a motor neuron (and thus motor unit) is related to the maximum force of the muscle fibers that the motor neuron innervates. The result is that motor units are recruited in the order of their maximum force, from weakest first to strongest last, which is known as orderly recruitment and is part of the size principle theory. In other words, the higher the motor unit strength, the higher its motor neuron threshold. As a side note, the size principle theory [7] is criticized for holding the motor neuron size responsible for motor neuron threshold [8, 9], but not for the idea of orderly recruitment. The relation between motor neuron size and MU-threshold is not used in this study. Only orderly recruitment is considered.

1.3 Force production

When an action potential of a motor neuron reaches the muscle fibers that the motor neuron innervates, the fibers will contract. Note that this study will not dive into the contraction mechanism of the muscle fibers. A single action potential will elicit a single contraction of the muscle fibers after which the fibers relax. Such a single contraction (and relaxation) of the muscle fibers of a single motor unit is called a motor unit twitch and is depicted in figures 1.3 and 1.4. Although the motor unit twitches in the figures are obtained from a mouse and a cat, the assumption is that the motor unit twitches of mammals have similar shapes. All muscle force is built up from one or multiple twitches produced by one or more motor units.

Figure 1.3: Motor unit (mechanical) force twitch recording from a mouse (triceps surae muscle) by Manuel and Heckman [10]. The figure shows the average of 10 motor unit twitches of a single motor unit.

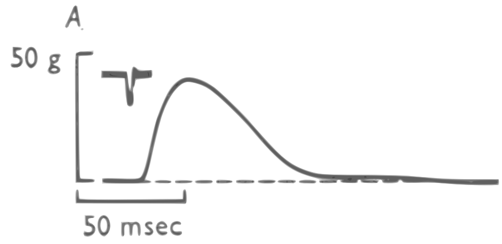

Figure 1.4: Motor unit (mechanical) force twitch recording from a cat (gastrocnemius muscles) by Burke et al. [11] with the corresponding EMG recording (50 [g] ≈ 0.49 [N]).

As earlier stated, the number of muscle fibers per motor unit can vary. The number of muscle fibers determine the maximum force that a motor unit can produce although maximum force also depends on the type of muscle fiber the motor unit is composed of. One method to differentiate between muscle fiber types is using the twitch contraction time (TCT), maximum force (also known as maximum tetanic tension (MTT)) and susceptibility to fatigue of their muscle fibers [12]. The TCT is the time duration of a single motor unit twitch and the MTT is as the name suggest, the maximum force that a motor unit can produce. Closely related to the TCT is the time to peak (TTP) which is the time that passes before the peak is reached of the motor unit twitch. The susceptibility to fatigue is omitted for this current study. Considering the TCT and MTT there are two main categories of muscle fiber types namely, 1) slow twitching, low force units (type S) and 2) fast twitching high force units (type F). The slow muscle fiber twitch duration is longer and produces a lower force than the twitch of the fast muscle fiber. Important to notice is that fast muscle fibers take less time to reach peak twitch force than slow muscle fibers. Within each group of muscle fiber types, the TCT and MTT also varies, resulting in a large variation of possible muscle force outputs.

Motor neurons are able to produce action potentials at a higher frequency than muscle fibers can produce twitches. When the discharge frequency of a motor neuron reaches a certain frequency, the resulting muscle fiber twitches start to overlap (see figure 1.5 and 1.6). As twitches overlap, the peak force will be higher than that of a single twitch. In general the higher the frequency, the higher the force that is developed. In the extreme case this leads to the maximum force a motor unit can produce also known as maximum tetanic tension. A motor unit produces its maximum force when the motor neuron fires with such a rate that the muscle fibers no longer get time to relax. As F type muscle fibers have a shorter TCT the frequency of the motor neuron that drives the F type fibers needs to be higher than that of S type muscle fibers to be able to evoke twitch fusion.

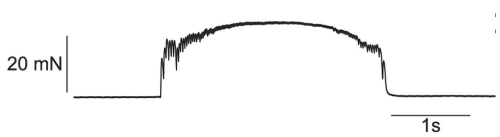

Figure 1.5: Motor unit force recording from a mouse (triceps surae muscle) by Manuel and Heckman [10]. The figure shows the force recording of a single motor unit over a brief period of time. Right at the beginning the twitches start to overlap although individual twitches can still be distinguished. As the motor unit gets closer to the maximum producible force the individual twitches become less visible.

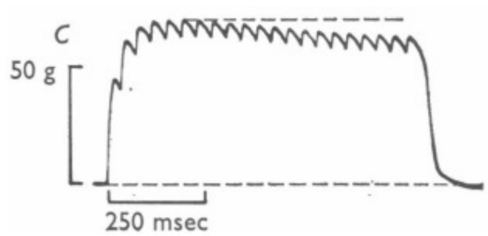

Figure 1.6: Motor unit force recording from a cat (gastrocnemius muscles) by Burke et al. [11]. Recruitment rate of the motor unit is high enough for the twitches to overlap, but not cause maximum motor unit force. The individual motor unit twitches are visible over the full recording. The decline in force over time is due to motor unit fatigue (50 [g] ≈ 0.49 [N]).

1.4 Motor unit properties

Depending on the excitation level at the motor neuron pool, one, two or more than a thousand motor units produce twitches in a rate that also depends on that same excitation level. Summing the force produced by the recruited motor units leads to the total force produced by the muscle at a certain excitation level. The excitation-force relation of a muscle therefor greatly depends on the properties of the motor units that are present in the muscle. The MU-threshold and the maximum force of the motor units are therefor expected to have a strong effect on the excitation-force relation. For example a muscle that contains motor units of which most are low force and have low MU-thresholds is expected to have a different excitation-force relation profile than a muscle containing mostly motor units with high force, high MU-thresholds. Then the question is how the motor unit properties are distributed among the human muscles.

In humans the motor unit property distribution was found not only to vary per muscle, but also vary in the same muscle between different persons [13]. If that is true than there is no such thing as a general motor unit distribution for each muscle. The question is if there is a way to determine the distribution of motor unit properties of a human muscle. There have been studies that were able to obtain motor unit properties (and their distribution) of cats [14, 15, 16, 11], but these studies used experiments that required partly dissecting the cats and ultimately kill them.

1.5 Goals

The excitation-force profile of a muscle depends on the properties of the motor units that are present in the muscle. In theory there is a chance that the MU-threshold and maximum force distributions can be derived from force recordings of a muscle. The idea is that such a feature is possible if the excitation-force profiles of muscles show characteristics that can be linked to either the MU-threshold or maximum force distributions among the motor units. To determine if such characteristics exist, the effect of the MU-threshold and maximum force distributions among the motor units of a muscle on the excitation-force profile of the muscle must first be understood. In a research question formulation: what relation do the MU-threshold and maximum force distributions among the motor units of a muscle have with the excitation-force profile of the muscle. As a reminder, the goal of this study is to predict how the distribution of the recruitment threshold (MU-threshold) and maximum force (MU-force) among the motor units of a muscle affect the excitation-force relation.

The research question and chosen method led to the following specific (sub-) goals for this study:

- Determine the individual relations of the MU-threshold and maximum force distributions with the excitation-force relation.
- Determine if the effect of the MU-threshold and maximum force distributions on the excitation-force profile result in unique characteristics that allow for estimation and differentiation of the distributions from muscle force recordings.
- Build a computer model representing a group of motor units that can be used to simulate the excitation-force relation of a muscle with the MU-threshold and MU-force distribution among the motor units as independent variables.

2 Method

Computer model simulations were chosen as the method to investigate the research question. In the past there have already been cases where computer model simulations have proven to produce reliable and useful results [17, 18, 19, 20]. The possibility of reliable results was not the only argument to use computer model simulations. Creating a computer model involves considering which elements are required to be able to accurately simulate the target system. Deciding which elements to include or exclude is basically to hypothesize which elements are important for the system that is being simulated which could lead to new research questions. A strong argument for the current study to use simulations is that the values of the parameters of a computer model can be changed which gives the possibility to create and test different scenarios. In contrast to experiments on humans where changing parameters is not always possible, desirable or considered ethical.

2.1 Computer model

To simulate the force output of a group of motor units a computer model was developed. The computer model was build and simulated using the MATLAB and Simulink programming environment (The Mathworks, Natick, MA). Before the group of motor units was turned into a computer model the group of motor units was first represented in the form of a block scheme (figure 2.1) for a more engineering perspective. The block scheme was used as a blueprint to construct the computer model and will be explained from left (input) to right (output). The input was modeled as a continuous neural excitation signal rather than an impulse train representing the action potentials. Although the use of impulses would be more biological correct, the use of a continuous signal made it possible to create a less complex model without affecting the results. The first block with the neural excitation as the input represents the recruitment mechanism which produces the action potentials corresponding to the neural excitation level as the output. The action potentials are modeled as impulses that can form so called impulse trains when more than one action potential takes place during a simulation. Modeling the action potentials as impulses is justified as an action potential duration of a skeletal muscle (< 10 [ms]) is negligible compared to the twitch contraction time of a motor unit (> 30 [ms]). The number of impulse trains is equal to the number of recruited motor units and form the input for the second block. The second block represents the force production that produces the force as an output that corresponds to the incoming impulse trains.

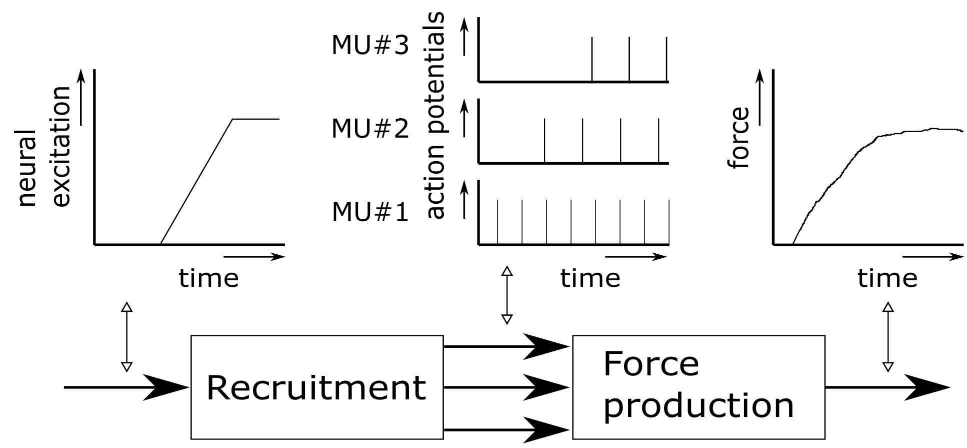

Figure 2.1: Block diagram describing the process from neural excitation input to force output. The first block contains the recruitment mechanism (i.e. production of action potentials by the recruited motor units corresponding to the incoming neural excitation at the motor neuron pool). The second block contains the force production (i.e. production of force by the muscle fibers of the recruited motor units corresponding to the incoming action potentials). The three plots in the top of the figure represent the in- and out-going signals of the blocks (left: neural excitation, middle: action potentials, right: force).

The block scheme can be expanded to show the individual motor units, each containing a motor neuron and the corresponding muscle fibers as in figure 2.2. Following from figure 2.2 the motor units all receive the same level of neural excitation [6, 7, 21] and operate independent from each other.

