Biol. Cybern. 76, 11–22 (1997)

Biological
Cybernetics

Size principle and information theory

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Received: 26 January 1996 / Accepted in revised form: 17 September 1996

Abstract. The motor units of a skeletal muscle may be recruited according to different strategies. From all possible recruitment strategies nature selected the simplest one: in most actions of vertebrate skeletal muscles the recruitment of its motor units is by increasing size. This so-called size principle permits a high precision in muscle force generation since small muscle forces are produced exclusively by small motor units. Larger motor units are activated only if the total muscle force has already reached certain critical levels. We show that this recruitment by size is not only optimal in precision but also optimal in an information theoretical sense. We consider the motoneuron pool as an encoder generating a parallel binary code from a common input to that pool. The generated motoneuron code is sent down through the motoneuron axons to the muscle. We establish that an optimization of this motoneuron code with respect to its information content is equivalent to the recruitment of motor units by size. Moreover, maximal information content of the motoneuron code is equivalent to a minimal expected error in muscle force generation.

1 Introduction

1.1 Recruitment of motor units by size

A skeletal muscle together with the motoneurons controlling it consists of several hundred motor units of different sizes. A motor unit (MU) itself is defined as a motoneuron together with its innervated muscle fibers. In the human medial gastrocnemius muscle there are about 300 motor units with tetanic forces ranging from 0.63 to 203.5 g (Garnett et al. 1979). The force output of a muscle is determined by the sum of the force outputs of the active motor units. Due to the large number and different properties of these units, their recruitment must be specified in a suitable way. This task is automatically performed by the motoneuron pool in the spinal cord. The pool as a whole receives input from the central nervous system and from peripheral receptors which is distributed to its individual motoneurons (MNs). If the common input to the pool exceeds the threshold of a motoneuron, this motoneuron will fire action potentials and consequently activate the muscle fibers which it innervates (Fig. 1). For a more detailed model of the motoneuron pool including, for example, inhibitory Renshaw circuits, the reader is referred to Akazawa and Kato (1990) and the references therein. From physiological experiments one knows that with increasing input motoneurons are recruited in order of their size and hence their force-generating properties. This order of recruitment is known as the *size principle* (Henneman et al. 1965). Thus, smaller units producing less tension are recruited at a lower level of input into the pool, while larger units are recruited at progressively higher levels.

A large number of experimental studies have been devoted to the possible physiological mechanisms leading to the size principle [see Henneman and Mendell (1981), Lüscher and Clamann (1992) and the citations therein]. Here, we investigate the benefit of recruitment by size instead of its physiological explanation. We are interested in the internal logic by which the motoneuron pool is guided to the activation of motor units according to their sizes. Our questions are: What are the possible underlying optimization principles governing the recruitment of motor units? How can optimal precision in force generation and maximal information transfer be realized simultaneously?

1.2 Shannon's information transmission theorem and motor unit encoding

In an information transmission system a source message is processed by an encoder, fed through a channel and reconstructed by a decoder. A user at the end of the transmission system specifies a maximal distortion (error) which is permitted in the received message. Depending on this distortion bound, the source message is first compressed into a source code and the information not needed to satisfy the bound is discarded. The source code is then processed by the channel encoder which adapts it to the characteristics of the channel and adds some redundancy to protect against noise. After this second encoding step one obtains the channel code,

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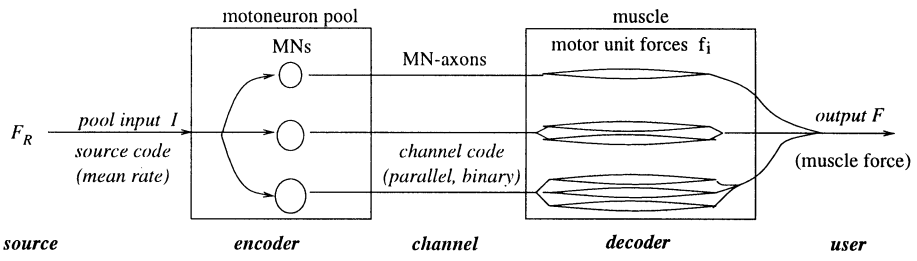

Fig. 1. The transmission system of muscle innervation. It consists of the motoneuron (MN) pool which encodes the firing rate of a central neural input I, the motoneuron axons which transmit the parallel binary code and the muscle which converts this code to a force F. The muscle fibers are innervated by α-motoneurons lying in a common motoneuron pool in the spinal cord. The figure shows three motor units each consisting of a motoneuron and the muscle fibers it innervates

which is transmitted through the channel and thereby probably contaminated by noise. The decoder performs the inverse operations, reconstructing the channel code, the source code and finally reproducing the original message up to the information lost by the source compression (see the diagram below). Within this framework Shannon's *information transmission theorem* tells us what maximal rate of information transmission (measured in bits per seconds or, alternatively, in bits per channel symbol) can be achieved. This rate depends on the channel capacity and on the distortion allowed at the end of the transmission system (Shannon and Weaver 1949; Blahut 1987).

In order to apply the information theoretical paradigm to the situation of muscle activation we have to make several choices. As a source message we assume a signal representing some reference force F_R, which may be generated by the motor cortex, for example, and which determines the muscle force to be produced. The reference force F_R is encoded in a mean firing rate representing the source code which is sent by an efferent fiber to the spinal cord where it is distributed to the motoneuron pool as an input I. The motoneuron pool acts as a second encoder, translating the source code into the channel code. By restricting ourselves to pure recruitment modulation in the absence of rate modulation we have only two states of the motoneuron i corresponding to its activation $x_i = 1$, or inactivation $x_i = 0$. With N motoneurons we obtain a parallel binary channel code in which each codeword is characterized by a motoneuron state $x \in \{0, 1\}^N$. We shall refer to this channel code as the *motoneuron code*. The motoneuron code is transmitted to the muscle through the motoneuron axons, which are assumed to represent a noiseless parallel channel. As long as consideration is restricted to a binary code with either zero or constant frequency for each motoneuron, the noise-free assumption is reasonable. The muscle decodes the received signal x by producing a muscle force F. We assume that the total muscle force is a linear superposition of the forces of the individual motor units. This muscle force at the end of the transmission system should correspond, within some limits, to the original reference force. The distortion of the original message (i.e., the deviation from the output characteristics) is small if F is close to F_R. The stages of the transmission system are summarized in the following diagram (cf. Fig. 1):

$$\begin{array}{ccccccccc}
\text{message} & & \text{source code} & & \text{channel code} & & \text{channel code} & & \text{system output}\\
\text{intended force} & & \text{pool input} & & \text{MN states} & & \text{MU states} & & \text{muscle force}\\
F_R & \longrightarrow & I & \longrightarrow & x & \Rrightarrow & x & \longrightarrow & F\\
\text{source} & \text{encoder I} & & \text{encoder II} & & \text{channel} & & \text{decoder} & \text{user}
\end{array}$$

To apply Shannon's statistical theory we introduce a probability distribution $p(F_R)$ of the reference force F_R which we assume to be monotonically decreasing. Thus, small muscle forces are assumed to be produced more frequently than larger ones. The distribution p induces a probability distribution of the motoneuron states x and this directly permits calculation of the information content of a word x of the motoneuron code. Since at this stage we are dealing with a parallel binary code, each codeword x requires the same transmission time and this allows us to measure the information transmission of the channel code in bits per codeword. Let us emphasize that Shannon's information transmission theorem was derived for the steady state, thereby ignoring dynamic changes of the encoder and decoder which may be prominent in our application to motor circuits.

The rate at which the relevant information is transmitted from the central nervous system to the muscle can be enhanced in both encoding steps. First, the source code may improve the rate by mapping the continuum of choices for F_R to a finite, well-chosen set of firing frequencies I. Second, the channel or motoneuron code may improve the rate by choosing codewords x with large information content. As we shall see, the compression of the source code will limit the number of possible combinations of active motor units and the combination finally selected is determined by the information maximization of the channel code.

Our work is organized as follows. In Sect. 2 we introduce the model of motor unit recruitment and formalize the classical point of view that the size principle generates precision for producing an optimal muscle force. In Sect. 3 we turn to information theory and show that the size principle follows from maximizing the information transmission. As in Sect. 2 we address the question of the optimal distribution of the motor unit forces. In Sect. 4 we combine these results and propose a learning rule to enhance muscle force precision based on the local information theoretical principle. In Sect. 5 we discuss and summarize our results and review other approaches. The proofs of the theorems are given in the Appendix.

