PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Preface to Mechanisms of neuromuscular control. A Theme organized and edited by J. L. van Leeuwen

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Preface

This issue addresses mechanisms and evolutionary aspects of neuromuscular control found in insects and vertebrates. It is also concerned with applied aspects, such as the design of neuroprostheses (Riener) and the design of biologically inspired robots (Papantoniou *et al.*). The contributions are based on a symposium held on the 24 March 1998 during the Annual Meeting of the Society for Experimental Biology (SEB), University of York, UK. The meeting was organized on behalf of The Biomechanics Group and The Neurobiology Group of the SEB. Both groups have a broad comparative scope. The Biomechanics Group has, apart from its obvious experimental nature, a strong interest in theoretical models. These interests were reflected by a diverse, stimulating, and lively meeting.

There were nine presentations by invited speakers. In addition, four others contributed lectures and one poster exhibit was included in the programme. The abstracts of all contributions were published in *Abstracts of animal and cell biology*, The Society for Experimental Biology, Annual Meeting, University of York, 23–27 March 1998. All invited speakers contributed a paper to the present issue. Each paper is briefly introduced below. More detailed comments are provided in my introductory paper. All contributed papers are listed at the end of this foreword.

Progress in this interdisciplinary field is supported best by combinations of experimental work and quantitative modelling. Several of the papers have applied such a fruitful combination in their analyses. Studies of neuromuscular control have to deal with several levels of structural organization, from the molecular and ultrastructural level up to the level of the whole body and its interactions with the environment. These levels of organization were also represented at the Meeting. For instance, Graham *et al.* (contributed paper) considered the role of calcium and cAMP in the contractility of muscles from the liver fluke, *Fasciola hepatica*. Heldoorn *et al.* (contributed paper) presented a model study of the neuronal control of a single muscle, the external urethral sphincter of mammals. Ting *et al.* (contributed paper) discussed the neuromuscular control of human pedalling. Their results indicate that the control of each limb is not achieved with independent neuronal oscillators, but instead suggest that common neuronal elements are used for both limbs. This observation is similar to a recent study of bimanual coordination in rhesus monkeys (Donchin *et al.* 1998). Most neurons in the primary motor cortex responded specifically to bimanual movements. Activities of the same neurons during unimanual movements were significantly different. Several other authors discussed aspects of whole-body control such as swimming.

The first paper of this issue (Van Leeuwen) provides a short introduction, intended to help general readers to understand the more specialized topics by outlining basic principles that apply to the other papers. The following four papers consider the control mechanism of terrestrial locomotion. Insects have to be 'designed' for very short response times of their controllers, demanding a geometrical design of body and legs (the sprawled posture) that provides inherent good stability (Kubow & Full), and local fast neural-control mechanisms of the legs (see Schmitz *et al.* 1998). Balancing of standing humans has often been described with inverted pendulum models. Otten shows that the inverted pendulum model is not applicable to a balancing task in which a subject is standing with one foot on a narrow ridge. His inverse dynamics analysis indicates that hip-joint moments of the stance leg are crucial in controlling the position of the centre of mass. If one attempts to design a neural controller or a walking robot it soon becomes clear that details really matter. Riener discusses the clinical use of neuroprostheses. He describes how mathematical models can be used to gain better insight into the artificially stimulated musculo-tendon system and to develop and test different stimulation strategies. Such a model-based approach aims to accelerate the development of neuroprostheses and to reduce the required number of experiments with human subjects. Louison *et al.* (contributed paper) considered strategies of functional electrostimulation as an aid in quiet standing in physically impaired patients. Gharooni *et al.* (contributed paper) discussed the design and control of a hip and knee orthosis. Papantoniou *et al.* describe the design of an autonomously moving robot dinosaur based on fossils of *Iguanodon atherfieldensis*. The design team was faced with several problems and practical limitations. Stability control is difficult due to a narrow trackway and a high centre of mass. In addition, the robot has to carry its own energy-supply system, in the form of a battery pack. So far, the limitations of energy supply result in unrealistically slow movements. The next three papers consider control of swimming and flying. Ekeberg & Grillner discuss the swimming apparatus of the lamprey. The central nervous system of lampreys is considerably simpler than that of fish, and therefore forms an attractive object for control studies of swimming. This study attempts to integrate basic anatomical, physiological and physical aspects in one overall quantitative model for locomotion. The model displays a remarkably rich and interesting set of swimming behaviours. Even more than in terrestrial locomotion, flying insects have to be designed for very short response times and inherent stability of the mechanical system. Dickinson considers the sensory role of the halteres during flight control in flies (Diptera). The miniaturized integrative design and manoeuvrability of flying insects is impressive. A much better understanding of flying insects than is currently available would be most helpful (if not vital) for the design of small flying robots. Sokoloff & Goslow provide new insights into the organization of the motor units of the pectoralis muscle, the major flight muscle in birds. Muscle fibres in the pectoralis muscle are arranged in series between the tendons. This design leads to several, so far unsolved, problems of force transfer and concerted activation of motor units. Suthers *et al.* provide an overview of the control of bird vocalization.

Recent experiments (in particular endoscopic filming) have shed new light on the mechanical role of the tympaniform membranes and the labia of the syrinx, the principal vocal organ. In the final paper, Nishikawa considers the control of protrusible tongues during prey capture in frogs. She shows that two derived mechanisms of tongue protraction (inertial elongation and hydrostatic elongation, each requiring very different neuronal controllers) have evolved several times independently among frogs.

Finally, I wish to acknowledge several people and organizations that contributed to this issue. The Society for Experimental Biology is thanked for financial support and for taking care of many organizational aspects. This issue would never have been completed without the enthusiasm of the authors, who had to complete their papers within a short time. I thank the Royal Society for its support in publishing this issue, and especially Janet Clifford and her colleagues on the production staff of *Philosophical Transactions* B for their efforts and patience.

Leiden, 18 January 1999 — Johan L. van Leeuwen

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Contributed papers

(Abstracts published in *Abstracts of Animal and Cell Biology*, The Society for Experimental Biology, Annual Meeting, University of York, 23–27 March 1998.)

Gharooni, S., Heller, B. & Tokhi, M. O. 1998 The spring-brake orthosis: a new technique for generating hip flexion during the swing phase of gait.

Graham, M. K., McGeown, J. G. & Fairweather, I. 1998 Ionic mechanisms responsible for spontaneous mechanical activity in isolated muscle strips from the liver fluke, *Fasciola hepatica*.

Heldoorn, M., Feierabend, H. K. P. & Van Leeuwen, J. L. 1998 Neuromuscular control of sphincter muscles.

Louison, K., Wilson, A. J. & Heller, B. W. 1998 Strategies for the improvement of FES-elicited quiet standing.

Ting, T. H., Kautz, S. A., Brown, D. A. & Zajac, F. E. 1998 Neuromuscular organisation of interlimb coordination in human pedalling.

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