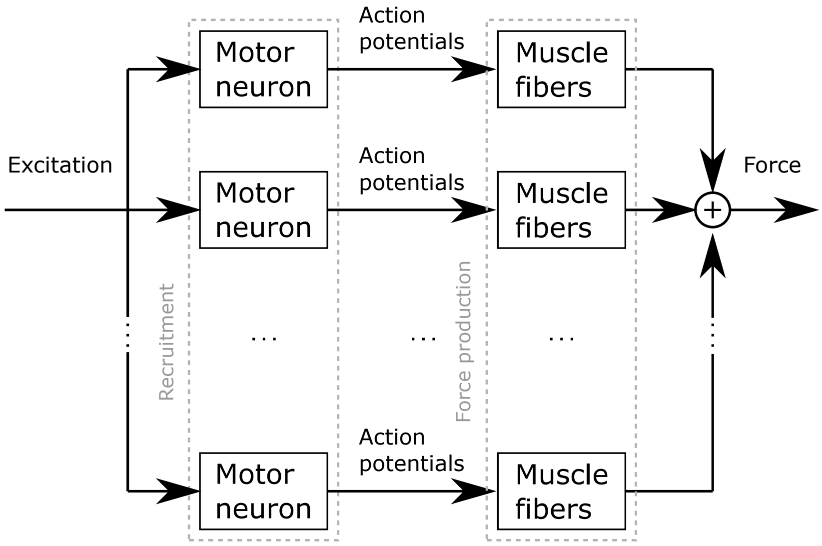

Figure 2.2: A block diagram representing a group of motor units. In this figure there are three motor units each consisting of a motor neuron and its corresponding muscle fibers as well as the in- and out-going signals. The with dashed lines bordered rectangles show to which part from figure 2.1 the enclosed elements belong to.

A non-trivial matter was how many motor units there should be modeled. The number of motor units was decided not to be a variable that will be tested in the current study. As a consequence the number of motor units had to be set to a predetermined value. The model was tested with different numbers of motor units. Using less than 50 motor units resulted in a force of which development was considered to increase too abruptly with each newly recruited motor unit (with the tested MU-threshold and MU-force distributionss). Using more than 100 motor units improves the smoothness of the force development, but increases the computation time. The number of motor units for the simulations was set to 100 as a 100 is a plausible number mentioned in the literature [4] and an acceptable compromise between smoothness of the force output and the computation time.

2.1.1 Recruitment

There are already several models available that are able to simulate (motor) neuron behaviour and therefor the recruitment mechanism. One of these models is the repetitive firing neuron model [22] that simulates the ion flow across the neuron membrane. This ion flow across the membrane determines the neuron membrane electric potential which when reaching a level equal to the threshold causes the neuron to discharge. The repetitive firing neuron model has proven to be useful in earlier studies that made use of computer simulations [23, 18, 17]. Although this repetitive firing model is able to simulate neuron behaviour in a realistic manner, the model contained too many variables irrelevant for the current study, which made matters more complicated than necessary without giving useful insight for the goal of the current study. Therefor a simpler model that could simulate motor neuron recruitment was made that uses only a few parameters.

The recruitment model had to comply to a few requirements deduced from the introduction (section 1.2). With increasing neural excitation the number of recruited motor units increases. The firing rate of motor neurons of already recruited motor units increases (until maximum value is reached). This led to the following recruitment model.

Each motor unit was given an unique value for the MU-threshold set between 0 and 100 with an arbitrary unit (au). The neural excitation input level therefor could also take a value in the range of 0 to 100. The neural excitation input was no longer defined as a single impulse or impulse train as would be more true to the biological environment. This was no longer necessary due to the design of the computer model and was expected to have no further consequences for the results. Each motor unit received the same level of neural excitation (as shown in figure 2.2) which is important as an equal level of neural excitation for each motor unit means that only the MU-threshold was responsible for the recruitment order of the motor units in the computer model. The motor units were also assigned a firing rate bandwidth. A motor neuron fired at its minimal firing rate if a constant neural excitation would be applied equal in strength to the motor neuron's threshold. An assumption had to be made for the level of neural excitation required to elicit the maximum firing rate. While the literature suggest the next motor unit is recruited before the previous motor unit has reached its maximum firing rate [6] the choice was made to use a sequential recruitment pattern of the motor units. As a result, the level of neural excitation required for a motor unit to reach its maximum firing rate was set equal to the MU-threshold of the next motor unit. If the moment of recruitment for the next motor unit was based on the literature the question would then be what the firing rate of the previous motor unit had to be which was not found in the literature and would therefor still be an arbitrary choice.

Important for the research question was how to distribute the values for the MU-thresholds. Without the existence of a generic MU-threshold distribution [13] many options were possible. According to the size principle theory a direct proportional relation exists between the conduction velocity (traveling speed of action potentials along the nerves) of motor neurons and the MU-threshold of the corresponding motor units [7]. Experiments on cat muscles led to conduction velocity distributions among motor units in cat muscles [15, 14] and therefor, according to the size principle, to equivalent MU-threshold distributions. One of the experimentally obtained conduction velocity distributions had more motor units with conduction velocities in the lower region than in the higher region. The MU-threshold distribution that followed from the conduction velocity distribution using the size principle, was considered a starting point to base a MU-threshold distribution on for the current study.

In the human body a latency between the discharge of an action potential and force development exist partly due to the conduction of the action potential over the nerve. The latency therefor depends on the conduction velocity and length of the nerve. The length of a nerve in turn depends on the location of a muscle in the body as the more distal the muscle is located (from the central nervous system) the longer the nerves and thus the path the action potentials need to 'travel'. The effect of the differences in conduction velocity for each motor unit on the excitation-force relation was assumed to be negligible for the goal of the current study and therefor of no further interest. However the choice was made to incorporate a latency for more realistic results. For the simulations of the current study the latency was set equal for all motor units to 10 [ms] based on literature findings [15], hence omitting the theory of different conduction velocities between the motor units. The latency is expected not to be important for the goal of the current study as the latency is the same in all simulations.

In this study two 'types' of MU-threshold options were investigated with the computer model. Both options are shown in figure 2.3. One of the options was to have the MU-threshold increase exponential with the motor unit number. An exponential MU-threshold distribution results in more motor neurons with relatively 'low' MU-thresholds then with relatively 'high' MU-thresholds as found in one of the studies on cat muscles [15]. To see the effect of an exponential MU-threshold distribution the computer model had to be simulated with another 'type' of MU-threshold distribution for reference. For comparison of the exponential threshold distribution a linear threshold distribution was chosen. With an increase in MU-threshold that is linear with the motor unit number results in as many motor neurons with 'low' MU-thresholds as there are with 'high' MU-thresholds. No literature was found that presented evidence of a MU-threshold distribution among motor units of a muscle with more motor units with relatively 'high' MU-thresholds than motor units with relatively 'low' MU-thresholds.

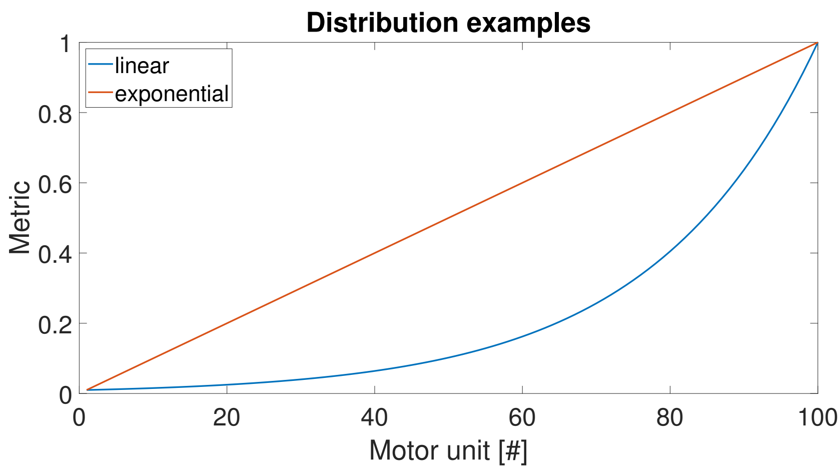

Figure 2.3: Two ways to distribute MU properties values among the motor units. The horizontal axis indicates the MU number. The vertical axis indicates the metric of an arbitrary MU property. The blue line shows a linear relation between the arbitrary MU property and motor unit number. The red line shows an exponential relation between the arbitrary MU property and motor unit number.

The two MU-threshold distributions were modeled using a few equations. The linear spread of the motor neuron firing thresholds is given by equation (2.1). The firing threshold of the ith motor neuron number is represented by TH_i and is equal to the ith motor neuron i divided by the total number of motor neurons N plus 1. The reason for the plus one was that the motor neuron with the highest MU-threshold was able to increase its firing frequency. If the plus 1 would be omitted the last motor neuron would be triggered at the highest neural excitation level (1 [au]), but would not be able to increase its firing frequency as the neural excitation level would not further increase.

$$TH_{lin}(i) = \frac{i}{N+1} \tag{2.1}$$

The exponential distribution of the motor neurons MU-thresholds is given by equations (2.2), (2.3) and (2.4) which are based on the equation used by Potvin J.R. and Fuglevand A.J. [19] to set the MU-thresholds of motor units. Again TH_i is the MU-threshold of the ith motor neuron, i the ith motor neuron number and N is the total number of motor neurons. The symbol α determines the curve of the exponential and thus the degree of the exponential distribution. Equation (2.3) is used to scale equation (2.2) such that the rules in equation (2.5) are applicable. The scaling ensures a better comparison between threshold distributions with different values for α.

$$TH_1(i) = \frac{e^{\frac{\alpha}{N}(i-1)}}{e^{\alpha}} \tag{2.2}$$

$$TH_2(i) = \frac{1 - \frac{e^{\alpha}}{N+1}}{N}(i-1) + \frac{e^{\alpha}}{N+1} \tag{2.3}$$

$$TH_{exp}(i) = TH_1(i) \cdot TH_2(i) \tag{2.4}$$

$$\text{for } \alpha > 0 \begin{cases} TH_{exp} = \frac{e^{\alpha}}{N+1} & \text{for } i = 1 \\ TH_{exp} = 1 & \text{for } i = N+1 \end{cases} \tag{2.5}$$

The values of α used in the simulations were 0, 1, 2, 3 and 4. The case of $\alpha = 0$ resulted in a linear MU-threshold distribution (TH_{lin}) as in equation (2.1). The cases $\alpha = 1$, 2, 3 and 4 resulted in exponential MU-threshold distributions, where the higher the number for α the more exponential the distribution. A value for α higher than 4 did not result in a significant increase of the exponential shape of the MU-threshold distribution.

Figure 2.4 shows what different values for α (both 0, 1, 2, 3 and 4) did for the threshold distribution. Note that the total number of motor units in the figure is 101 ($N + 1$) although no motor unit with number 101 existed. The threshold of the last motor unit (100) should not be 1 [au] as explained in section 2.1.1 to have that motor unit the ability to increase its firing rate to its maximum (at neural excitation level 1 [au]).

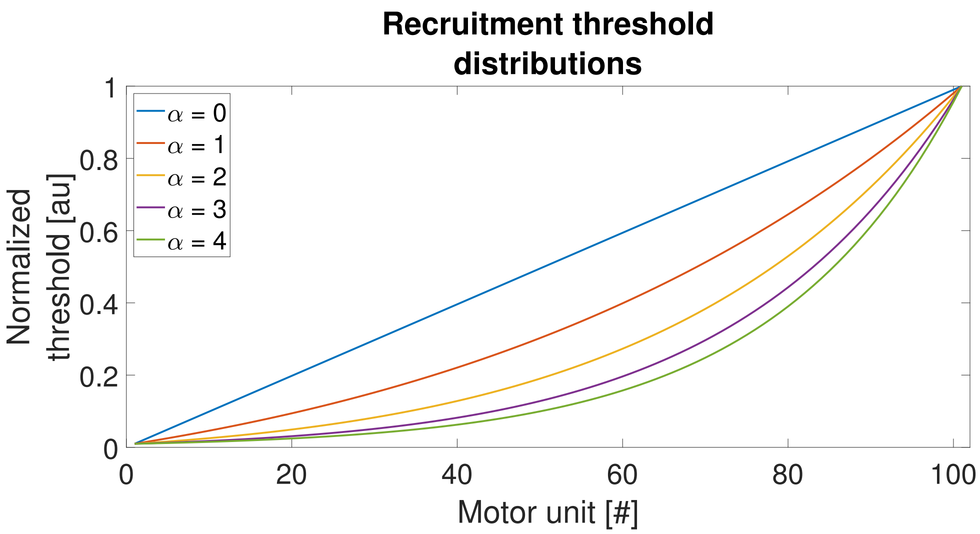

Figure 2.4: The number of motor units (N) is set to 100. The different threshold distributions (TH_α) are determined by α. For all α the first motor unit has a MU-threshold of $TH(1) = 0.0099$. For $\alpha = 0$: $TH_0(100) = 0.9901$ and 50% of the motor units has a TH value below the average TH_0 value. For $\alpha = 1$: $TH_1(100) = 0.9804$ and 57% of the motor units has a TH value below the average TH_1 value. For $\alpha = 2$: $TH_2(100) = 0.9711$ and 61% of the motor units has a TH value below the average TH_2 value. For $\alpha = 3$: $TH_3(100) = 0.9627$ and 64% of the motor units has a TH value below the average TH_3 value. For $\alpha = 4$: $TH_4(100) = 0.9564$ and 66% of the motor units has a TH value below the average TH_4 value.

