The neural mechanisms that organize and control movements have been the subject of extensive investigations over the past decades. Motor neurons innervating the muscles, feedback loops carrying proprioceptive information from the muscle spindles to stabilize the muscle-effector system, motor, premotor and parietal cortical structures organizing the movements at a higher level have all been identified within the mammal motor system, and detailed studies of the motor control system for various effectors in different species have been published. Most of these studies, however, were based on relatively simple single limb movements made in artificial laboratory situations. Moreover, simultaneous movements were often severely restricted to prevent contamination of the data by movements of other body parts than the effector being studied.

In more natural situations, however, one usually observes much more complex movement patterns involving various motor structures. For example, when a cat chases a prey, it almost simultaneously turns its eyes, head, and body towards the prey while stretching its body for a jump. When humans pick up or plan to manipulate an object located beside the midline, a fast saccadic eye movement is made, followed by a combination of head, trunk and arm movements in a perfectly organized pattern. Many natural manipulatory tasks also require a perfect orchestration of the movements of the eyes, head and arms, while the trunk and legs may be involved as well. In driving a car, for example, one can control the steering wheel, look in the rear mirror and push the pedals at the same time without much effort.

Knowledge about motor control obtained in studies of single movements in isolation may well have to be reconsidered in the light of new findings with regard to neural mechanisms controlling more common and natural synergetic movement patterns. Recently, first attempts have been made to understand these mechanisms. