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Optimality in the encoding/decoding relations of motoneurones and muscle units

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Abstract

Experimental data indicate the existence of a matching between many motoneurone characteristics and those of the corresponding innervated muscle fibres. This association between the properties of motoneurones and muscle fibres is quite important for the adequate and efficient functioning of the motor system. We present a view of motoneurones and muscle fibres as encoders and decoders of signals. An analysis of some of the encoding/decoding relations performed by motoneurones and muscle fibres in functionally relevant situations indicates that they are optimal and we indicate in the paper what performance measures are optimised. Besides its relevance in the study of motor control, the encoding/ decoding framework should also be useful in the task of model validation.

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1. Introduction

Several coding stages occur in the nervous system when an 'internal' decision is reached to enact a certain motor action. The desired action is encoded into spike trains of a large number of neurones in prefrontal, premotor and supplementary motor cortices as well as in other areas such as the basal ganglia and cerebellum. Another coding stage translates all those spike trains into the spike trains of descending pathways to the spinal cord. These are next encoded into the spike trains of motoneurones from several motoneurone pools in the spinal cord that will activate axial and limb muscles involved in the desired movement. Quite obviously, observing only the spike trains of a single motoneurone will only give us a very partial view of the encoding rules that map the descending spike trains onto the firing activity of the motoneurone pools associated with a given movement. Nevertheless, there is an interest in studying spike trains from single motoneurones and from the ensemble of motoneurones from a given motoneurone pool because their 'message' will be decoded in a final stage that will result in a measurable muscle contraction. Experiments

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have indicated that there is a degree of matching between characteristics of a given motoneurone and the muscle fibres it innervates—the muscle unit (e.g. Kernell, 1990). For example, when a current step (or an approximation to it) is applied to a motoneurone, the first few interspike intervals are shorter than at steady state (adaptation), which is exactly what is required by the muscle unit to generate a fast force buildup. Other instances of these matchings will be presented later.

Motoneurones encode input synaptic currents into spike trains, i.e. there is a mapping from the set of all possible input signals to a set of corresponding spike trains. This set of inputs contains the set of naturally occurring inputs and a set of experimentally generated inputs (Segundo, 1970). If the encoder is linear (e.g. in restricted conditions) then it is irrelevant which inputs are utilised experimentally to identify the coding. For the study of the much more difficult nonlinear encoders it would be desirable to employ experimental signals that approximate naturally occurring signals, mainly those that have a clear functional relevance. In the motoneurone-muscle system a few functionally relevant inputs are easily suggested by the knowledge of functionally relevant muscle outputs. Particular cases to be covered later are fast force development for ballistic movements and step-like input currents, periodic force development for rhythmic movements and sinusoidal input currents, constant force for quiet posture and constant input currents. What is worthy of note is that for the cases above the encoding and decoding stages are matched for optimal performance, as described in the next section.

These issues are interesting both in terms of theoretical studies of information transmission and coding in neuromuscular systems as well as in terms of neuronal model validation. In terms of the former aspects, it should be interesting to remember that a standard communication system may be described by an information source followed by a transmitter or encoder whose output feeds a communication channel. The channel usually is noisy and its output is applied to a receiver or decoder whose output is connected to the destination. The transmitter in a technological communication system (Adámek, 1991) may encode the source's output to optimise the code efficiency (e.g. mean code word length) and to provide a protection for the interferences that occur in the channel. In any of the cases, there is a specific performance measure that has to be optimised by the encoder. The receiver decodes the channel output generating the overall system output. This decoding process in the case of a noisy channel has to be designed for optimal performance, for example to minimise probability of error. The motoneurone-muscle-unit system may be viewed in a somewhat similar general framework. The information source may be viewed as the set of all presynaptic neurones to a given motoneurone. The source output will activate the motoneurone through the current reaching its soma from the multitude of synaptic contacts occurring on its dendritic tree and soma (Binder, 2000). The motoneurone encodes this input current into a spike train that is sent to the corresponding muscle unit by means of an axon. The muscle unit will decode this spike train, interpolating between the action potential firings, and act on the environment by means of a force waveform. If one looks only at the signals involved in this system, there is the input somatic current waveform, the channel spike train or channel code word and the output waveform. The encoding from the first to the second and the decoding from the second to the third are of main interest in the study of the motor system at this level. As will be described in what follows, there is an optimal matching of the encoding and decoding realised by the motoneurone and the muscle when involving some functionally relevant behaviours.