The discharge frequency of the motor neurons were based on literature findings. In many of the studies that did experiments to obtain data on motor unit properties electric shocks were used as neural excitation to trigger motor unit recruitment. [11, 15, 14]. The found literature presented values for the neural excitation rate that resulted in maximum (fused) tetanic tension in the range of 100 to 200 [Hz] [11, 15, 14]. As can be noted, the unit for the level of neural excitation was usually expressed in a rate (pulses per second) rather than a magnitude (e.g. Volts). There is no clarity from the same literature whether the neural excitation rate elicited the same value for the discharge frequency of the motor neurons.

The maximum discharge frequencies in the model are divided among the motor neurons according to the 'reversed onion skin' [20] which means the higher the maximum force of a motor unit, the higher the maximum discharge frequency of that motor unit. The reason for distributing the discharge frequencies proportional to the maximum force of the motor units is the assumption that a motor unit with a shorter twitch time to peak requires a higher frequency to reach maximum force (maximum tetanic tension) and the twitch time to peak (TTP) and thus twitch contraction time (TCT) is also set proportional related to the maximum force of the motor units. The maximum discharge frequencies are divided among the motor neurons proportional to the maximum force of the motor units where the motor neuron with the lowest MU-threshold has a maximum discharge frequency of 25 [Hz] and the motor neuron with the highest MU-threshold has a maximum discharge frequency of 100 [Hz]. A few other maximum discharge frequency ranges were tested, but lead to minimal changes in the force output curve (see appendix A.3; figure A.4; note that the muscle force was normalized).

The minimal discharge frequency of a motor unit which happens when the neural excitation is at a (constant) level that is equal to the MU-threshold of that motor unit, is set to 1 [Hz] for every motor neuron. The chosen minimal discharge frequency is an assumption and is expected to have a negligible effect as the chosen neural excitation signals quickly surpass the MU-thresholds of the motor units. The neural excitation-frequency relation of a motor unit is modeled as a linear relation. The result is with an linear increasing neural excitation input, the discharge frequencies of the recruited motor neurons also increase linearly (within their range) and with an exponential increasing neural excitation, the discharge frequencies of the recruited motor neurons increase exponentially (within their range). The choice for a linear neural excitation-frequency relation of a motor unit is an assumption. Setting the neural excitation-frequency relation of a motor unit as exponential would add another exponential element to the model which in case of an exponential neural excitation input is expected to result in an excitation-force relation of the muscle that is not able to approximate measured muscle force.

When the neural excitation equals or surpasses the MU-threshold of a motor unit the motor neuron of the motor unit starts to discharge action potentials at the prescribed frequency. An action potential is an all or nothing phenomenon meaning that the output of the simulated motor neurons is either 0 or the set amplitude. The amplitude of an action potential was set to 1 [arbitary unit (au)] for all motor neurons. The choice of setting the action potential amplitude to 1 [au] can be justified by the reason that there is no necessity to know the exact action potential amplitude value for the current research. The duration of an action potential (especially the time required to reach peak value) was considered negligible compared to the time duration of the muscle fiber contractions. Only the moment of discharge of the action potential was relevant in case of a comparison between the timing of the simulated discharges with the timing of recorded EMG data is desired. The part of the computer model responsible for the force production is sensitive for the amplitude of the action potential which is another reason why the action potential amplitude is set to 1 [au] for all motor neurons (see section 2.1.2).

2.1.2 Force production

The muscle fibers turn the incoming impulses into force twitches. A twitch has a distinctive force profile shown in figure 1.3 and 1.4. The course of the force production is a relatively quick rise in force towards the peak force followed by a relatively slow decline in force till no more force is produced. In the computer model the twitch force profile was approximated by the impulse response of a critically damped second order system. An example of a simulated motor unit twitch using a critically damped second order system is depicted in figure 2.5. A Comparison between figure 2.5 and the figures (1.3 and 1.4) from section 1.3 shows distinct similarities between the simulated motor unit twitch and the experimentally recorded motor unit twitches.

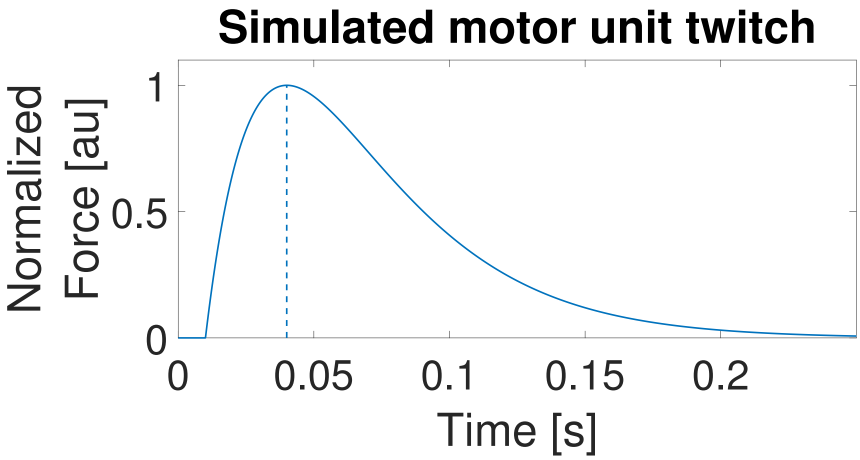

Figure 2.5: A simulated motor unit twitch using a critically damped second order system. The simulated twitch has a relatively fast rise until the maximum twitch force is attained (indicated by the dashed line; TTP = 0.03 [s]) after which a relatively slow decline in force starts until resting conditions are met. Note that the force starts to develop at t = 0.01 [s] due to the latency that represents the conduction time of the action potentials along the nerves.

The critically damped second order system (in the Laplace domain) that simulated the muscle fibers is given by equation (2.6) and a solution (in the time domain) to the impulse response of that system is given by equation (2.7). For more details see the appendix (A.1).

$$H(s) = \frac{1}{s^2 + 2\omega_n s + \omega_n^2} \tag{2.6}$$

$$F(t) = te^{-\omega_n t} \tag{2.7}$$

$$\omega_n = \frac{1}{TTP} \tag{2.8}$$

From equation (2.7) follows that the ω_n is the only adjustable parameter. Consequently the value of the parameter ω_n fully determines the twitch behaviour including the time to peak (TTP) and the to the TTP related twitch contraction time (TCT). The relation between ω_n and the TTP is given by equation (2.8). The parameter ω_n gives the possibility to vary the TTP (time to peak) and therefor the twitch contraction time (TCT) among the motor units. In several studies the TTP of a motor unit was found to be proportional related to the maximum force of that motor unit [12, 15, 14]. For the computer model the proportional relation between the TTP and maximum force of the motor unit resulted in the relatively same distribution of the TTP and maximum force among motor units. The range of the TTP values was set between 30 [ms] for the motor unit with the highest maximum force and 70 [ms] for the motor unit with the lowest maximum force conform to values found in the literature [12, 15, 14]. Other plausible ranges (lowest-highest TTP: 20-80 [ms], 30-70 [ms], 40-60 [ms] and 50-50 [ms]) for the TTP were tested, but the differences were considered to be too small for the TTP to be of any concern for the current study (see appendix A.3, figure A.5).

From equation (2.7) the deduction can be made that the value for ω_n influences the maximum force of a twitch. The shorter the TTP, the lower the peak force of the twitch which should be the shorter the TTP, the higher the peak force of the twitch according to the literature [12, 15, 14]. A correction is implemented that sets the maximum force equal for all motor units after which weight factors can be applied that lead to the desired MU-force distributions. The influence of the input (action potential) on the force output is eliminated by the choice of setting the action potential amplitude to 1 for all motor units. Equation (2.9) gives the force output as in equation (2.7) with the correction (C_{corr}) for ω_n and the weight factor (C) to achieve the desired MU-force distributions among the motor units.

$$F(t) = C_{corr} C t e^{-\omega_n t} \tag{2.9}$$

The weight factor determined the maximum force of a motor unit. As for the MU-thresholds, the question was how to distribute the weight factors and thus the maximum force among the motor units. The earlier mentioned studies that experimented on cat muscles also presented measured data on how the maximum force was distributed in two muscles of the cat [15, 14]. Although the experiments were done on cat muscles the found distribution of the maximum force among the motor units was considered the base for MU-force distributions for the computer model. The found MU-force distributionss among the motor units of the cat muscles had more relatively low force motor units than relatively high force motor units. An exponential distribution was used as an approximation of the found distribution of the maximum force among motor units. As stated before, in humans the distribution of motor unit properties was found not only to vary per muscle, but also vary in the same muscle between different persons [13] and an exponential distribution of the maximum force among motor units is not unthinkable. To compare the exponential distribution, a linear distribution of the maximum force among the motor units was also simulated.

Equation (2.10) was used for the linear distribution of the weight factors. The highest weight factor was always equal to 1 and the lowest weight factor was set by β as it determined the steepness of the linear increase. To compare the linear with the exponential distribution β was set to equal the number of motor units N. Other values for β (10, 20, 50, 100, 200) were tested but the number had to be extremely different to have a significant effect (see appendix A.3; figure A.3).

$$C_{lin}(i) = \frac{1}{\beta} + \frac{1 - \frac{1}{\beta}}{N - 1}(i - 1) \tag{2.10}$$

Equation (2.13) was used for the exponential distribution of the weight factors that is a modified version of an equation used by Potvin J.R. and Fuglevand A.J. [19]. The equation closely resembles that of the exponential distribution of the MU-thresholds. A difference is that the highest outcome is always 1 for $i = N$ no matter the value for N. Equation (2.11) is normalized by equation (2.12) for the same reason as with the MU-thresholds. The result of the normalization is given by equation (2.14) Again an element, in this case γ, was used to determine the degree of the exponential curve. The higher the γ, the steeper the exponential curve.

$$C_1(i) = \frac{e^{\frac{\gamma}{N-1}(i-1)}}{e^{\gamma}} \tag{2.11}$$

$$C_2(i) = \frac{1 - \frac{e^{\gamma}}{N}}{N - 1}(i - 1) + \frac{e^{\gamma}}{N} \tag{2.12}$$

$$C_{exp}(i) = C_1 \cdot C_2 \tag{2.13}$$

$$\text{for } \gamma > 0 \begin{cases} C_{exp} = \frac{1}{N} & \text{for } i = 1 \\ C_{exp} = 1 & \text{for } i = N \end{cases} \tag{2.14}$$

The values of γ used in the simulations were 0, 1, 2, 3 and 4. The case of $\gamma = 0$ resulted in a linear MU-force distributions (C_{lin}) as in equation (2.10). The cases $\gamma = 1$, 2, 3 and 4 resulted in exponential MU-force distributionss among the motor units, where the higher the number for γ the more exponential the distribution. A value for γ higher than 4 did not result in a significant increase of the exponential shape of the MU-force distributions.

To see what different values for γ (both 0, 1, 2, 3 and 4) did for the MU-force distributions, the different distribution patterns were plotted in a single figure. Figure 2.6 shows the different MU-force distributionss. The shown MU-force distributionss are as intended and the weight factors are therefor without the correction explained in section 2.1.2.

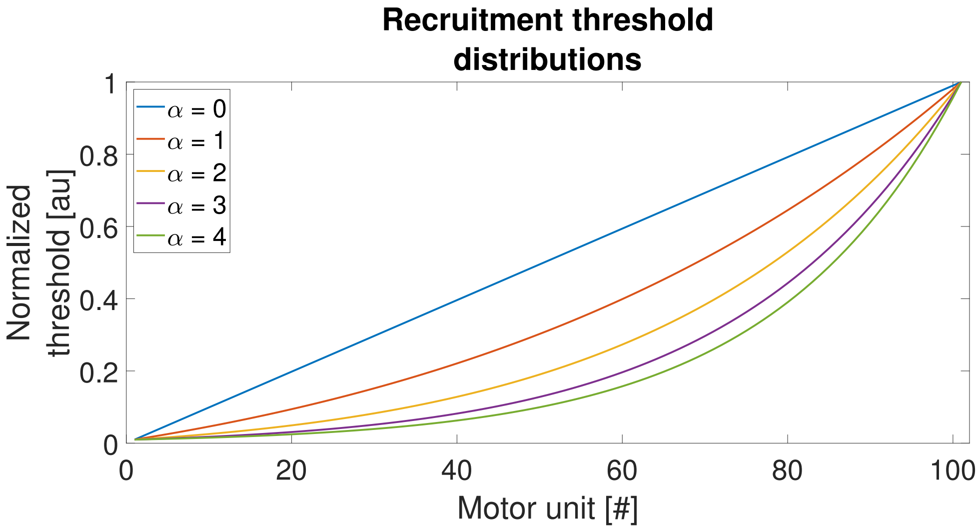

Figure 2.6: The number of motor units (N) is set to 100. The different MU-force distributions (C_γ) are determined by γ. For all γ the force of the first motor unit has a weight factor of $C(1) = 0.0099$ and the force of the last motor unit has a weight factor of $C(100) = 1$. For $\gamma = 0$: 50% of the motor units has a C value below the average C_0 value. Using $\gamma = 0$ is the same as using a linear distribution ($\beta = 100$) for the weight factors. For $\gamma = 1$: 57% of the motor units has a C value below the average C_1 value. For $\gamma = 2$: 61% of the motor units has a C value below the average C_2 value. For $\gamma = 3$: 64% of the motor units has a C value below the average C_3 value. For $\gamma = 4$: 66% of the motor units has a C value below the average C_4 value.

A few remarks about the force production. To get the intended MU-force distribution a small correction was required due to the (mathematical) influence of the ω_n on the force output. The function of the correction was to set the maximum force of all motor units equal after which the weight factors were applied ensuring the desired MU-force distributions among the motor units. The consequence was that the model had to be simulated twice. First to determine the extra correction values and second to obtain the force data. For the unit of force the choice was made to use an arbitrary unit. Expressing the force of the motor units in realistic quantitative values would require an extra effort that was considered not worth the trouble for the current study as realistic quantitative values were not required for the investigation of the research question. There is no distinction made between motor units with different muscle fiber types (S and F; section 1.3). The maximum strength is set by the weight factors and increases (gradually) from minimum to maximum according to the chosen weight factor distribution. To obtain the (total) muscle force, the force of each recruited motor unit was summed. The muscle force was subsequently normalized such that the steady state of the force was close to 1. The normalization was required to be able to compare the muscle force from different simulations.

2.2 Simulation

2.2.1 Graphical validation

Important for a computer model is the reliability of the results that simulations with that computer model produce. A common criteria for the reliability of the results is the validity of the computer model. In the ideal situation an experiment is specifically designed to obtain data that can be compared one on one with the simulated data from the computer model to validate the computer model. If the computer model simulations can produce data that is considered similar as data found using experiments with human test subjects that computer model is a valid representation of the simulated system of process. For practical reasons the choice was made to use a graphical validation. This meant no experimental data was available for comparison with the simulated data and no quantitative validation techniques such as the variance accounted for (VAF) could be used.

The graphical validation consisted of a visual comparison of the results from the computer simulations with the results from studies that did experiments with human test subjects [5, 24] given by the figures 2.7 and 2.8.

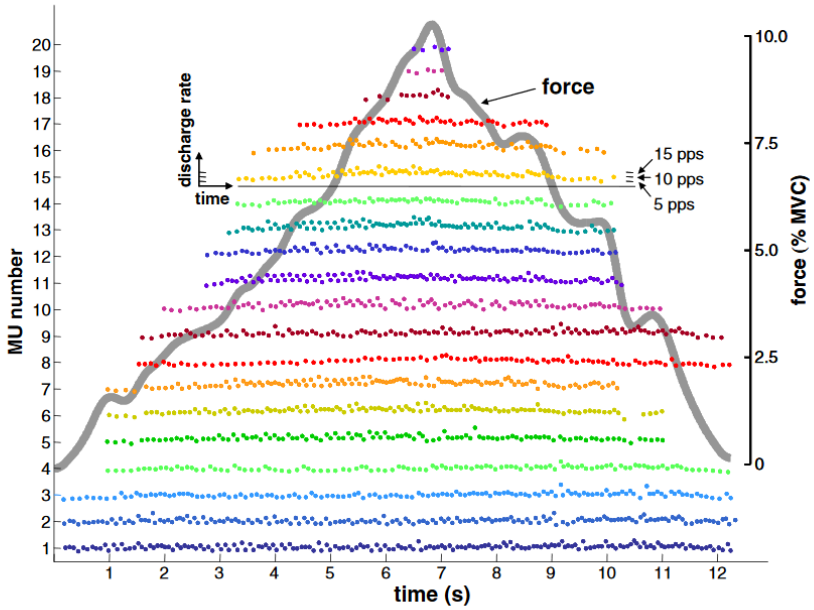

Figure 2.7: Recordings of the Abductor Pollicis Brevis muscle from [5]. The colored dots represent the recruitment of the motor units obtained using (surface) EMG in combination with EMG decomposition techniques. The gray colored line is the muscle force which has a maximum of 10% MVC. The recordings were obtained by having a human test subject slowly increase the muscle force up to 10% MVC and then slow decrease the muscle force back to fully relaxed.

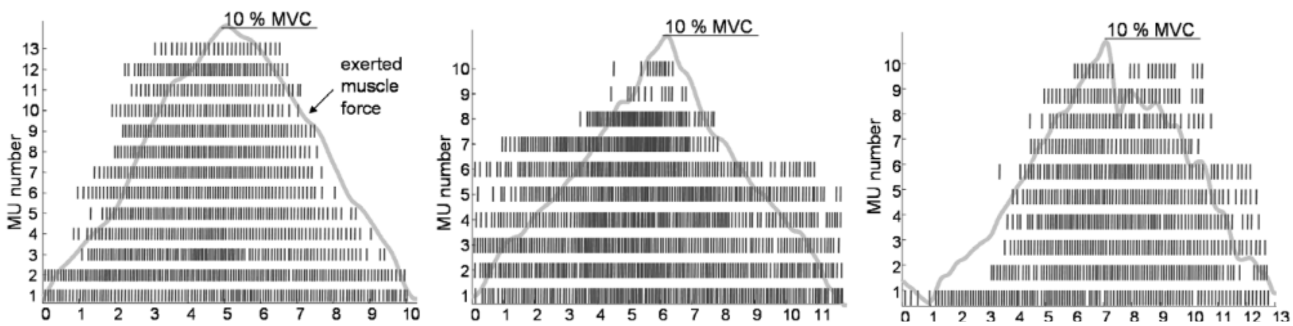

Figure 2.8: From left to right are recordings of the Biceps Brachii, Upper Trapezius and Vastus Lateralis muscles from [24]. The vertical lines (barcodes) represent recruitment of the motor units recorded using (surface) EMG in combination with EMG decomposition techniques. The continuous gray line is the muscle force which has a maximum of 10% MVC. The recordings were obtained by having a human test subject slowly increase the muscle force up to 10% MVC and then slow decrease the muscle force back to fully relaxed.

Important to know is that the maximum force in all the plots in figures 2.7 and 2.8 is 10% of the maximum voluntary contraction due to the limitation of the EMG decomposition technology. The plots in the figures suggest that the shape of the muscle force curve during the force increase is close to linear independent of the recruitment pattern for the motor units. The shape of the muscle force curve during the force decrease does not show a clear similarity between the plots. The pattern of motor unit recruitment is significantly different in each plot which seems on the eye to vary from being concave to linear and can be different during the force increase and decrease. The lack of general recruitment and force patterns from the figures strengthens the theory that in humans the motor unit property distribution at least varies per muscle.

Although not ideal, a visual comparison of force curves and motor unit recruitment can strengthen the plausibility of the computer model (proof of concept). The motor unit recruitment and the total muscle force from the experiments and simulations were compared as these were the two output variables of interest. Motor unit recruitment in the experiments was measured using (surface) EMG and EMG decomposition techniques to distinguish individual motor unit activity and the force was measured using a load cell. Several simulations were executed with different configurations for the MU-threshold and MU-force distributionss as the MU-threshold and MU-force distributionss among the motor units of the muscles from the experiments were unknown. The combination of the MU-threshold distribution and MU-force distributions that led to results most similar to the experimental findings was used for the visual validation validation of the computer model.

2.2.2 Ramp response

An important part of the simulations was the neural excitation input. A common way to experimentally obtain muscle properties is having test subjects do a ramp and hold task [17, 18, 19, 20]. During a ramp and hold task, the subject has to hold and maintain a joint (e.g. ankle, wrist) in a certain position or orientation while a (unidirectional) load is applied that linearly increases to a certain value. At the same time multiple quantities are recorded such as force, muscle activity using electromyography (EMG) and the (angular) position. A benefit of a ramp and hold task is that the relation between independent and dependent variables can be established over a wide range of the independent variable(s). As for the computer model the independent-dependent relation of interest was the excitation-force relation, a linear increasing or ramp neural excitation was modeled as the input (figure 2.9). A linear ramp input for the computer model does not necessarily results in a linear force output of the computer model.

A mathematical description of a ramp signal as used for the simulations is given by equations (2.15). From the equations there can been seen that the ramp input has two variables. The start time t_s and the increase rate a that sets the steepness of the ramp. The amplitude of the ramp is normalized and starts at 0 [au] where 0% of the motor units are recruited and increases to 1 [au] where 100% of the motor units (at their maximum discharge rate) are recruited.

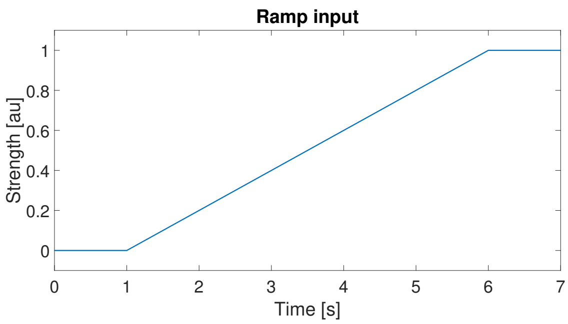

Figure 2.9: The profile of the ramp input used during the simulations. The ramp start at $t_s = 1$ [s] and has an increase rate of $a = 0.2$ [au s^{-1}].

$$r_{ramp} = \begin{cases} 0 & \text{for } t < t_s \\ a(t - t_s) & \text{for } t_s \leq t \leq t_s + \frac{1}{a} \\ 1 & \text{for } t > t_s + \frac{1}{a} \end{cases} \tag{2.15}$$

To be able to give an answer to the research question, multiple simulations with a ramp input (figure 2.9) as the neural excitation were executed with different combinations of the MU-threshold and MU-force distributionss. As the force lagged behind the neural excitation due to the simulated dynamics a direct excitation-force plot was difficult to create. Therefor the simulated forces were plotted against the simulation time which meant the neural excitation input curve had to be kept in mind while evaluating the force plots. The simulations with unique combinations of the MU-threshold and MU-force distributionss (α and γ) resulted in 25 muscle force profiles or excitation-force relations of a muscle. The visual inspection of the simulated forces revealed the influence of the MU-threshold and MU-force distributionss (α and γ) on the force. The results that showed the influence of the MU-threshold and MU-force distributionss the most clear came from the cases the linear and most exponentially tested MU-threshold and MU-force distributionss were used.

To accomplish the goal of finding the influence of the MU-threshold and MU-force distributionss among motor units of a muscle a maximum level of neural excitation for the ramp input (1 [au]) was used during the simulations which resulted in 100% maximum voluntary contraction (MVC). A 10% level of neural excitation (0.1 [au]) did not correspond to 10% MVC and each combination of MU-threshold and MU-force distributionss required a different level of neural excitation to reach 10% MVC. To achieve 10% MVC used for the graphical validation of the model the corresponding level of neural excitation was obtained from the 100% MVC simulations. Furthermore simulations were run with neural excitation inputs resulting in 20% and 50% MVC. To achieve 20% and 50% MVC the corresponding levels of neural excitation were also obtained from the 100% MVC simulation runs. Note that the input for the graphical validation consisted of an increasing ramp until 10% MVC was reached directly followed by a decreasing ramp back to zero (0 [au] or 0% MVC) forming a triangular input . For the levels of neural excitation corresponding to 10%, 20% and 50% MVC see table 2.4.

2.2.3 Distinguishable excitation-force curves

To be able to estimate the MU-threshold or MU-force distributions from the excitation-force relation of a muscle the individual effect of each distribution has to lead to a unique excitation-force relation curve. If two different combinations of the distributions result in excitation-force curves that cannot be distinguished from each other, the possibility of giving an estimation of the distributions based on and corresponding to an excitation-force curve is slim. The excitation-force relation curves from the 25 ramp input simulations (1 [au]; 100% MVC) were compared by calculating the variance of the difference between the excitation-force curves. The variance was an important measure as a low value for the variance meant the compared excitation-force curves had a similar shape. The value for the variance at which (and below) two curves were deemed similar was a subjective choice for simulation data. In case of experimental data that choice would likely depend on the data resolution and recorded noise. Having 25 excitation-force curves resulted in 300 comparisons ((25 $\times$ 25 - 25)/2).

The result from the comparisons indicated that several MU-threshold and MU-force distributions combinations led to similar shaped excitation-force curves. The finding of similar shaped excitation-force curves implies that at least one other quantity than force is required to be able to distinguish and estimate MU-threshold and MU-force distributions from experiments. Besides the force another quantity that can be simulated with the computer model and also recorded from humans (using EMG) are the action potential discharges of the motor units. The idea is that if from the action potentials the MU-threshold distribution can be obtained than in theory that should leave a single option for the MU-force distributions which could than be obtained from the (recorded) force.

2.2.4 Impulse response

The ramp and hold task during experiments makes use of voluntary muscle contractions. Humans also experience involuntary muscle contractions in the form of reflexes. A muscle reflex is a short, but intense contraction of the muscle often as response to a sensory input (for example in the form of pain). Simulating a muscle during a reflex with the computer model requires the appropriate neural excitation for the computer model. An impulse signal (figure 2.10) is assumed to trigger the computer model response that can simulate a muscle reflex. As the neural excitation is at a high level in an instant and all motor units receive the same level of neural excitation, high threshold motor units are recruited at the same time as low threshold motor units.

The impulse instantly changes input levels at time $t_{impulse}$ as described by equation (2.16). The impulse amplitude is normalized and can therefor take values between 0 [au] where 0% of the motor units are recruited or 1 [au] where 100% of the motor units are recruited.

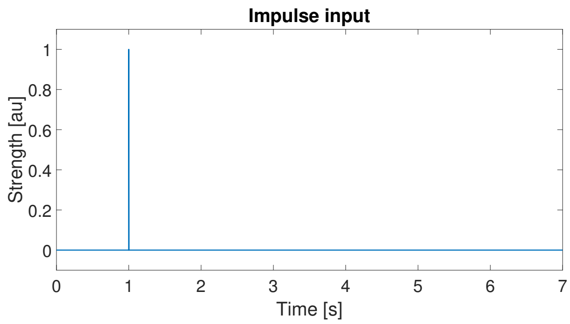

Figure 2.10: Impulse input occurs at $t = 1$ [s] with an amplitude of 1 [au].

$$r_{impulse} = \begin{cases} 0 & \text{for } t \neq t_{impulse} \\ 1 & \text{for } t = t_{impulse} \end{cases} \tag{2.16}$$

As with the ramp input, multiple combinations of MU-threshold and MU-force distributionss (α and γ) were simulated with the impulse signal as an input for the computer model. In contrast to the ramp input were the effects of using different combinations of the MU-threshold and MU-force distributionss on the force output. The differences on the force output were considered too small to be useful for the current study and therefor the impulse response was not further tested with the presented version of the computer model.

2.3 Model overview

A summary of the computer model with the most important parameters and signals used during the simulations. The susceptibility to fatigue of motor units and a feedback loop represent proprioception have been modeled. No (clear) distinction is made between different types of motor units (F or S type). The simulations were done with a fixed step size of $1{\cdot}10^{-4}$ [s]. The chosen step size was small enough to prevent computational errors such as aliasing, but large enough to have acceptable computation times. The simulated time was set to 7 [s] for every simulation run. The part of the model responsible for the recruitment was programmed directly in a MATLAB script while the force production was programmed using Simulink (see appendix A.2). Programming the recruitment model part directly in a MATLAB script turned out to be easier than programming the whole model in Simulink.

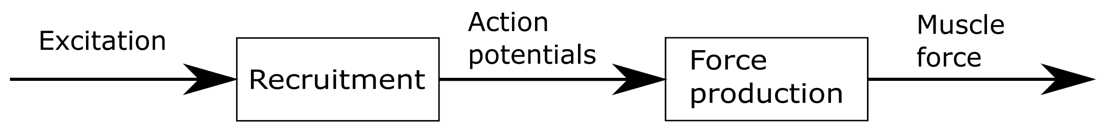

Figure 2.11: Block diagram of the model with block and signal names. The block diagram corresponds with tables 2.1 and 2.2.

Model part	Variable name	Variable type	Value	Based on
Recruitment	MU-threshold distribution (TH)	Independent	Linear or exponential distributed among motor units (α = 0, 1, 2 or 4) Equations (2.1) - (2.5)	[15]
	Minimal discharge frequency	Control	Set to 1 [Hz] for all motor units	Assumption
	Discharge frequency (DF)	Dependent	Proportional related to the maximum force	[11, 15, 14]
	neural excitation-frequency relation of the individual motor units	Control	Linear	Assumption
MU-force distribution (C)	Maximum force	Independent	Linear or exponential distributed among motor units (γ = 0, 1, 2 or 4) Equations (2.10) - (2.14)	[15, 14]
	Twitch time to peak	Dependent	Proportional related to the maximum force (TTP = $1/\omega_n$ [s])	[12]
Entire model	Number of motor units (N)	Control	Set to 100	[4]
	Recruitment order	Control	Orderly recruitment (from lowest maximum force to highest maximum force)	[7, 21, 8, 9]

Table 2.1: Overview of the model parameters. The table corresponds with figure 2.11.

Model part	Variable name	Variable type	Value	Based on
Recruitment (input)	neural excitation	Independent	[0, 1] (Normalized)	[17, 18, 19, 20]
Recruitment (output), Force production (input)	Action potentials	Dependent	0 or 1 (Normalized)	N.A.
Force production (output)	Muscle force	Dependent	[0, 1] (Normalized)	N.A.

Table 2.2: Overview of the signals. The table corresponds with figure 2.11.

Target MVC level	**neural excitation input**	**Values for α (MU-threshold distribution)**	**Values for γ (MU-force distributions)**	**Number of simulation runs (number of α and γ combinations)**
10%	triangle	0, 4	0, 4	4
20%	ramp	0, 4	0, 4	4
50%	ramp	0, 4	0, 4	4
100%	ramp	0, 1, 2, 3, 4	0, 1, 2, 3, 4	25

Table 2.3: The maximum voluntary contraction (MVC) target values during the simulations and the used values for the α and γ leading to a number of simulation runs for the corresponding MVC level. The MU-threshold distribution is determined by α and the MU-force distribution is determined by γ. For α and γ: 0 is linear distribution, 4 is strongest exponential distribution and the numbers in between are intermediate steps.

distribution combination	normalization factor	MVC level	neural excitation level
$\alpha = 0$, $\gamma = 0$	50	10%	0.325
		20%	0.450
		50%	0.709
$\alpha = 0$, $\gamma = 4$	22	10%	0.530
		20%	0.662
		50%	0.851
$\alpha = 4$, $\gamma = 0$	50	10%	0.044
		20%	0.081
		50%	0.267
$\alpha = 4$, $\gamma = 4$	22	10%	0.115
		20%	0.215
		50%	0.512

Table 2.4: This table contains a few computer model parameters used to simulate ramp responses at different levels of maximum voluntary contractions (MVCs) with different distribution combinations. The MU-threshold distribution is determined by α and the MU-force distribution is determined by γ. For α and γ: 0 is linear distribution, 4 is strongest exponential distribution.

3 Results

3.1 Simulation

3.1.1 Graphical validation

Four simulations were run with the combinations of the extreme values for α and γ. In other words, the combinations contained the linear and most exponential distributions for the MU-threshold and maximum force among the motor units. A (single period) of a triangle wave was used to try and create similar results as in figures 2.7 and 2.8. The minimum level of neural excitation was set to 0% (zero recruited motor units) and the maximum level of neural excitation had to be pre-determined by finding the level that corresponds to 10% maximum voluntary contraction (MVC) for each α-γ combination. The pre-determination was done by simulating each α-γ combination with a full range ramp input and find the level of neural excitation at which 10% MVC was reached.

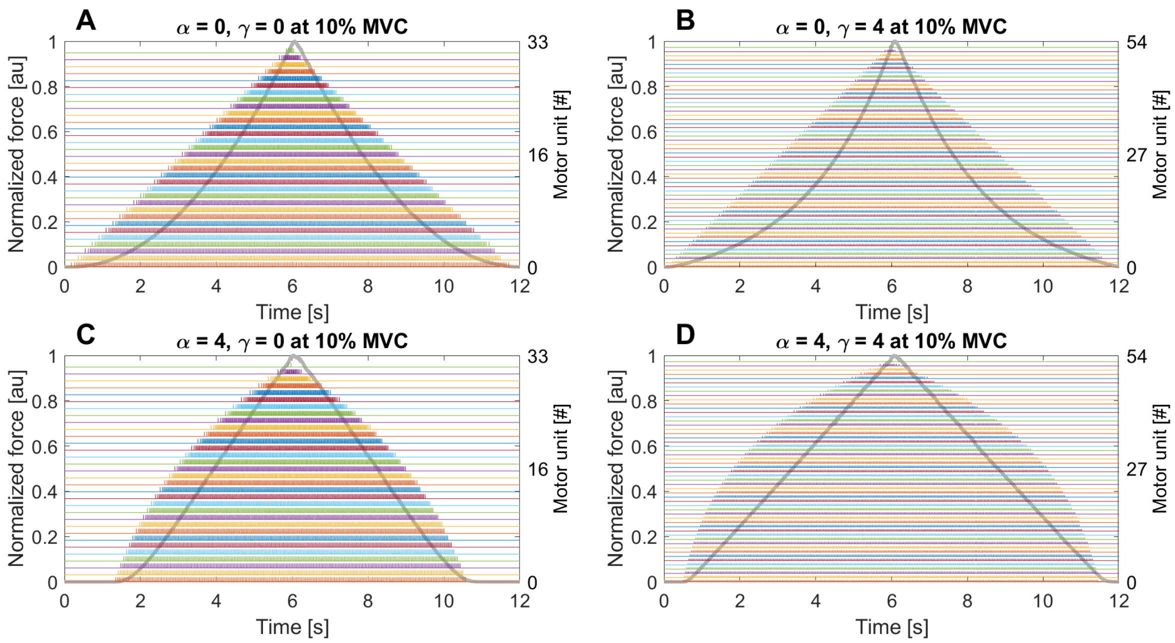

Figure 3.1: Four plots of the simulated muscle force (MVC $\approx$ 10%) and action potentials of the individual recruited motor units. Each plot is made with a different combination of the MU-threshold and MU-force distributions. The colored lines are the motor neuron discharge trains (action potentials) where each vertical line is a discharge of an action potential. The gray colored curve is the muscle force.