2 Minimizing the expected error in muscle force generation

Recruitment by size may be seen as a strategy to solve the following combinatorial problem (Henneman 1990, p. viii): 'How can the different tensions that individual motor units develop be combined by activating appropriate motoneurons to produce any total force that is required with the necessary *precision* and (computational) *speed*?'

Concerning *speed*, the pool is restricted to a fixed recruitment order according to which the motor units are activated.

A predetermined order of recruitment provides economies in neural circuits and reduces the computing time needed to select an appropriate combination of active motor units. Concerning *precision,* such a predetermined order must be an ascending order to provide the desired high precision.

2.1 The model of motor unit recruitment

Upon receiving a common global input $I(F_R)$ represented as a firing rate (Mendell and Henneman 1971), the pool must assemble a total muscle force $F(I)$ as close as possible to the given reference force F_R. The input I is assumed to be a monotonic function of the reference force F_R. If F_R increases, I will increase as well and the pool must recruit a further motor unit as soon as the reference force F_R rises above $F(I)$. Which one of the motor units will be recruited next is fixed by the predetermined order of recruitment. Let N be the total number of motor units and let us enumerate them according to increasing 'size', i.e., according to increasing tetanic forces (which may all be assumed to be different from each other). We define a *recruitment order* π to be a permutation $\pi : \{1, \ldots, N\} \to \{1, \ldots, N\}$ of the N motor units onto themselves. *Recruitment by size* is defined by $\pi = \mathrm{Id}$, i.e., by the order according to the basic enumeration. The mechanism of recruitment assigns to the ith motor unit within the recruitment order π a threshold θ_i^π. Depending on π this threshold specifies at which level of global input I the unit $\pi(i)$ must be activated in order to produce the intended muscle force. Let us write the force of motor unit $\pi(i)$ in the form $f_{\pi(i)}(I - \theta_i^\pi)$. Defining the supra-threshold input $\tilde{I} = I - \theta_i^\pi$, one has $f_{\pi(i)}(\tilde{I}) = 0$ for $\tilde{I} < 0$ and $f_{\pi(i)}(\tilde{I}) > 0$ for $\tilde{I} > 0$. Moreover, $f_{\pi(i)}(\tilde{I})$ is monotonically increasing in $\tilde{I}$. In the model of Heckman and Binder [see (2) below] the input-force relation $f_{\pi(i)}(\tilde{I})$ is even strictly increasing for the suprathreshold input $\tilde{I} > 0$. The (total) *muscle force* depends on the recruitment order π and is defined as a superposition of the individual motor unit forces according to

$$F(I) \equiv F^\pi(I) = \sum_{i=1}^{N} f_{\pi(i)}(I - \theta_i^\pi) \tag{1}$$

2.2 Example. The motor units of the cat medial gastrocnemius

To give an example, we have chosen the input-force relation according to Heckman and Binder (1991):

$$f_i(\tilde{I}) = F_{max,i} \cdot (1 - e^{-(freq_i(\tilde{I})/T_i)^{P_i}})$$
$$\text{for } \tilde{I} \geq 0 \; , \quad i = 1, \ldots, N \tag{2}$$

The function $freq_i(\tilde{I}) = freq_{thres,i} + G \cdot \tilde{I}$ represents the firing frequency of motoneuron i at relative input $\tilde{I} = I - \theta_i^{Id}$. The firing frequency is zero below θ_i^{Id}, jumps at this point to some threshold-frequency $freq_{thres,i}$ and then increases at a rate given by the gain G. The positive constants T_i and P_i are additional parameters. Using the same data as Heckman and Binder (1991, Table 2) for their 21 motor units [$freq_{thres,i} \in (8, 17.5)$, $G = 2.25$, $T_i \in (20, 56.5)$ and $P_i \in (2.1, 2.6)$], we calculated the actual muscle forces $F^\pi(I)$ when a reference force F_R is given. Note that the correspondence $F_R \to I$ may be inverted due to its monotonicity. This allows us to compare the two functions $F^\pi(I)$ and $F_R(I)$ (Fig. 2). The recruitment order π was chosen once to be recruitment by size ($\pi = \mathrm{Id}$) and once to be the reverse of that order. It should be stressed that for these data the contributions of the motor units merge into a nearly smooth curve $F^\pi(I)$ if the reference force F_R is a suitable sigmoidal function with a larger slope adapted to the slopes of the motor unit forces $f_i(I)$.

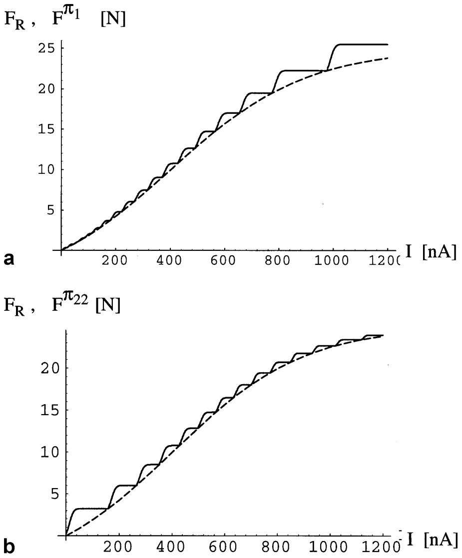

Fig. 2a,b. The total muscle force $F^\pi(I)$ (*continuous line*) approximating the smooth reference force $F_R(I)$ (*dashed line*). Whenever the reference force rises above the muscle force actually exerted, an additional motor unit is recruited. For the data in Heckman and Binder (1991) several of the 21 motor units are recruited at nearly the same time. **a** Recruitment by size according to the order $\pi_1 = \mathrm{Id}$ in Fig. 3. This recruitment order minimizes the deviation from the reference force. **b** Recruitment according to the reverse order π_{22}

Given a recruitment order π, the (relative) *error* $\mathscr{E}^\pi(F_R)$ is defined by the relative difference between the muscle force output F^π and the corresponding reference force F_R:

$$\mathscr{E}^\pi(F_R) \doteq \frac{|F^\pi(I(F_R)) - F_R|}{F_R} \tag{3}$$

Next we introduce the probability density $p(F_R)$ describing the relative frequency with which the reference force F_R must be encoded. This allows us to quantify the average error in muscle force production according to

$$\langle \mathscr{E}^\pi \rangle = \int_{F_{min}}^{F_{max}} \mathscr{E}^\pi(F_R) \cdot p(F_R) \, dF_R \tag{4}$$

To illustrate the dependence of the expected error $\langle \mathscr{E}^\pi \rangle$ on the recruitment order π we chose a sequence of permutations $\pi_1 \ldots \pi_{22}$ leading from the ascending to the descending order. For each of these permutations we calculated the expected error $\langle \mathscr{E}^\pi \rangle$ with respect to the constant probability density $p(F_R) = $ const. As Fig. 3 reveals, the minimal expected error is achieved for recruitment by increasing size.

π_1=(1, 2, 3, 4, 5, 6, 7, …, 20, 21)
π_2=(2, 1, 4, 3, 6, 5, 8, …, 19, 21)
π_3=(2, 4, 1, 6, 3, 8, 5, …, 21, 19)
π_4=(4, 2, 6, 1, 8, 3, 10, …, 17, 19)
π_5=(4, 6, 2, 8, 1, 10, 3, …, 19, 17)
⋮
π_{20}=(20, 18, 21, 16, 19, 14, …, 1, 3)
π_{21}=(20, 21, 18, 19, 16, 17, …, 3, 1)
π_{22}=(21, 20, 19, 18, 17, 16, …, 2, 1)

a

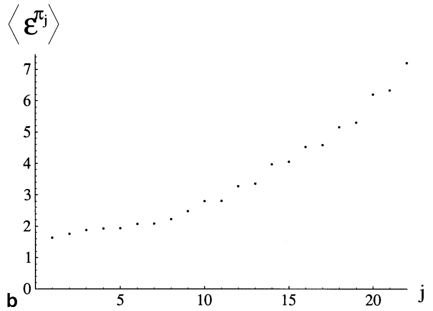

Fig. 3. **a** A sequence of permutations leading from order by (increasing) size to the reverse. **b** The expected errors $\langle \mathscr{E}^{\pi_j} \rangle$ for the corresponding sequence of recruitment orders π_j. $\langle \mathscr{E}^{\pi_j} \rangle$ was calculated according to *(4)* with a uniform distribution of the reference forces F_R. Since, according to the table, larger motor units are recruited successively earlier, $\langle \mathscr{E}^{\pi_j} \rangle$ increases with index j (cf. Fig. 2)

2.3 Error-optimal recruitment of motor units

To prove that recruitment by size is optimal in precision we restrict ourselves to the case of pure recruitment modulation and assume that the motor unit forces $f_i(\tilde{I})$, $\tilde{I} = I - \theta_i^{Id}$, are step functions of the form

$$f_i(\tilde{I}) = \begin{cases} 0 & ; \quad \tilde{I} < 0 \\ f_i = \text{const} & ; \quad \tilde{I} \geq 0 \,, \quad i = 1, \ldots, N \end{cases} \tag{5}$$

Pure recruitment modulation takes place at the beginning of the activation of certain finger muscles where motor units are first recruited and discharge at nearly constant frequencies. Rate modulation in these movements only occurs later, at higher force levels (Milner-Brown et al. 1973).