2. Experimental results from the literature and the optimal matching in motoneurone encoding and muscle decoding

In fast movements, for example, changing a joint angle from A_1 to A_2 as fast as possible, the target muscle must overcome the inertia of the limb segment and hence it should generate a force increase with a short rise time. This may be

achieved either by a very fast and constant discharge rate of the motoneurone or, alternatively, by an adapting firing pattern, starting with a higher instantaneous rate and decaying towards lower steady firing rate (Baldissera and Parmigianni, 1975). This phenomenon is related to the nonlinear property of muscle fibres, studied under isometric contractions, called the 'catch property' (Burke et al., 1976), which consists of a fast force rise to high peaks if the input has short interspike intervals at the onset (see also Grottel and Celichowski, 1999). By analysing data from the literature (e.g. Figure 1 in Baldissera and Parmigianni, 1975), one notices that quite similar force output waveforms are obtained by either a 98 per s constant rate spike train or a spike train with adaptation having a steady firing rate of about 65 per s. This would mean in the communication system analogy that there is a similar overall inputoutput relation (the input waveform would be a step function) but with a different channel code word. In other words, the decoding process is not one-to-one but that there are two different encoders for the two spike trains. The first encoder would be a motoneurone without spike rate adaptation, e.g. without calcium dependent potassium channels. The second encoder would be a realistic motoneurone containing all channels responsible for adaptation (Powers et al., 1999). The first encoder would be an inefficient encoder from the point of view of metabolic expenditure, as the firing rates involved would have to be quite high for normal force waveforms at the system output. Therefore, we can see that there is an optimisation in the encoding/decoding maps in motoneurones and muscle units that involves energy minimisation in the motoneurones and force rise-time minimisation in muscle units. Additional data (Figure 3 in Baldissera and Parmigianni, 1975) shows that a motoneurone (MN) firing pattern showing rate adaptation results in higher force plateaus than motoneurone with constant rate firing (for firing rates below 60 Hz). This would mean that (for this firing rate range) another optimality criterion was the maximisation of force amplitude. Fig. 1 synthesises the encoding/decoding pairs found in nature that



Fig. 1. Optimal matching of motoneurone encoding and muscle unit decoding for very fast movements.

follow the optimisation of performance measures described above.

Muscle fibres with a slow (fast) twitch under isometric conditions have a higher sensitivity in force production when the input firing rate is in a lower (higher) frequency range. There is a rough match between the primary firing rate range of motoneurones to constant injected current and the muscle fibre's steepest part of the isometric tension-frequency curve (Kernell, 1965, 1990; McDonagh et al., 1999). In other words, the motoneurones (types S and F) encode naturally occurring 'constant' input currents into firing rate ranges that fit the preferential range in the decoding from motor fibre firing rate into contraction force. Fig. 2 shows a matching of the primary range of firing (from the minimum firing rate up to a frequency f2) of a given motoneurone (either S or F) and the range of higher sensitivity of the



Fig. 2. Optimal matching of motoneurone encoding of steady state input current I into firing rate f and muscle unit decoding of steady firing rate inputs f into force F, under isometric conditions.

firing rate $f \times$ force F relation of the corresponding muscle fibres. If we assume that Fig. 2 shows curves for a type S motor unit (MU), then a type F motoneurone would have an $f \times I$ curve displaced to the right and upwards, yielding a higher minimum discharge rate than for S type MN, with the corresponding $f \times F$ curve also displaced to the right and upwards. The optimisation realised in these relations is the maximisation of the input current dynamic range corresponding to a high sensitivity in force production.

The rather slow contracting dynamics of muscle as well as the propagation delay of action potentials from the spinal cord to the muscles are partially compensated for by motoneurone properties (Baldissera et al., 1998; Matthews, 1997). The frequency response of motoneurone instantaneous rates has a gain curve that increases with frequency and a phase response curve with phase advance (Baldissera et al., 1984). The first property corrects partially the lowpass filtering of the muscle contraction dynamics while the second tries to compensate the phase lag caused by the finite conduction velocity of the action potential through the motoneurone axon. Hence, the encoder/decoder relations achieve an optimisation of the input/output frequency response by maximising the bandwidth (the frequency range corresponding to an almost flat gain curve) and minimising the phase delay.

From the standpoint of neuronal modelling, motoneurone models must encode sinusoidal-like current inputs into spike trains with specific frequency responses (Baldissera et al., 1984; Goroso et al., 2000). An important aspect has to be considered in these discussions: the dendritic filtering effect. If it has a lowpass filter characteristic, with lower cutoff frequencies for distally occurring synapses, then it is clear that synaptic inputs related to voluntary commands perhaps could not be very distal, because their effect at the initial segment could be insufficient to cause a periodic bursting at the repetition rate necessary for the enactment of a given fast oscillatory movement. Therefore, it is important to determine the frequency response from synaptic inputs occurring at different dendritic sites to the soma. The general idea of this encoding/decoding rela-



Fig. 3. Optimal matching of motoneurone encoding of sinusoidal input current and muscle unit decoding of sinusoidally varying rate inputs.

tion is shown in Fig. 3, on the left showing an increasing gain and phase for higher frequencies in the motoneuronal encoding of sinusoidal inputs compensating in part the decreasing gain and phase of the muscle decoding.