Figure 3.1 shows the results of the simulations used for the graphical validation of which a few interesting aspects can be noted. All plots (A, B, C and D) are symmetric (both the recruitment and force) around the point (6 [s] mark) where the triangular input changes from an increasing shape to a decreasing shape which does not show in the findings from the literature. The part during the neural excitation increase (basically the ramp input) seems to be a more accurate representation which makes sense as only the activation dynamics were considered for the model and not the deactivation dynamics. The number of motor units required to reach 10% MVC differs most between the linear and exponential distribution of the maximum force among the motor units. Looking at figure 3.1 the plots with the exponential MU-threshold distribution (C and D) are the most similar to the figures from the literature. Whether the distribution for the maximum force among the motor units is linear or exponential is not so clear by comparing the figure 3.1 and the figures from the literature (section 2.2; figures 2.7 and 2.8).

3.1.2 Ramp response

The first input to be used to create simulation data for the research question was the ramp input as described in section 2.2.2. To get an idea of the influence of the MU-threshold and MU-force distributions (α and γ), the muscle force with combinations of the linear and most exponential MU-threshold and MU-force distributions were simulated for different levels of MVC.. The result is given by figure 3.2 and allows for a visual analysis of the produced force curves.

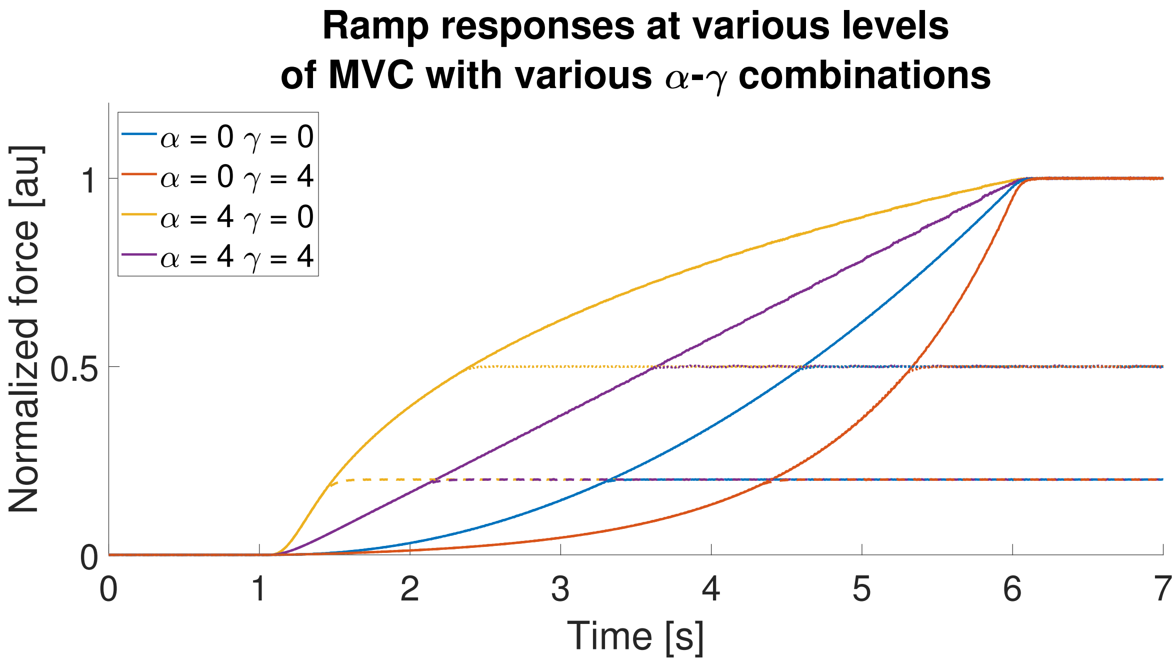

Figure 3.2: The ramp responses of four different combinations of MU-threshold and MU-force output distributions at different levels of MVC. The combinations contain the linear and most exponential MU property distributions (α and γ: 0 and 4) and can be distinguished by the four different colors. The different levels of MVC can be distinguished by the line style. The dashed lines indicate 20% MVC, the dotted lines indicate 50% MVC and the solid lines indicate 100% MVC.

3.1.3 Distinguishable excitation-force curves

All other combinations of the MU-threshold and MU-force distributions within the set range of α and γ were simulated with the ramp input as the neural excitation. Figure 3.3 gives an example of two force curves with different MU-threshold and MU-force distributions, but visually appear the same.

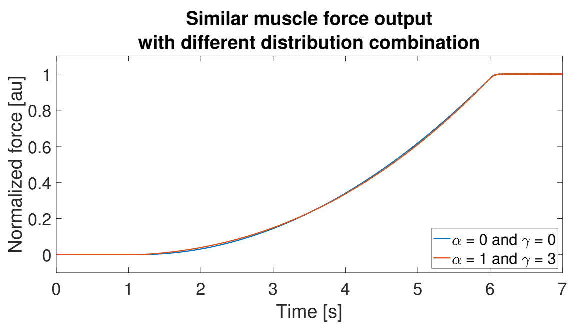

Figure 3.3: Example of two simulated force curves with different combinations of the MU-threshold and MU-force distributions (α and γ). Subtracting the force curves results in a difference of which the variance is only $2.3{\cdot}10^{-5}$ suggesting both force curves are similar.

variance criteria	number of similar forces
$1{\cdot}10^{-2}$	180
$1{\cdot}10^{-3}$	57
$1{\cdot}10^{-4}$	9

Table 3.1: If the value for the variance is below the criteria value, the compared simulated forces are considered to be similar. Three different criteria for the variance and the corresponding number of force pairs that are considered to be similar.

A quantitative test for similarity of the simulated force curves with all combinations of the MU-threshold and MU-force distributions resulted in a number of similar force curves depending on the criteria at which a curve was considered the same. The results of the similarity test is given by table 3.1.

The action potential discharges of the motor units are an optional output of the computer model. From the simulated discharges the MU-threshold distribution could be obtained by determining the first moment of recruitment of the motor units as a response to a ramp input. The result is shown in figures 3.4 and 3.5 for two different MU-threshold distribution patterns.

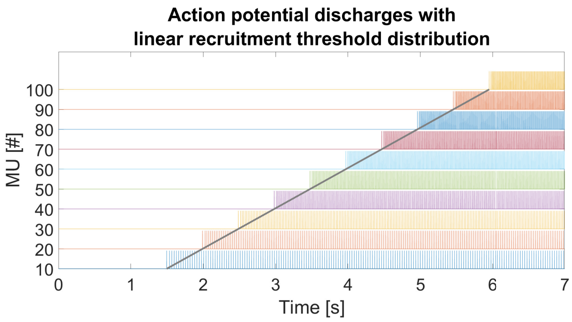

Figure 3.4: The impulse trains as a result of a ramp input. Only the discharges of every 10th motor neuron are shown. The MU-threshold distribution is linear ($\alpha = 0$; indicated by the gray line) as the difference in neural excitation level between recruitment of each motor neuron is equal.

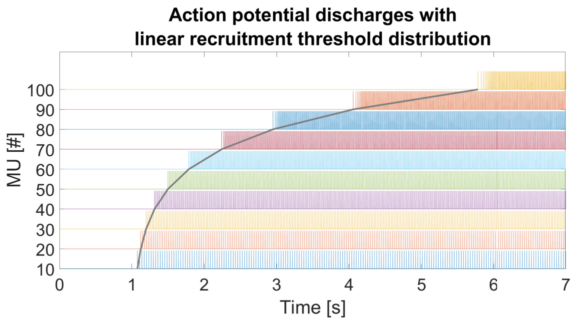

Figure 3.5: The impulse trains as a result of a ramp input. Only the discharges of every 10th motor neuron are shown. The MU-threshold distribution is exponential ($\alpha = 4$; indicated by the gray line) as the increase in neural excitation that is required to recruit the next motor neuron increases exponentially.

3.1.4 Impulse response

The other tested input was the impulse introduced in section 2.2.4. Again combinations were made with the chosen outer values for the MU-threshold and MU-force distributions (linear and most exponential; α and γ: 0 and 4). The results of the impulse responses are given by figure 3.6.

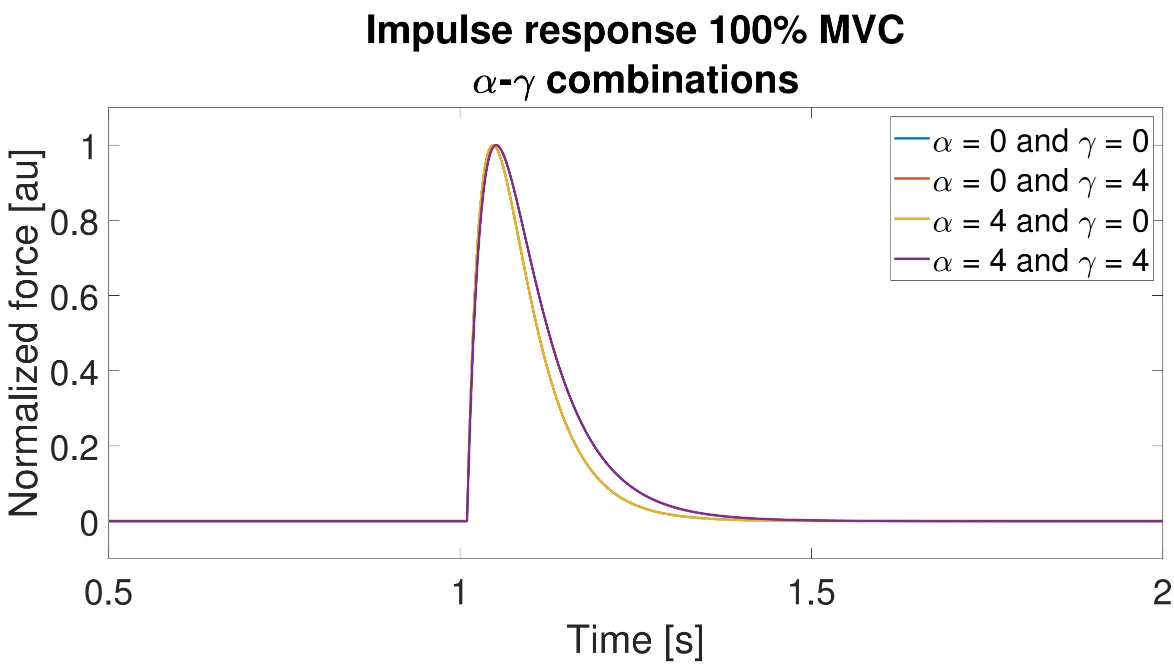

Figure 3.6: The muscle force output of the impulse response simulations using the four combinations with the outer values for α and γ. Only two force curves are visible as they exactly overlay the other two force curves. Different values for α has no noticeable effect on the shape of the force curve which suggest that the MU-threshold distribution does not play a role for the force during an impulse input. Different value for γ has a slight effect on the shape of the force curve. The force curves with a linear MU-force distribution reach peak force and resting position a bit quicker than the force curves with an exponential MU-force distribution.

4 Discussion

4.1 Graphical validation

The forces and action potential discharges simulated for the graphical validation of the computer model show similarities with the experimental results found in the presented literature [5, 24]. Although the simulated results are not exactly the same as the results from the literature, the simulated force and action potentials are already a rough approximation of the those found in the literature, with basically arbitrary MU-threshold and MU-force distributions. The force curves in plots C ($\alpha = 4$, $\gamma = 0$) and D ($\alpha = 4$, $\gamma = 4$) from figure 3.1 resemble the force curves in figures 2.7 and 2.8. The MU-recruitment is harder to compare with a graphical comparison only. The MU-recruitment from the literature [5, 24] examples do not seem to be linear and would suggest a more exponential distribution which could explain why plots C and D from figure 3.1 give the more similar force curves.

Some important difference between the literature results and the results from the current study can be noted. The results from the literature show a different course for the decrease of the force than the simulated results. The results from the literature demonstrate that the force curve during the force decrease can be irregular compared to the smoother curve during increase. For the simulated results the action potential discharge pattern during the force decrease is the mirror image of the action potential discharge pattern during the force increase while the results from the literature seem to show a difference between the action potential discharge patterns during force increase and force decrease. The deviations might be explained by a neurological cause such as proprioception (feedback) which has not been incorporated in the computer model, but was present in the experiments from the literature. Proprioception can influence the recruitment of motor units (not the distribution) in a response to joint parameters such as force, angle (position) and velocity.