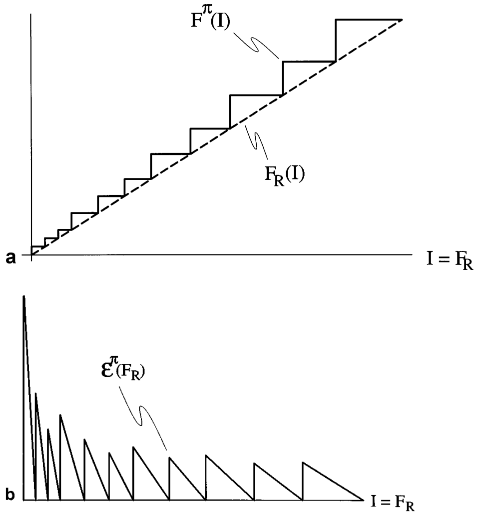

Fig. 4. **a** The total muscle force $F^\pi(I)$ (*continuous line*) and the reference force $F_R(I) \equiv I$ (*dashed line*) for motor unit forces as defined in *(5)*. The recruitment order π is recruitment by size, i.e., π = Id and thus $f_{\pi(1)} \leq \ldots \leq f_{\pi(N)}$. As soon as the reference force $F_R(I)$ reaches the actual muscle force $F^\pi(I)$ the next motor unit is recruited ('next' according to the recruitment order π). Alternately one could postulate a more symmetrical scenario where the next motor unit is activated as soon as the difference $|F^\pi(I) - F_R(I)|$ reached half the tetanic force of that next motor unit. Although in such a scenario the average error would be smaller, our qualitative statements would not change. Notice that there are intermediate parts of the output characteristics that may not be reached by any coding. **b** The error function $\mathscr{E}^\pi(F_R \equiv I)$ [cf. (6) corresponding to the force production $F^\pi(I)$ in **a**. Note that deviations from the output characteristics at large muscle forces contribute less to the (relative) error $\mathscr{E}^\pi$

Let us assume that the relation between input I and intended muscle force F_R is linear, say $I = F_R$. A linear relationship between supraspinal motor commands and muscle force production has indeed been confirmed experimentally. Ruegg and Bongioanni (1989) demonstrated such a linearity for the human soleus and tibialis anterior. Moreover, we assume that some minimal tone or 'background' force $f_0 > 0$ is always present. According to our model of recruitment, the kth motor unit within π is activated at that moment when the increasing reference force F_R becomes just larger than the sum of the motor unit forces actually produced, i.e., just beyond the point at which the equality $F_R = \sum_{i=0}^{k-1} f_{\pi(i)}$ holds. Due to the identity $I = F_R$, the force $\sum_{i=0}^{k-1} f_{\pi(i)}$ corresponds to the input threshold θ_k^π of the kth motor unit within the recruitment order π. Since after recruiting this kth unit the actual force becomes $F^\pi(I) = \theta_k^\pi + f_k = \theta_{k+1}^\pi$, the error $\mathscr{E}^\pi$ (3) becomes

$$\mathscr{E}^\pi(F_R) = \frac{\theta_{k+1}^\pi - F_R}{F_R} \tag{6}$$

where $k+1$ is the smallest index such that the force $\theta_{k+1}^\pi = F^\pi(I(F_R))$ is greater than or equal to the reference force F_R. The functions F^π, F_R and $\mathscr{E}^\pi$ are illustrated in Fig. 4 for π = Id.

Setting $F_{max} = \sum_{i=0}^{N} f_i$, the reference force F_R is assumed to vary within the range $[f_0, F_{max}]$ and (4) transforms to

$$\langle \mathscr{E}^\pi \rangle = \int_{f_0}^{F_{max}} \mathscr{E}_\pi(F_R) \cdot p(F_R)\, dF_R \tag{7}$$

Definition 1 (Error-optimality). *A recruitment order π is* optimal *in precision (short: error-optimal) if the expected error $\langle \mathscr{E}^\pi \rangle$ is minimal with respect to all possible recruitment orders π. More formally, π is error-optimal if $\langle \mathscr{E}^\pi \rangle \leq \langle \mathscr{E}^{\tilde{\pi}} \rangle$ for any recruitment order $\tilde{\pi} : \{1, \ldots, N\} \to \{1, \ldots, N\}$.*

For the case of pure recruitment modulation with step functions (5) as motor unit forces we now have:

Theorem 2.1 (Size principle from error optimization). *Let $p(F_R)$ be any monotonically decreasing probability density on the reference forces F_R. Then, recruitment by size is the only recruitment order which is error-optimal. In other words: the order of recruitment π is error-optimal if and only if $f_{\pi(1)} \leq f_{\pi(2)} \leq \cdots \leq f_{\pi(N)}$.*

To give an idea of the proof, note that $\mathscr{E}^\pi(F_R)$ is a saw-tooth map as depicted in Fig. 4b. Since the 'weighting function'

$p(F_R)$ of these teeth monotonically decreases, the teeth must be arranged in an ascending order to minimize the integral (7). For more detailed arguments see the Appendix.

2.4 Error-optimal motor unit density

From physiological experiments one also knows not only that the forces of activated motor units increase with increasing input, but also that they increase progressively, i.e., the differences $f_i - f_{i-1}$ increase with i. This is reflected in the distribution of the motor unit forces: for a skeletal muscle, the number of motor units $n(f)$ with tetanic force f within some fixed interval $\triangle f$ typically decreases. Figure 5a shows this function $n(f)$ for the human medial gastrocnemius (Garnett et al. 1979). The tetanic forces are chosen to be the discrete values $f = 4, 8, 12, 16, \ldots, 40$ and $n(f)$ is the number of motor units lying in an interval of length $4\,g$ around these values. To test our model we ask the same question within our mathematical framework: Given the total number N of motor units, a 'background' force f_0 and some total force F_{max}, what is the optimal distribution of the motor unit forces $f_1 \leq f_2 \leq \ldots \leq f_N$ under the constraint that their sum $\sum_{i=0}^{N} f_i$ is equal to F_{max} ?

In order to treat this question analytically we define the notion of motor unit density $d(f)$ in our present discrete case. Intuitively, the density $d(f_i)$ of motor units with tetanic force f_i should be proportional to the number $n(f_i)$ of motor unit forces lying within the interval (f_{i-1}, f_i) and inversely proportional to the length of this interval itself. Since in our case there is only one motor unit lying within this interval, $n(f_i) = 1$, we have the following definition:

Definition 2 (Motor unit density). *Consider a pool with a finite number of motor units of tetanic forces* $(f_0 <) f_1 < \ldots < f_N$. *The density* $d(f)$ *of the motor units is defined at the points* f_i *as* $d(f_i) \doteq 1/(f_i - f_{i-1})$, $i = 1, \ldots, N$.

In the reminder of this section we investigate the relation between the probability $p(F_R)$ of the reference forces F_R and the *optimal motor unit density* $d(f)$, i.e., the density leading to a minimal expected error $\langle \mathscr{E}^{\pi} \rangle$. We first establish that a decreasing probability density $p(F_R)$ leads to a decreasing optimal density $d(f)$ of motor units. Consider the family of probability densities $p_\alpha(F_R) \propto 1/(F_R)^\alpha$ with real numbers α and let $d_\alpha(f)$ be the corresponding optimal motor unit density. This optimal motor unit density is found by adjusting the f_i values in order to minimize the expected error $\langle \mathscr{E}^{Id} \rangle$. Since, by Theorem 2.1, $\langle \mathscr{E}^{\pi} \rangle$ can only be minimal for recruitment by size, we assume $\pi =$ Id. Numerical simulations show that $d_\alpha(f)$ only decreases if $\alpha \geq 0$. If $-1 < \alpha < 0$, i.e., if the probability density of the reference forces increases slightly, the optimal density $d_\alpha(f)$ has a minimum in the middle range of the motor unit forces f (Fig. 5). For $\alpha < -1$ corresponding to a superlinear increase of the reference force density, the optimal motor unit density $d_\alpha(f)$ is monotonically increasing. It appears that the probability density $p(F_R) = \text{const}$, corresponding to measuring the relative error $|F - F_R|/F_R$, is the limiting probability density which just guarantees a decreasing density function $d(f)$ of the motor unit forces. Knowing that the measured motor unit density is indeed decreasing we can conclude that nature needs an average precision for large forces F which is smaller than $1/F$.