From the perspective of a population of MNs that innervate a given muscle, there are also some optimality conditions associated with the spike trains of the ensemble of MNs. Recruitment of motor units usually follows an ordered sequence, from type S to type FF. For low force, only type S (low threshold MNs and slow muscle units) are recruited while for larger force type FF are also recruited. The innervation ratio of type S MUs is usually smaller than for FF MUs, which makes the low force/fine movement control situation well mapped in the recruitment order and force \times firing rate relations in the motoneurone pool. During quiet standing, mostly type S motor units are active in leg muscles, which is optimal for minimising muscle fatigue.

3. Validation of motoneurone models by the use of specific encodings found in nature

Nonlinear encoders may be extremely complex and hence quite difficult to validate. Even the Wiener kernel approach may not be of much help due to its dependence on the input noise standard deviation (S.D.), the difficult interpretation of the higher order kernels besides estimation difficulties. The proposal here is to use naturally occurring inputs which have functional relevance and that present some optimality in the matching in the encoding and posterior decoding stages. We shall use such an approach in the validation of motoneurone (and muscle) models being developed in our laboratory.

Improved models of type S, FR and FF motoneurones have been developed and shall be described elsewhere (Vieira and Kohn, in preparation). They are composed of several dendritic compartments besides those for the soma and the initial segment. The soma and the initial segment are described by several ionic conductances in parallel. In view of the specific optimality of motoneurone encoding it seems quite relevant to employ such relations as validation conditions for each model.

As pointed out before, in very fast and forceful contractions, an important input is a current step or an approximation to it. The resultant spike train from a model of a type FF motoneurone had a very short initial interspike interval followed by a pronounced adaptation, as shown in Fig. 4. As mentioned before, a muscle would decode such a train by generating a short rise time and large forces. However, a motoneurone model with an inadequate representation of the dynamics of the calcium channels and the calcium-dependent po-



Fig. 4. Simulation result from a motoneurone model showing firing rate adaptation. Figure shows instantaneous rate as a function of time for a current step input.

tassium channels could lead to slow muscle force development when coupled to a muscle model, i.e. something quite different from the optimal matching of encoding and decoding found in nature.

As presented in a previous section, the firing rate under steady state as a function of the current intensity is also of relevance for motoneurone– muscle function. A result obtained from the mathematical model simulation is shown in Fig. 5 for FF and FR type motoneurone models. The resultant slopes, current and frequency ranges are within those found in real motoneurones, which optimise the force \times frequency curve of a muscle.

The motoneurone firing rates illustrated in Fig. 5 are typically sufficient to assure a maintained fused muscular contraction. In humans a voluntarily commanded maintained isometric contraction is associated with a nearly periodic firing pattern of each motoneurone (e.g. with $CV \approx 0.1$), with fusion occurring above a certain firing rate value.

4. Discussion

The information theory framework has been applied to Neuroscience problems primarily in the study of sensory systems (e.g. Rieke et al., 1997). In the field of motor control, one of the few instances of the application of the coding framework is the work done by Georgopoulos et al.



Fig. 5. Simulation result from motoneurone models of type FF and FR showing the encoding of firing rate for constant input current.

(1999) who have been very successful in the analysis of population encoding in the motor cortex of monkeys.

Our contribution is focused on the final pathway of the motor system, i.e. the motor unit (motoneurone+muscle fibres innervated). The analysis presented of the optimality of certain matched encoding/decoding relations seems to be new in the literature and adds relevant concepts to the study of motor control and to the validation of mathematical models of motoneurones and muscle. The relations described above are relevant to normal behaviours, such as escape (fast movements) and locomotion (periodic movements). The optimality of some experimentally found encoding/decoding relations might arise in nature through a blend of genetic and plasticity mechanisms, both having been shaped by slow evolutionary forces.

An interesting question regarding optimally matched motoneurone encoding and muscle decoding is with respect to plasticity caused either by increased or decreased activity in the motoneurones, as happens during disease, sport training or physical therapy (Munson et al., 1997; Roy et al., 1999; Cuppini et al., 1999; Nakano and Katsuta, 2000). In the case of diseased states, some motor dysfunctions may arise from the mismatch of the encoding/decoding realised by the motoneurone/ muscle system.

Optimality has been used quite frequently in the analysis of the motor system either from a biomechanical or from a behavioural viewpoint (e.g. Kuo, 1995; Winters and Crago, 2000). The optimally matched encoding and decoding realised by the motoneurone/muscle pair is an observation at a more microscopic level and is useful in a bottom-up study of motor control, as contrasted to the top-down view of previous work found in the literature.

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