Another difference between the results from the literature and the simulated results are the number of recruited motor units to produce the force (10% MVC). With an 'arbitrary' chosen number of motor units, as the number of motor units in a muscle is unknown, the difference in recruited motor units can be expected. However the shape of the simulated force curve is expected not to depend on the exact number of motor units as long as the amount of motor units that is simulated is above a certain number (about 50 see section 2.1). For the current study the exact number of motor units is not of interest as only the shapes of the force curves are of interest.

The graphical validation shows that a computer model that can simulate a group of motor units is potentially able to produce results similar to that of an actual muscle. For the current study the graphical validation is considered acceptable.

4.2 Force curve shapes

From the simulations with the ramp input as the neural excitation for the computer model the influence of the MU-threshold and MU-force distributions on the muscle force can be obtained. As a reminder two types of distributions were used for the MU-threshold as well as the MU-force among the motor units. A linear MU-threshold distribution (i.e. as many motor units with a 'low' MU-threshold as there are motor units with a 'high' MU-threshold) and exponential distributions (i.e. more motor units with a 'low' MU-threshold than there are motor units with a 'high' MU-threshold). The same holds for the MU-force distribution. When the MU-threshold distribution is linear and is changed to a more exponential pattern while keeping the MU-force distribution constant, the muscle excitation-force relation (shape) becomes more concave. When the MU-force distribution is linear and is changed to a more exponential pattern while keeping the MU-threshold distribution constant, the muscle force excitation-force relation becomes more convex. With convex and concave being opposite shapes means that the MU-threshold and MU-force have opposite effects on the excitation-force relation of a muscle. In other words the MU-threshold distribution is able to cancel out the effect of the MU-force distribution on the excitation-force relation and vice versa.

The convex or concave shapes of the excitation-force relation of a muscle have different consequences for the muscle functioning. A convex shaped excitation-force relation means that in the lower neural excitation region the increments in force are smaller (with a ramp input) allowing for more precision. A convex excitation-force relation is ideal to perform low force precision tasks while still being able to produce high forces for tasks that emphasize more on high force than precision. For a concave excitation-force relation the increments in force in the lower neural excitation region are now larger than in the higher neural excitation region resulting in a more precise control of the force in the higher force range. Whether having a muscle with a concave excitation-force relation is useful is questionable. A convex force curve is assumed to be preferable as precision tasks often require low muscle forces. Precision is usually of less importance in high force tasks (that a human can handle in terms of force). Then again the ideal excitation-force curve for a muscle could probably also depend on the muscle's location in the body. For example for a hand muscle there are more benefits to have precision over (almost) the full range of the force spectrum of that hand muscle as the hand is mostly used for low force high precision tasks. On the other hand, a back muscle could do with a less convex excitation-force relation as precision is expected to be of less importance as compared to the hand muscle.

An interesting question is: which tested motor unit property distribution has a stronger influence on the excitation-force relation of a muscle, the MU-threshold or MU-force distribution. If both distributions would have the same amount of influence on the excitation-force relation of a muscle than an equal change in both motor unit property distribution patterns would result in the same excitation-force relation curve as no change was applied. However equally changing both motor unit property distribution patterns (for example α and γ from 0 to 4) clearly results in two different shapes of the excitation-force curve. The effect of a change in the MU-threshold distribution pattern on the excitation-force relation is stronger than the effect of a change in the MU-force distribution pattern. I.e. the excitation-force curve with α and γ set to 4 is more concave than the excitation-force curve with α and γ set to 0. Comparing the two force curves, suggests that the MU-threshold distribution has a stronger influence on the excitation-force relation for the computer model. Whether the stronger influence of the MU-threshold can also be found in human muscles cannot be determined from the current simulation results.

4.3 Recognisable excitation-force curves

As stated, the excitation-force curves corresponding to a MU-threshold and MU-force distribution combination (α-γ) are not necessarily unique. Several simulated excitation-force curves with different combinations of the MU-threshold and MU-force distribution resulted in similar excitation-force curves. Similar excitation-force curves makes estimating the MU-threshold and MU-force distributions from the recorded force (excitation-force relation) alone impossible as a recorded force curve by itself has multiple options for the corresponding MU-threshold and MU-force distribution combination.

This study has shown that from the simulated action potentials of individual motor units, the MU-threshold distribution (pattern) can be retrieved. With the MU-threshold distribution known, the remaining MU-force distribution can be obtained from the simulated force. In theory the same feature should be possible with the appropriate experimental setup and EMG-decomposition techniques as studies have shown that EMG-decomposition techniques [5, 24] allow for differentiation of action potentials of individual motor units. The main limitation at this moment is the maximum voluntary contraction (MVC) at which EMG decomposition techniques can distinguish action potentials from individual motor units. The current level at which EMG decomposition is around 30% MVC although there have been studies that were able to get results up to 50% MVC [25, 26]. EMG-decomposition techniques are expected to improve in the future which would increase the potential of computer model aided methods as used in the current study.

4.4 Applications

The findings of the current study could be interesting for certain groups of population such as athletes or physicians treating people suffering from muscle related diseases. The distribution of motor unit properties has already been proven to not only vary per muscle, but per person [13] which therefor very likely also holds for the excitation-force relation of muscles. The assumption is that in healthy people only the MU-force distribution is expected to change. Therefor there can be assumed that the maximum force that a muscle is able to produce only changes if the maximum force of the motor units in the muscle changes. Maximum muscle force is usually increased through repeated exercise, but that does not mean all increase in muscle force is the same. Looking at athletes from different sport disciplines perhaps different exercises result in different (shapes of) excitation-force relations of the muscle. As for certain sport disciplines (or tasks in general) a specific excitation-force relation of the muscle might be preferred, knowing if or which exercise can achieve the preferred excitation-force relation of the muscle might be the difference between winning or losing, which is especially crucial for professional athletes. Another question is when achieving a specific excitation-force relation through training is possible, which motor unit properties change. Does only the maximum force of motor units change or is the MU-threshold of a motor unit not a permanent set value? A further developed version of the presented computer model could in theory give an answer to the questions in this section.

A group of people where the recruitment of motor units can most certainly be affected are people that have a muscle related disease or condition. For a disease such as ALS that affects the recruitment of motor units rather than the force production of the muscle there is not a clear or fast diagnosis available at this moment. Tracking the changes in muscle force (loss in force) and being able to identify the cause as either neural of mechanical could assist in making a diagnose for a disease such as ALS. For example, in case there is a loss in muscle force, a comparison can be done between the MU-threshold and MU-force distributions from subjects recorded at different instances in time. The cause of the loss in muscle force can the be identified as either to a change in the MU-threshold distribution, the MU-force distribution or a combination of the two. A change in the MU-threshold distribution suggests a neural cause while a change in the MU-force distribution suggests a mechanical cause for the loss in muscle force. It should be noted that for a proper comparison of distributions from different time instances, normalization of the force must not be applied.

4.5 Remarks & recommendations

The computer model needs a quantitative validation to proof if the model is a realistic representation of a group of motor units. An option is to use optimization algorithms to estimate the values of the computer model parameters based on recorded force and EMG data. With estimated values for the parameters the model can then be simulated after which quantitative validation and verification is possible using the same recorded force and EMG data.

With the results from the current study showing that the method utilizing a computer model has the potential of estimating the MU-threshold and MU-force distributions, justifies to further research and develop the computer model. Further developments can be made at different levels of the model.

The model in its current form does not incorporate a feedback loop with the reason to keep the complexity for this study within certain limits. In the human body (real life biological environment) this feedback is present in the form of proprioception (muscle spindles and golgi tendon organs). As proprioception influences the recruitment of motor units, adding a feedback loop that simulates the proprioception process is recommended for further research. In the computer model the proprioception adds a 'connection' between joint parameters (velocity, force etc.) and the neural excitation input.

In this study only linear and exponential distributions among the motor units were investigated for the MU-threshold and MU-force. Although the distributions used for the computer model are based on results from studies involving cat muscles and not human muscles, the assumption is that the distribution possibilities of the investigated parameters will not differ that much from the findings in those studies. If these type of distributions turn out to be far apart from the linear or exponential patterns the model will need to be modified to allow for other distribution patterns.

The sensitivity to fatigue is not the same for every motor unit. Depending on the type of muscle fibers that a motor unit contains, the decline in its force production can be quite significant after extended use of the corresponding motor unit. During experiments with human test subjects the decline in muscle force will be reflected in muscle force recordings. Incorporating this decline in the computer model is therefor advised especially if the experiments to obtain muscle recordings involve repeated and/or long duration tasks.

The comparison with the results from the literature proved the computer model is only suitable for increasing neural excitation inputs. Makint the model suitable for a wider range of neural excitation inputs, requires investigation of the deactivation dynamics. Most improvement is expected to be gained in the recruitment part of the model. Besides proprioception, a more accurate representation of the motor neuron in the form of a leaky integrator might be important.

For future validation of the computer model, experiments with forces at higher MVC should be done. New EMG decomposition techniques have already shown that decomposition up to 50% of MVC is possible [25, 26].

5 Conclusion

The goals at the beginning in the introduction (section 1.5) were set to answer the research question. A recap of the research question and goals are given.

Research question: "What relation do the MU-threshold and MU-force distributions among the motor units of a muscle have with the excitation-force profile of the same muscle?"

Goals:

- Determine the individual relations of the MU-threshold and maximum force distributions with the excitation-force relation.
- Determine if the effect of the MU-threshold and maximum force distributions on the excitation-force profile result in unique characteristics that allow for estimation and differentiation of the distributions from muscle force recordings.
- Build a computer model representing a group of motor units that can be used to simulate the excitation-force relation of a muscle with the MU-threshold and MU-force distribution among the motor units as independent variables.

Each of the goals has been achieved and the outcome is summarized for each goal. The outcomes together also form the answer to the research question.

Outcomes:

- A computer model representing a group of motor units was build for simulating the excitation-force relation of a muscle with the MU-threshold and MU-force distributions among the motor units as independent variables.
- Changing the MU-threshold and MU-force distributions from linear to exponential results in a more concave, respectively convex shape of the excitation-force profile.
- The individual contributions of the MU-threshold and MU-force distributions among the motor units of a muscle do not lead to unique muscle excitation-force profiles that allow for estimation and differentiation of the MU-threshold and MU-force distributions. As a consequence, the MU-threshold and MU-force distributions cannot be obtained from muscle force recordings alone. Using a combination of force and (surface) EMG recordings with the built computer model has the potential to estimate (non-invasive) the MU-recruitment and MU-force distributions among the MUs of a muscle.