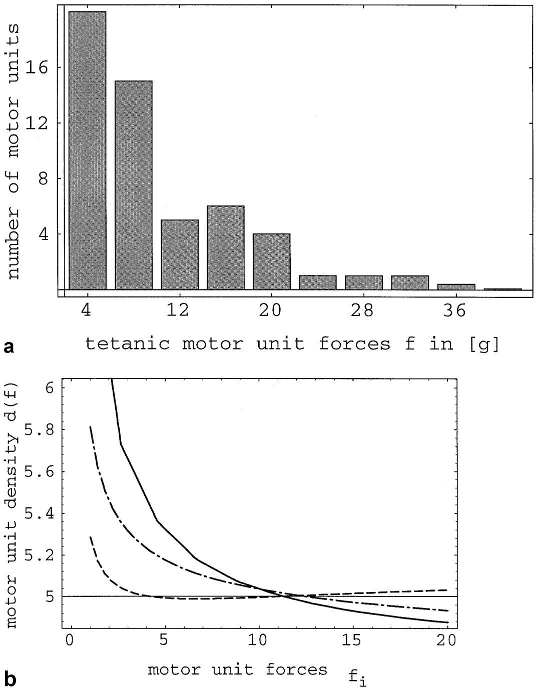

Fig. 5. **a** The distribution of motor units characterized by their tetanic force f in the human medial gastrocnemius (Garnett et al. 1979). **b** Optimal densities $d_\alpha(f)$ of the motor units for the probability densities $p_\alpha(F_R) \propto 1/(F_R)^\alpha$ with $\alpha = -0.01$ (*dashed line*), $\alpha = 0$ (*continuous line*) and $\alpha = 1$ (*dot-dashed line*). If $\alpha = -1$, the density would be constant (= 5). All densities are normalized to yield a total force $F_{max} = \int f d_\alpha(f)\, df = 100$ within the interval $f \in [1, 20]$. For the 'background' force we chose $f_0 = 1$

Let us consider in more detail the case $\alpha = 1$ in which an analytical solution to the optimization problem can be given.

Theorem 2.2 (Error-optimal motor unit density). *Let* N *be the number of motor units,* $f_0 > 0$ *a non-vanishing 'background' force and* $F_{max} = \sum_{i=0}^{N} f_i$ *the sum of the unknown motor unit forces. Let us assume a probability density* $p(F_R) \propto 1/F_R$. *Then, the forces* f_i *minimizing the expected error* $\langle \mathscr{E}^{Id} \rangle$ *in (7) increase exponentially according to* $f_i = (c-1) f_0 c^{i-1}$, $i = 1, \ldots, N$, *with some appropriate constant* $c > 1$. *The optimal motor unit density is given by* $d(f) = \frac{c}{c-1} \cdot \frac{1}{f}$.

For the proof we refer to the Appendix. We can readily show that $c = \sqrt[N]{(F_{max}/f_0)}$.

According to the theorem and its assumptions, the density of motor units $d(f) \propto 1/f$ is optimal in precision if one assumes an appropriately decreasing probability distribution for the reference forces. We are not the first to deduce such a motor unit density: Tax and coworkers (Tax and van der Gon 1991) derived the same motor unit density from their model, which – like ours – requires a linear input-force relationship.

3 Maximizing the rate of information transmission

3.1 Compressing the source code

According to Shannon, the rate of information transmission can be improved by compressing the source code and/or by enhancing the information content of the channel code. We first show that the source code may be compressed essentially to the number of motor units by reducing the number of source codewords. This permits a shorter sampling time to identify a source codeword, which is given by the mean rate of the global input I. A shorter sampling time makes it possible to increase the rate of information transmission to the pool.

Let us assume that an input fiber must encode reference forces F_R within some fixed range of firing frequencies. A receiver (in our case the motoneuron pool) has to estimate (e.g., implicitly by a leaky integrator) the time between two successive spikes. If we assume that these spike intervals characterizing a frequency are slightly perturbed it has to measure k spike intervals in order to reduce the error of the frequency estimate to the order $O(1/\sqrt{k})$ (this follows from the Chebyshev inequality applied to the arithmetic mean of the spike intervals). Assuming a bounded domain of possible firing frequencies this implies that the receiver cannot distinguish reliably more than $O(\sqrt{k})$ different frequency inputs.

Now, assuming a binary channel code formed by N motoneurons, the pool has at its disposal a maximum of 2^N different states and thus can resolve not more than the same amount of different source codewords. To identify reliably one out of 2^N [$= O(\sqrt{k_0})$] different firing frequencies as its input, the pool must wait and integrate on the order of $k_0 = 2^{2N}$ spike intervals. Indeed, with 2^{2N} measurements, the receiver can reduce the error of the frequency estimate to the necessary resolution of $1/2^N$.

However, as the experiments of Henneman showed, the pool does not exploit all possible combinations of motor units and thus cannot resolve 2^N different inputs by pure recruitment modulation (Henneman et al. 1965, 1974). Instead, the activation of the motor units follows a well-defined recruitment order leading to only $N+1$ different states, namely $(0,\ldots,0)$, $(1,0,\ldots,0)$, $(1,1,0,\ldots,0)$, $\ldots$, $(1,\ldots,1)$. Each of these states represents a channel codeword and specifies up to which cell within the recruitment order the motoneurons are activated. This motoneuron code again requires a source code of $N+1$ words which are expressed by different input frequencies. But to resolve $N+1$ frequencies the pool must wait and integrate $k_1 = (N+1)^2$ spike intervals in order to reduce the expected error to $1/(N+1)$. This leads to a compression factor of

$$\frac{k_1}{k_0} \;\leq\; \frac{(N+1)^2}{2^{2N}} \;\leq\; e^{-\frac{N}{3}} \qquad (N \geq 3)$$

compared with a source code with 2^N codewords. The restriction to a fixed recruitment order enhances the rate of codeword transmission to the pool. On the other hand, the compression of the source code leads to a loss in muscle force precision. This, however, seems to lie within the tolerance defined by the user at the end of the communication system.

3.2 Maximizing the information content of the motoneuron code

By exploiting the maximal information content offered by a motoneuron code restricted to $N+1$ words, the rate of information transmission could again be improved. Let X_k denote the random variable which takes the value 1 if motor unit k is active and 0 otherwise. By p_k^π we denote the probability that the kth motor unit within the recruitment order π is activated at a random reference force F_R. Since we assume that $F_R = I$ this is just the probability that F_R is larger than the threshold θ_k^π of the kth unit within π and we have

$$p_k^\pi \doteq \mathscr{P}(X_k = 1) = \int_{\theta_k^\pi}^{F_{max}} p(F_R)\, dF_R \ , \quad k = 1, \ldots, N \ .$$

The recruitment probabilities p_k^π induce the joint probability p_Ω^π on the space $\Omega = \{0,1\}^N$ encoding the states of the N motor units. The *motoneuron code* corresponding to the recruitment order π consists of the subset of codewords $x = (x_1, \ldots, x_N) \in \Omega$ with $p_\Omega^\pi(x) > 0$. We now define the *information content* of the motoneuron code to be the Shannon entropy H_{MN}^π of the probability distribution on the motoneuron states:

$$H_{MN}^\pi \doteq H(X_1, \ldots, X_N) = -\sum_{x \in \Omega} p_\Omega^\pi(x) \log_2 p_\Omega^\pi(x) \ . \qquad (8)$$

One may interpret H_{MN}^π as the *average information per state* $x = (x_1, \ldots, x_N)$ of the pool. Recall that $J(x) \doteq -\log_2 p_\Omega^\pi(x)$ is the information in bits provided by the observation that the pool is in the particular state x. On the average, the information provided by such an observation is $\sum_{x \in \Omega} p_\Omega^\pi(x) J(x)$ and this is equal to H_{MN}^π.

Fixing the tetanic forces f_i of the individual motor units, we establish that among all recruitment orders, recruitment by size provides the maximal Shannon information of the motoneuron code:

Theorem 3.1 (Size principle from information optimization). *Let the probability density $p(F_R)$ of the reference forces F_R be strictly decreasing. Then, the information content H_{MN}^π of the motoneuron code corresponding to the recruitment order π is maximal if and only if π = Id, i.e., if π is recruitment by size.*

3.3 Information-optimal motor unit density

As in the previous approach, one may ask not only for the optimal order, but for the optimal *distribution* of the f_i values. To do so, we now fix the order of recruitment π = Id and let the motor unit forces f_i adapt (and with them the thresholds $\theta_i = \sum_{j=i}^{i-1} f_j$.) To simplify the notation we drop the supscript π = Id for the rest of the paper. In Theorem 2.2 we have seen that the probability density $p(F_R) \propto 1/F_R$ yields a minimal expected error if the density $d(f)$ of motor units is proportional to $1/f$. In this information theoretical approach we confirm that the density $d(f) \propto 1/f$ is optimal, now in the sense of the maximal information content of the motoneuron code.

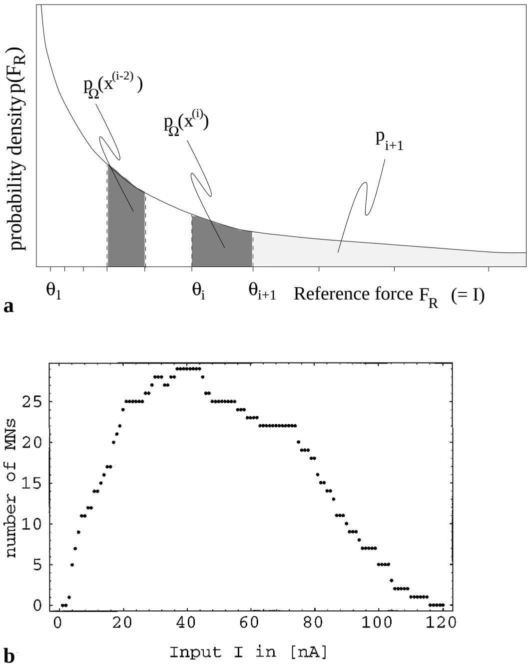

Fig. 6. **a** For an information-optimal motor unit distribution the motoneuron states $x^{(i)}$ must be equally probable. The two *dark grey* regions must therefore have equal area. Put differently, the probability density $p(F_R)$ of the reference forces F_R leads to a maximal information content H_{MN} if $p(\theta_i) \approx const/f_i = const/(\theta_{i+1} - \theta_i)$ (cf. Lemma 3.1). **b** Considering motor units with rate modulation, the optimal probability density $p(F_R)$ has its maximum where most units are sensitive to changes in F_R or, more precisely in $I(F_R)$. For each input I we counted the number of motoneurons (MNS) in Table 1 of Graham and Redman (1993) having a strictly positive slope (≥ 1.5 *Hz/nA*) in the input-frequency relation $f_i(I)$ and plotted this number against I. Assuming a linear relation between the pool input I and the reference force F_R, the shape of the distribution qualitatively yields the optimal density $p(F_R)$ for which the pool extracts the maximum of information from the rate modulated input

Theorem 3.3 (Information-optimal motor unit density). *Consider a finite number N of motor units, some 'background' force f_0 and a sum F_{max} of the unknown motor unit forces f_i. The density $d(f) \propto 1/f$ of motor unit forces is optimal from an information theoretical point of view (i.e., leads to a maximal information content H_{MN} of the motoneuron code) if and only if the probability density $p(F_R)$ of reference forces itself is proportional to $1/F_R$. The optimal motor unit forces f_i are the same as in Theorem* 2.2.

The following lemma will be used in the proof of the preceding two theorems. It gives a condition under which the upper bound of $\log_2(N+1)$ bits is achieved by a motoneuron code restricted to $N+1$ words.

Lemma 3.1 (Maximal information content criterion). *Let N be a fixed number of motor units satisfying* (5) *and let the reference forces F_R vary randomly according to the distribution $p(F_R)$ within some interval $[F_{min} \equiv f_0, F_{max}]$. Then, the maximal information content $H_{MN} = \log_2(N+1)$ is reached for tetanic forces f_i satisfying*

$$p_\Omega(x^{(i)}) = \int_{\theta_i}^{\theta_i+f_i} p(F_R)\,dF_R$$

$$= constant\ \left(= \frac{1}{N+1}\right), \quad i = 0, 1, \ldots, N \qquad (9)$$

where $\theta_i = \sum_{j=0}^{i-1} f_j$. This 'equilibrium condition' holds approximately if $f_i \cdot p(\theta_i) \approx const.$ In particular, if the probability density p is monotonically decreasing, it follows that $f_1 \leq \ldots \leq f_N$.

Proof of the lemma. Denoting the possible states of the pool by $x^{(i)} = (1, \ldots, 1, 0, \ldots, 0)$ where i denotes the number of 1's, the information content H_{MN} reduces to

$$H_{MN} = H(X_1, \ldots, X_N)$$

$$= -\sum_{i=0}^{N} p_\Omega(x^{(i)}) \log_2 p_\Omega(x^{(i)}) \qquad (10)$$

This last expression is maximal [namely $\log_2(N+1)$] if and only if all the $p_\Omega(x^{(i)})$ are equal, i.e., if $p_\Omega(x^{(i)}) = 1/(N+1)$ for every i. Since the probability $p_\Omega(x^{(i)})$ of state $x^{(i)}$ may be written as the probability that the ith motor unit is activated minus the probability that the $(i+1)$th is activated, we get (cf. Fig. 6a)

$$p_\Omega(x^{(i)}) = p_i - p_{i+1} = \int_{\theta_i}^{\theta_{i+1}} p(F_R)\,dF_R$$

$$= \int_{\theta_i}^{\theta_i+f_i} p(F_R)\,dF_R\ , \quad i = 1, \ldots, N \qquad (11)$$

We set $\theta_1 = F_{min}$, $p_{N+1} = 0$ and $\theta_{N+1} = F_{max}$. To achieve the optimal values $p_\Omega(x^{(i)}) = 1/(N+1)$, we first tune f_1 so that this equality holds for $i = 1$ and get the threshold θ_2. Proceeding in the same way for $i = 2, 3, \ldots, N$ we determine iteratively the values of f_i. Moreover, since $\theta_i < \theta_{i+1}$ and since $p(F_R)$ monotonically decreases, the equalities (9) may only hold simultaneously for every i if $f_i \leq f_{i+1}$. $\square$

The lemma states the following: To obtain the motoneuron code with maximal information content, the probability that the reference force F_R falls into a bin $[\theta_i, \theta_i + f_i]$ must be equal for all $i = 0, 1, \ldots, N$. Conversely, given motor unit forces $f_1 \leq \ldots \leq f_N$ and corresponding thresholds $\theta_i = \sum_{j=0}^{i-1} f_j$, the pool best extracts information from an input $I(F_R)$ if the probability density $p(F_R)$ roughly satisfies $p(\theta_i) \approx const/f_i = const/(\theta_{i+1} - \theta_i)$. Thus, the information extraction from the continuous input signal I is maximal if the input probability density $p(I)$ is inversely proportional to the threshold differences or, in other words, directly proportional to the density of bins $[\theta_i, \theta_i + f_i]$ (cf. Fig. 6a).

The adaptation of the thresholds to the particular form of the reference force distribution is intuitively clear: In regions where the density $p(F_R)$ is large, the 'sample points' θ_i must move closer together in order to distribute the 'weight' $p(F_R)$ uniformly on the 'pillars' at θ_i, $i = 1 \ldots N$. This corresponds to the unfolding of a Kohonen map over some input space which has its highest resolution at regions of highest input density.

3.4 Generalization to motoneurons modulating their firing frequencies

Finally, we remark that the approach of maximizing information transmission can be extended to motor units with rate modulation. For simplicity we again assume a linear relationship between the pool input and the intended muscle force, $I = F_R$. If every motor unit i ($i = 1, \ldots, N$) can produce S different forces f_{ij} ($j = 1, \ldots, S$), the information content H_{MN} maximally reaches $\log_2 (N+1)S$, always assuming that a fixed order of recruitment pertains. The states of the neurons induce bins $[\theta_i + f_{ij}, \theta_i + f_{i,j+1}]$ on the input axes which are able to 'detect' inputs I with a granularity corresponding to the intersection of all these partially overlapping, bins. The upper bound $\approx \log_2 (N+1)S$ is attained for a probability density $p(F_R)$ which is proportional to the density of the intervals $[\theta_i + f_{ij}, \theta_i + f_{i,j+1}]$, now interpreted as bins on the F_R axes. The reason is the same as in Lemma 3.1: the maximal information content of the motoneuron code is reached if all $(N+1)S$ states of the pool have equal probability. This is only possible if a unit interval on the F_R axes with frequently used reference forces, i.e., large $p(F_R)$, induces a larger number of motoneuron states than a unit interval on the F_R axes with rarely used reference forces. The distribution in Fig. 6b shows the number of motor units in Table 1 of Graham and Redman (1993) which have a strictly increasing input-frequency relation at the point I (in the work cited the input-frequency relation has slope either 0, 1.5 or ∞). We conclude that the pool with the characteristics of Fig. 6b optimally extracts information from its input I if the density $p(F_R)$ has the same graph as in the figure. In terms of error optimization we find that the muscle achieves its maximal relative precision at an intermediate range of input corresponding to an intermediate range of force.