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A Appendix

A.1

The differential equation of a second order system.

$$F(t) = \ddot{x}(t) + 2\zeta\omega_n\dot{x}(t) + \omega_n^2 x(t)$$

With $\zeta = 1$ the system becomes a critically damped second order system.

$$F(t) = \ddot{x}(t) + 2\omega_n\dot{x}(t) + \omega_n^2 x(t)$$

The Laplace transformation of the differential equation.

$$\begin{aligned} F(s) &= s^2 X(s) + 2\omega_n s X(s) + \omega_n^2 X(s) \\ F(s) &= (s^2 + 2\omega_n s + \omega_n^2)X(s) \end{aligned}$$

The transfer function.

$$G(s) = \frac{F(s)}{X(s)} = s^2 + 2\omega_n s + \omega_n^2$$

Using transfer function properties to find the relation of interest between input $U(s)$ and output $F(s)$ instead of input $F(s)$ and output $X(s)$. The resulting transfer function is called $H(s)$.

$$\begin{aligned} G(s) &= s \rightarrow \frac{dy}{dt} = u \\ H(s) &= \frac{1}{s} \rightarrow y = \frac{du}{dt} \end{aligned}$$

$$\begin{aligned} H(s) &= \frac{F(s)}{U(s)} \\ H(s) &= \frac{1}{s^2 + 2\omega_n s + \omega_n^2} \end{aligned}$$

The unit impulse as an input.

$$u(t) = \delta(t) \longleftrightarrow U(s) = 1$$

The unit impulse input results in the following equation.

$$\begin{aligned} F(s) &= H(s)U(s) \\ F(s) &= H(s) \end{aligned}$$

Simplifying (factorization) the polynomial using the quadratic formula.

$$\begin{aligned} ax^2 + bx + c &\rightarrow s^2 + 2\omega_n s + \omega_n^2 \\ x = \frac{-b \pm \sqrt{b^2 - 4ac}}{2a} &\rightarrow s = \frac{-2w_n \pm \sqrt{(4w_n^2 - 4w_n^2}}{2} = -w_n \end{aligned}$$

Finding the unit impulse response in the time domain.

$$F(s) = \frac{1}{(s + w_n)^2} \longleftrightarrow F = te^{-w_n t}$$

A.2

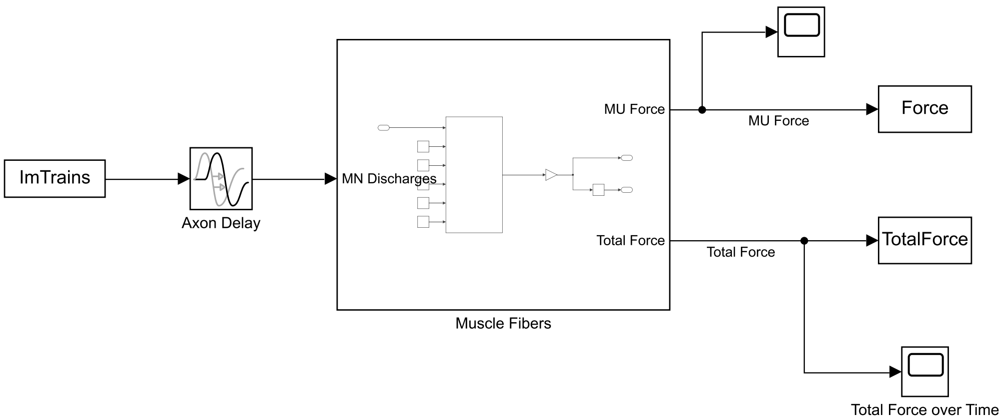

Figure A.1: The SIMULINK model responsible for the force production. The input (MN Discharges) is proviede by the impulse trains (ImTrains) that are created by the recruitment part. The outputs are the force of each individual MU as well as the summed total force. The block representing the muscle fibers can be further expanded which is shown in figure A.2. The block named 'Axon Delay' can be used to add a small delay on each impulse train to simulate the differences in conduction velocity of the nerves. In the current study the delay was set equal for all motor units.

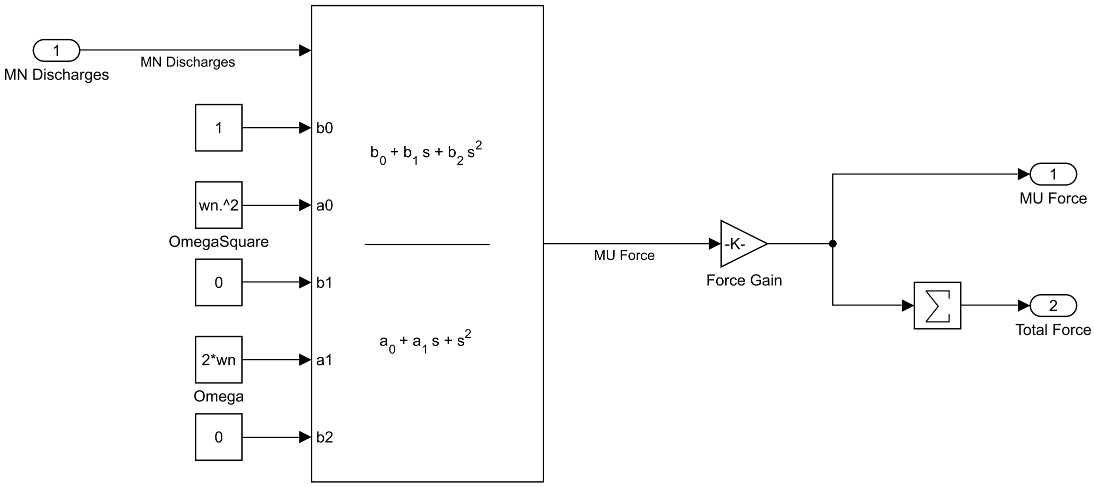

Figure A.2: The SIMULINK model that is responsible for simulating the force production of the muscle fibers. The signal input is the (delayed) impulse trains. The other inputs (a0, a1, b0, b1, b2) are the parameters that determine that the muscle fibers behave as a critically damped second order system. The outputs are the force produced by the individual MU's and the summed total force. The block named 'Force Gain' contains the force weight factors for each MU.

A.3

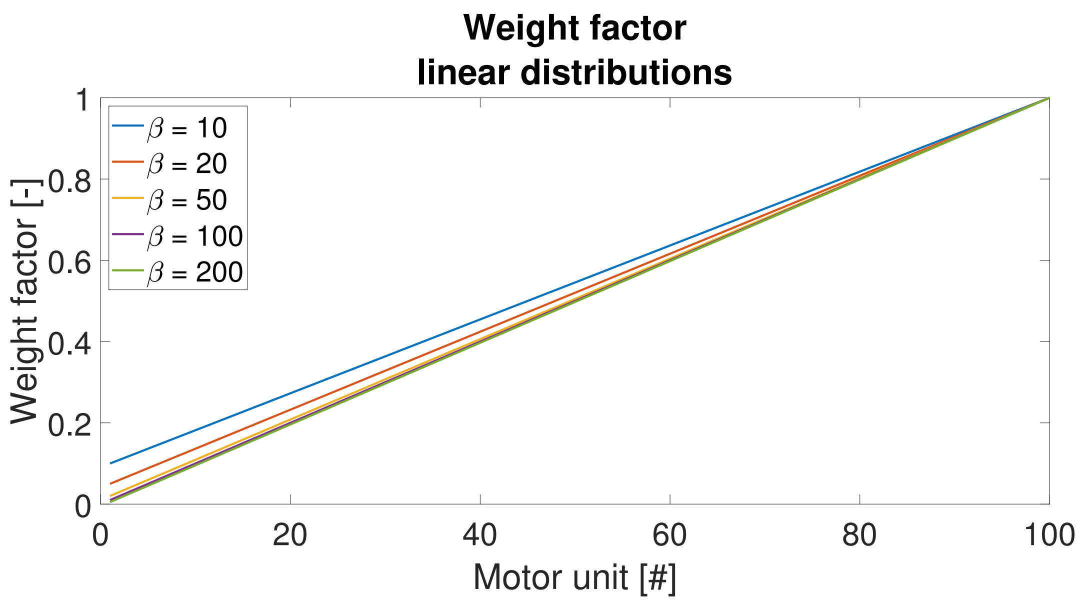

Figure A.3: The linear distribution of the weight factors C had a variable β. This figure shows that the influence of β is small.

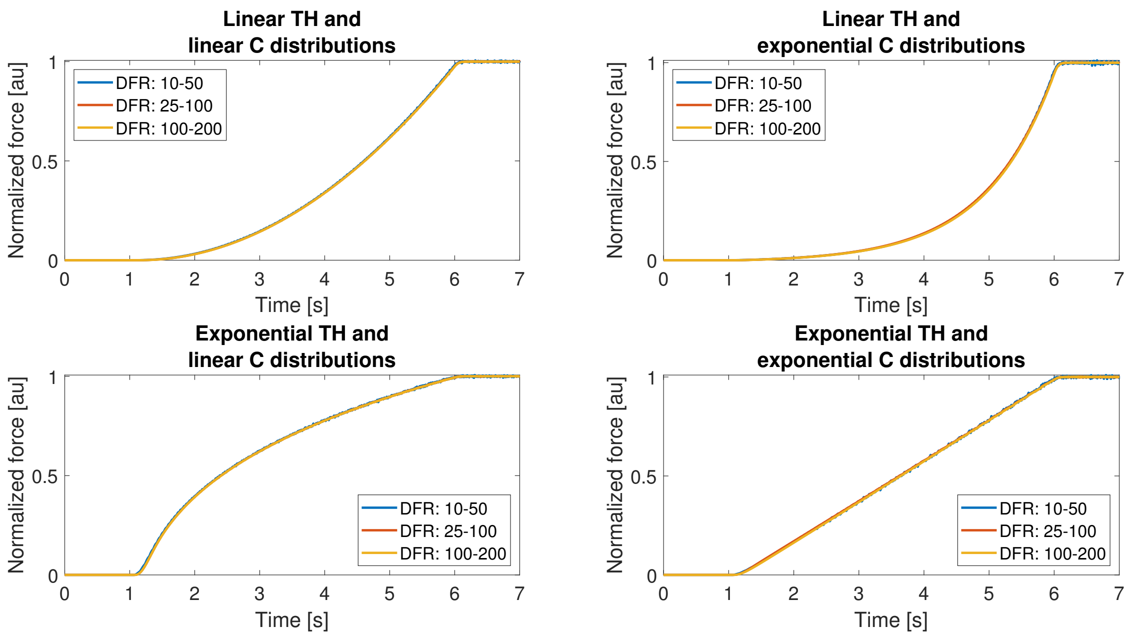

Figure A.4: Different discharge frequency ranges (DFR) were tested for four combinations of the MU-threshold and MU-force distribution combinations (α and γ: both 0 and 4). The tested DFR had little influence on the shape of the simulated excitation-force relation.

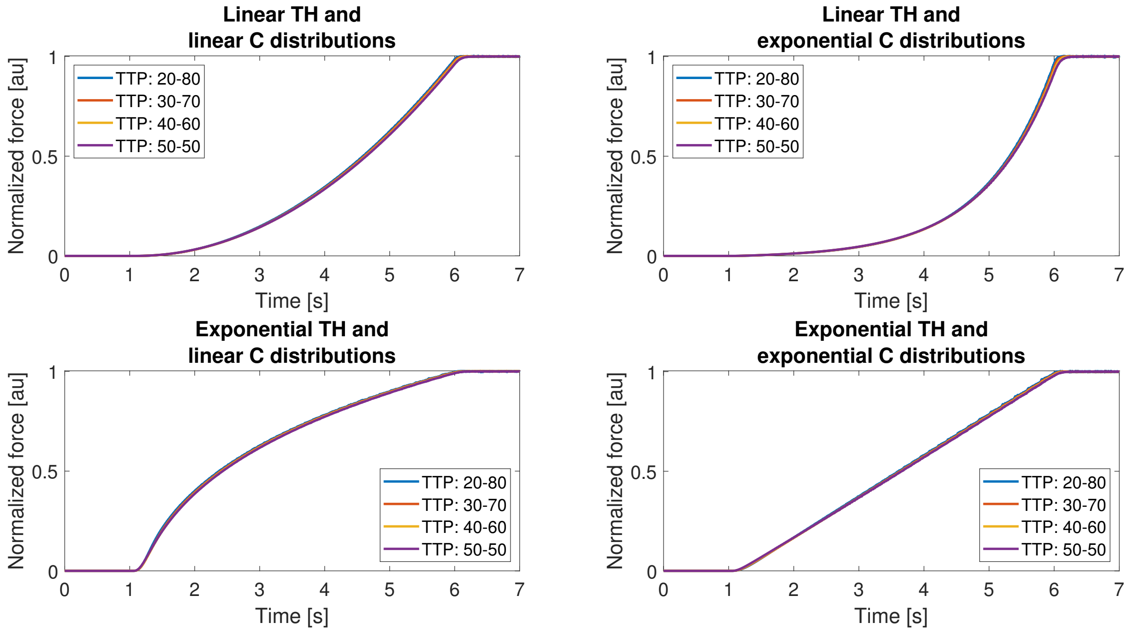

Figure A.5: Different twitch time to peak (TTP) ranges were tested for four combinations of the MU-threshold and MU-force distribution combinations (α and γ: both 0 and 4). The tested TTP ranges had little influence on the shape of the simulated excitation-force relation.