4 Combination of the error-minimizing and the information-maximizing approach

4.1 Equivalence of the two approaches

From Theorem 2.1 and Theorem 3.1 one directly concludes that the approach of error minimizing in muscle force generation is equivalent to the approach of information maximizing of the motoneuron code if only the order of recruitment is considered:

Corollary 4.1 (Equivalence of error minimizing and information maximizing). *Let $p(F_R)$ be any strictly decreasing probability density on the reference forces F_R and let us assume that the input I to the pool is proportional to F_R. Then, a recruitment order is optimal in precision if and only if it provides the maximal information content of the motoneuron code.*

Specifying the probability density $p(F_R)$ to be inversely proportional to F_R, the equivalence even extends to the optimal distribution of motor unit forces f_i. From Theorem 2.2 and Theorem 3.2 one deduces:

Corollary 4.2 (Equal motor unit distributions). *Assume $p(F_R) \propto 1/F_R$ and $I \propto F_R$. Then the optimal density $d(f)$ of motor unit forces f_i is the same in the sense of minimizing the expected error $\langle \mathcal{E} \rangle$ and in the sense of maximizing the information content H_{MN} of the motoneuron code.*

The common optimal density $d(f)$ is depicted in Fig. 5b by the dot-dashed curve.

4.2 A learning rule maximizing the information content of the motoneuron code

How could the optimal precision in muscle force generation be learned? The straightforward answer is that the relative error $\mathcal{E}$ between generated muscle force F and reference force F_R could be fed back to the motoneuron pool by certain receptors. However, the equivalence between the two approaches suggests a new learning rule. Instead of looking to the muscle one may concentrate on the motoneuron pool itself and try to enhance the information content of the motoneuron code by directly adapting the motoneuron thresholds θ_i. Let us write the time dependence of the thresholds by θ_i^t. The method of steepest ascent to maximize the information content H_{MN} leads to a *learning rule* of the form

$$\theta_i^{t+1} = \theta_i^t + \triangle\theta_i^t \ , \ \text{with} \ \ \triangle\theta_i^t = \eta \frac{\partial H_{MN}}{\partial \theta_i^t}$$

where $\eta > 0$ is some learning rate. Using (10) and (11), the adaption of the thresholds at each time step t may be calculated as

$$\begin{aligned}\triangle\theta_i &= \eta \frac{\partial H_{MN}}{\partial \theta_i} \\ &= \eta \cdot p(\theta_i) \cdot \left(\log_2 p_\Omega(x^{(i)}) - \log_2 p_\Omega(x^{(i-1)})\right)\end{aligned} \qquad (12)$$

where $p(\theta_i)$ is the reference force probability density at the level of the ith threshold. The value of $p_\Omega(x^{(i)})$ is given by (11) and represents the probability that the motoneurons are in state $x^{(i)} = (1, 1, .., 1, 0, .., 0)$ with i 1's at the beginning. Since according to (12) stationary thresholds θ_i are reached if $p_\Omega(x^{(i)}) = p_\Omega(x^{(i-1)})$, one recovers Lemma 3.1 stating that the maximal information content is achieved if the states of the motoneurons are uniformly distributed. Again, this last condition is satisfied if the 'sensitivity' of the cell group at the input $I(F_R)$ is proportional to the probability density $p(F_R)$ (cf. Fig. 6). Kohonen's learning algorithm produces exactly the same final thresholds θ_i when it unfolds the θ_i's in order to get a one-dimensional topological map of a large number of input samples $I(F_R)$ (cf. end of Sect. 3.3). According to this information theoretical learning rule, the size principle eventually develops and the highest possible precision in muscle force generation is guaranteed according to Corollaries 4.1 and 4.2. Let us again emphasize that such conclusions rely on our model of recruitment which connects the motor unit forces to the motoneuron thresholds and on the hypothesis that smaller muscle forces are more frequently used than large ones.

5 Discussion

5.1 The exceptional case of reversed recruitment order

How can we explain exceptional cases of muscle activation with recruitment other than in order of size? For most movements, the smoothness of muscle force production or the deviation from linear output characteristics is a reasonable measure of optimization. However, there are situations in which the objectives of the movement are not smoothness or linearity of the input-output relation, and which therefore require other optimization criteria. Examples of such tasks are the escape reflex of a fish or the paw shake of a cat to shed an object stuck to its paw.

In order to apply Shannon's steady-state theory to these altered information transmission systems one must redefine the distortion function and the probability density $p(F_R)$ of the reference forces. A more appropriate measure of distortion would then be the acceleration of muscle force generation rather than the smoothness of the muscle force itself. With respect to this new kind of distortion, the restriction to a binary motoneuron code of $N + 1$ words of a fixed recruitment order is too severe because it does not allow the activation of just one selected motor unit population. The motoneuron code must therefore be enlarged by additional words such as $(0, \ldots, 0, 1, 1)$ describing the activation of only the second-largest and largest motor unit. We argue that such a combination of motor units would need additional projections into the pool since it cannot be generated by tuning the common global input alone. In the case of teleost fish one finds that the Mauthner cell located in the brainstem projects its axon to the contralateral side of the spinal cord and there makes contact with the large and fast motoneurons along the entire length of the spinal cord. During the startle response these large motoneurons are activated at very short latencies (Yasargil and Diamond 1968). In the case of the rapid paw shake of a cat the movement frequency corresponds to the twitch contraction frequency of the larger and faster motor units in the pool (Smith et al. 1980). This indicates that strict recruitment by size is circumvented and larger motor units may well be activated without activating the smaller ones.

In order to recruit the larger motor units exclusively the source code must be extended by additional words as well. However, an extended source code requires a longer transmission time if the words are still encoded by mean frequencies and transmitted through one single input fiber. Since the transmission time is crucial in the case of the escape reflex, nature solved this dilemma by providing an additional parallel input fiber. An important event (which corresponds to a high probability of occurrence in Shannon's setting) is passed to the motoneuron pool by the Mauthner axon and thus allows for a shorter codeword length. It should be noted that the rate of information transmission from the sensory neuron to the Mauthner cell itself is also enhanced by the use of fast electrical synapses.

The situation of variable codeword lengths is reminiscent of Huffman codes in technical applications. For such codes the length l of a codeword is inversely related to its probability p of occurrence (roughly $l \propto \log 1/p$; see Blahut 1987).

5.2 Relation to other theoretical works

In different studies, models of the motoneuron pool have been proposed with different aims (Mendell and Henneman 1971; Akazawa and Ktao 1990; Heckman and Binder 1991). These workers begin with individual motor units and calculate the total muscle force by integrating over the input-output relationship of the motor units weighted by the motor unit densities. Others (Tax and van der Gon 1991; Studer 1994) begin with a linear input-output relationship for total muscle force and go back to calculate the motor unit densities and thresholds needed to reproduce this relationship. Our model of the motoneuron pool may be included in this latter class since we assume the same linear input–muscle force relationship of the muscle force and determine the appropriate recruitment thresholds of the individual motor units. In contrast to the models cited, however, we disregard rate modulation and consider pure recruitment modulation of the motor units, which leads us to a binary motoneuron code. A common feature of the cited models is that they do not derive the size principle but instead consider it as one of several properties which must be built into their description of the motoneuron pool.

It was Henneman himself, in his early work in 1965, who suggested several advantages of recruitment by size for solving a combinatorial problem (see beginning of Sect. 2). The size principle was investigated from a more theoretical point of view by Hatze and coworkers. By numerical simulations they showed that the size principle emerges from minimizing muscle energy consisting of mechanical work and different forms of heat production (Hatze and Buys 1977). In a second work, the size principle is shown to be a special case of the Weber-Fechner law for biosensors (Hatze 1979). This law states that the sensitivity of the biological sensor system scales inversely to the amount of input[1].

The size principle has not been investigated from the point of view of information theory before. In most work dealing with information theory, the information transmission of a single neuron is calculated assuming either a mean rate code or a spike interval code. Considering different stimuli (encoding different features) these works have tried to classify the temporal output patterns of a neuron and to quantify how much information an output pattern carries about the applied stimulus or feature (for an overview see de Ruyter van Steveninck and Bialek 1988). It appears, however, that a neuron may encode several features instead of only one, and that, in addition, a single feature may be encoded by a pool of distinct neurons (Gawne et al. 1991). In the case of the motoneuron pool the feature 'motor drive' is represented by a mean firing rate and supplied as a common input to the neuronal pool (Mendell and Henneman 1971). Since we consider motoneurons in the spinal cord we are in the fortunate situation that we know not only the common stimulus but also how the induced motoneuron code is interpreted: the weighted sum of the codeword components yields the total muscle force. In this sense we include semantic aspects of the neuronal code. Starting with the information theoretical principle we have deduced the optimal binary motoneuron code and find that this code is also optimal at the semantic level of muscle force precision.

There are further connections to optimization principles in motor control in which one tries to deduce the shape of a

---

[1] More formally, if $\triangle x$ is an increment of the input x and $\triangle y$ the corresponding increment of the output y of the biosensor, the Weber-Fechner law states that $\triangle y$ is proportional to $\triangle x/x$.

movement by minimizing its acceleration or jerk (Hogan and Flash 1987). It was pointed out by Hogan that such a principle of minimum jerk would be compatible with minimizing the information needed to represent motions internally. On the level of a single muscle, we have in fact established this same idea formally: the requirement of a minimal average jerk in muscle force generation leads to the size principle and this allows one to control the muscle activation with a minimal amount of input information.

5.3 Summary and concluding remarks

We have argued that recruitment by size improves the rate of information transmission from the motoneuron pool to the muscle. The restriction to a fixed recruitment order allows a compression of the source code and thus enhances information transmission to the pool. The fact that this order is by size enhances the information content of the channel or motoneuron code. We have shown that the maximal information content of the motoneuron code is equivalent to a minimal deviation from the intended muscle force (Fig. 4). Given the probability distribution of these intended muscle forces F_R, we inferred the optimal distribution of the individual motor unit forces f_i. This optimal force distribution is compatible with the condition in the human medial gastrocnemius (Fig. 5).

A fixed recruitment order allows for a simple connectivity pattern in the motoneuron pool: the common input only needs to be distributed uniformly to all motoneurons and these determine the order of recruitment by their thresholds. If rare motor tasks like high-frequency shaking have to be encoded, the motoneuron code must be enlarged by the exclusive activation of larger motor units. An extension of the motoneuron code is only possible if the preceding source code is less compressed. From the physiological point of view, an implementation of a larger motoneuron code would require further excitatory or inhibitory connections projecting onto the motoneurons. For instance, one could imagine additional interneurons or an alteration of the strong inhibitory feedback by Renshaw cells which under normal conditions are probably responsible for the linearization of the pool's output. In this sense, the compression of the source code sheds light on the 'hardware', i.e., the connectivity within the motoneuron pool. Enhancing the information content of the motoneuron code by adapting the thresholds of the motoneurons sheds light, in turn, on the 'software', i.e., the plasticity of the motoneurons.

Appendix

Proof of Theorem 2.1.

We must show that, whenever for a recruitment order π, two successive forces f_k, f_{k+1} satisfy $f_k > f_{k+1}$, the transposition $k \leftrightarrow k+1$ reduces the expected error $\langle \mathscr{E}^\pi \rangle$. Defining the new permutation $\tilde{\pi}$ by $\tilde{\pi}(k) = \pi(k+1)$, $\tilde{\pi}(k+1) = \pi(k)$ and $\tilde{\pi}(i) = \pi(i)$ otherwise, we need to prove that $\langle \mathscr{E}^{\tilde{\pi}} \rangle < \langle \mathscr{E}^\pi \rangle$. Note that all these transpositions eventually produce a recruitment such that $f_1 \leq \ldots \leq f_N$. Interchanging two neighboring units implies that in the graph of $\mathscr{E}^\pi$ (Fig. 4b) two neighboring teeth are interchanged while the remaining teeth do not change.

Since $\pi(j)$ and $\tilde{\pi}(j)$ only differ when $j = k$ and $j = k+1$, the thresholds $\theta_i^\pi = \sum_{j=0}^{i-1} f_{\pi(j)}$ and $\theta_i^{\tilde{\pi}} = \sum_{j=0}^{i-1} \tilde{f}_{\tilde{\pi}(j)}$ of π and $\tilde{\pi}$, respectively, are all equal up to $i = k+1$. For this index one has $\theta_{k+1}^\pi = \theta_k^\pi + f_k$ while $\theta_{k+1}^{\tilde{\pi}} = \theta_k^{\tilde{\pi}} + f_{k+1} = \theta_k^\pi + f_{k+1}$. With the help of Fig. A1a one finds

$$
\begin{aligned}
\langle \mathscr{E}^\pi \rangle - \langle \mathscr{E}^{\tilde{\pi}} \rangle = {} & \int_{\theta_k^{\tilde{\pi}}}^{\theta_{k+1}^{\tilde{\pi}}} \frac{(f_k - f_{k+1})}{F_R} \cdot p(F_R)\, dF_R \\
& - \int_{\theta_{k+1}^{\tilde{\pi}}}^{\theta_{k+1}^{\pi}} \frac{f_{k+1}}{F_R} \cdot p(F_R)\, dF_R \; > \\
& > \frac{(f_k - f_{k+1})}{F_R} \cdot p(\theta_{k+1}^{\tilde{\pi}}) \cdot f_{k+1} \\
& - \frac{f_{k+1}}{F_R} \cdot p(\theta_{k+1}^{\tilde{\pi}}) \cdot (f_k - f_{k+1}) = 0
\end{aligned}
$$

To obtain the inequality, we estimate the value of each of the integrals by means of their boundary values and the minimum and maximum value of $p(F_R)$ within the interval $[\theta_k^\pi, \theta_{k+1}^{\tilde{\pi}}]$ and $[\theta_{k+1}^{\tilde{\pi}}, \theta_{k+1}^\pi]$, respectively. Since $p(F_R)$ monotonically decreases, these values are equal to $p(\theta_{k+1}^{\tilde{\pi}})$ in both cases. In fact it is only required that $p(F_R)/F_R$ is strictly monotonically decreasing. Notice that the first interval has length f_{k+1} and that the second has length $f_k - f_{k+1}$. $\square$

Proof of Theorem 2.2.

Since we fix the recruitment order π to be $\pi = \mathrm{Id}$, we will drop the superscript index 'Id' of $\mathscr{E}$ and θ in the following. Necessary conditions that the motor unit forces f_k minimize the expected error $\langle \mathscr{E} \rangle$ are $\partial \langle \mathscr{E} \rangle / \partial f_k = 0$, $k = 1, \ldots, N$. We will deduce from these conditions that the f_k must have the form stated in the theorem. Instead of differentiating formally we consider the approximation $\partial \langle \mathscr{E} \rangle / \partial f_k \approx \triangle \langle \mathscr{E} \rangle / h$ by means of the difference quotient and let h approach 0 from above. Let us define the perturbation $\bar{f}_k = f_k + h$ and $\bar{f}_{k+1} = f_{k+1} - h$ and let us denote by $\langle \bar{\mathscr{E}} \rangle$ the expected error obtained with these new forces $\bar{f}_k$ and $\bar{f}_{k+1}$. Notice that the constraint $\sum_{i=0}^N f_i = F_{max}$ is still satisfied under this variation of f_k and f_{k+1}. Using (6), one calculates (cf. Fig. A1b)

$$
\begin{aligned}
\frac{\triangle \langle \mathscr{E} \rangle}{h} \equiv \frac{\langle \bar{\mathscr{E}} \rangle - \langle \mathscr{E} \rangle}{h} = \frac{1}{h} \Bigg(& \int_{\theta_k}^{\theta_{k+1}} h \cdot p(F_R)\, dF_R \\
& - \int_{\theta_{k+1}}^{\theta_{k+1}+h} (f_{k+1} - h) p(F_R)\, dF_R \Bigg) \approx \\
\approx {} & \int_{\theta_k}^{\theta_{k+1}} p(F_R)\, dF_R - f_{k+1} p(\theta_{k+1}) \\
= {} & \left(\frac{\text{const}}{\theta_k} - \frac{\text{const}}{\theta_{k+1}} \right) \\
& - f_{k+1} \frac{\text{const}}{(\theta_{k+1})^2} = \frac{\text{const}}{\theta_{k+1}} \left(\frac{f_k}{\theta_k} - \frac{f_{k+1}}{\theta_{k+1}} \right)
\end{aligned}
$$

The approximation is due to the neglect of the term $\int_{\theta_{k+1}}^{\theta_{k+1}+h} h \cdot p(F_R)\, dF_R$ in the parentheses which is roughly proportional to h^2. To obtain the second last equation we use the assumption $p(F_R) = \text{const}/(F_R)^2$ while for the last equation we use

$\theta_{k+1} = \theta_k + f_k$. In the limit $h \to 0$, the approximation $\approx$ turns into an equality and the conditions $\partial\langle\mathscr{E}\rangle/\partial f_k = 0$ are transformed to $f_k/\theta_k - f_{k+1}/\theta_{k+1} = 0$, or

$$\frac{f_{k+1}}{\theta_{k+1}} = \frac{f_k}{\theta_k} = \ldots = \frac{f_1}{\theta_1} = \text{constant} \doteq c - 1 \,. \qquad \text{(A.1)}$$

Let us check that the forces $f_i = (c-1)f_0 c^{i-1}$, $i = 1, \ldots, N$, satisfy these last conditions. Using the summation formula for the geometric series we calculate

$$\theta_{k+1} = \sum_{i=0}^{k} f_i = f_0 + (c-1)f_0 \sum_{i=1}^{k} c^{i-1} = f_0 + (c-1)f_0 \frac{c^k - 1}{c-1} = f_0 c^k \qquad \text{(A.2)}$$

and we indeed verify (A.1).

The constant $c = \sqrt[N]{F_{max}/f_0} > 1$ is deduced from the same equality (A.2) due to the definition of F_{max}. Finally, the density $d(f) = c/(c-1) \cdot 1/f$ at the points $f = f_i$, $i = 2, \ldots, N$, is obtained from

$$d(f_i) = \frac{1}{f_i - f_{i-1}} = \frac{1}{(c-1)f_0 c^{i-2}(c-1)} = \frac{c}{c-1}\frac{1}{f_i} \,. \qquad \text{(A.3)}$$

□

Proof of Theorem 3.1.

As in the proof of Theorem 2.1 we must show that, whenever two successive forces f_k, f_{k+1} of a recruitment order satisfy the (nonoptimal) relation $f_k > f_{k+1}$, the transposition $k \leftrightarrow k+1$ reduces the information content H^{π}_{MN}.

Let us consider the recruitment orders π and $\tilde{\pi}$ as defined in the proof of Theorem 2.1. For $i = 1, \ldots, N$ with $i \neq k$, $i \neq k+1$, one has $p^{\pi}_{\Omega}(x^{(i)}) = p^{\tilde{\pi}}_{\Omega}(x^{(i)})$ since the thresholds θ^{π}_i and $\theta^{\tilde{\pi}}_i$, $i \neq k+1$, corresponding to the recruitment orders π and $\tilde{\pi}$, respectively, are the same. For the index $i = k+1$, however, $\theta^{\pi}_{k+1} > \theta^{\tilde{\pi}}_{k+1}$, and it is only the sum $S = p_{\Omega}(x^{(k)}) + p_{\Omega}(x^{(k+1)})$ which is the same for π and $\tilde{\pi}$. We now define

$$H_S(\lambda) \doteq -(\lambda \log_2 \lambda + (S - \lambda)\log_2(S - \lambda)) \,, \lambda \in (0, S)$$

If, for example, $\lambda = p^{\pi}_{\Omega}(x^{(k)})$, $H_S(\lambda)$ is that part of the information content H^{π}_{MN} which is obtained by restricting the sum (10) to the two indices $i = k$ and $i = k+1$. The function $H_S(\lambda)$ has the property that $H_S(\tilde{\lambda}) > H_S(\lambda)$ whenever $|S/2 - \tilde{\lambda}| < |S/2 - \lambda|$. Using (11), the fact that $p(I)$ is monotonically decreasing and the assumption $f_k > f_{k+1}$, this same condition is verified for $\tilde{\lambda} = p^{\tilde{\pi}}_{\Omega}(x^{(k)})$ and $\lambda = p^{\pi}_{\Omega}(x^{(k)})$. Together with (10) we therefore obtain

$$H^{\tilde{\pi}}_{MN} - H^{\pi}_{MN} = H_S(p^{\tilde{\pi}}_{\Omega}(x^{(k)})) - H_S(p^{\pi}_{\Omega}(x^{(k)})) > 0$$

which was to be shown. □

Proof of Theorem 3.3.

Let us first assume that $p(\theta_i) = c_1/\theta_i$ with some constant $c_1 > 0$. Since Lemma 3.1 states that $f_i \cdot p(\theta_i) \approx c_2$ with some $c_2 > 0$, one gets $f_i \approx (c-1)\cdot\theta_i$ where $c - 1 = c_2/c_1$. This is, up to the approximation $\approx$, equivalent to (A.1). Using the calculation (A.2) we conclude that $f_i = (c-1)f_0 c^{i-1}$, $i = 1, \ldots, N$. The density $d(f) \propto 1/f$ is now deduced from (A.3).

Conversely, if $d(f_i) = c/(c-1) \cdot 1/f_i$ for $i = 2, \ldots, N$, we conclude from the definition $d(f_i) = 1/(f_i - f_{i-1})$ that $f_i = c \cdot f_{i-1}$ $(i = 2, \ldots, N)$. For the thresholds $\theta_i = \sum_{j=0}^{i-1} f_j$ one calculates $\theta_i = f_0 + f_1 \sum_{j=1}^{i-1} c^{j-1} = f_0 + f_1 \cdot (c^{i-1} - 1)/(c - 1)$. Setting $f_1 = (c-1)f_0$ we get $(c-1)\theta_i = f_1 c^{i-1} = f_i$ which is equivalent to $f_i \cdot c_1/\theta_i = c_2$. With Lemma 3.1 we conclude that $p(\theta_i) \approx c_1/\theta_i$. □

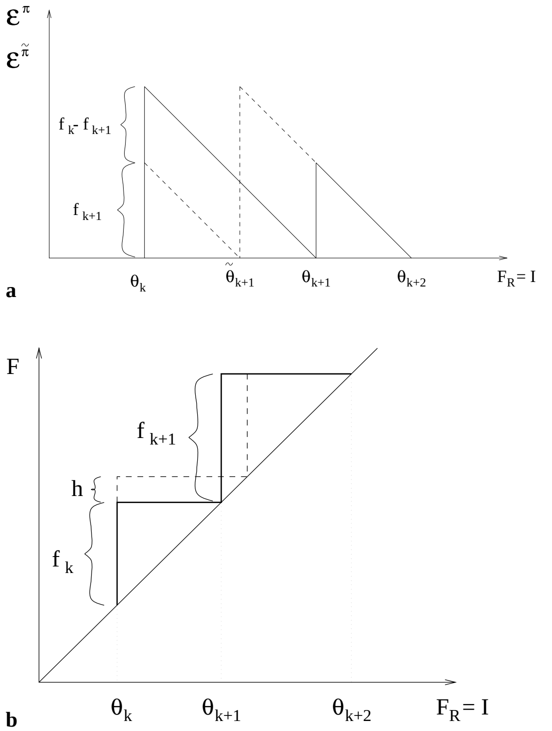

Fig. A1. **a** The error functions $\mathscr{E}^{\pi}(F_R)$ (*continuous line*) and $\mathscr{E}^{\tilde{\pi}}(F_R)$ (*dashed line*), $F_R = I$, within the interval $[\theta^{\pi}_k, \theta^{\pi}_{k+2}]$. Since the recruitment order $\tilde{\pi}$ emerges from π by exchanging only $i \leftrightarrow i+1$, the two functions are equal outside this interval. **b** The actual force $F(F_R)$, $F_R = I$, within the interval $[\theta_k, \theta_{k+2}]$, once for f_k, f_{k+1} and once for $\underline{f}_k = f_k + h$, $\underline{f}_{k+1} = f_{k+1} - h$. If $\langle\mathscr{E}\rangle$ is minimal, the local condition $(\langle\underline{\mathscr{E}}\rangle - \langle\mathscr{E}\rangle)/h \approx 0$ is satisfied

Acknowledgements. This work was supported by the Swiss National Science Foundation under the research grant no. 5002-03793 (Schwerpunktprogramm Biotechnologie). The authors would like to thank the anonymous referees for valuable and helpful critical comments.

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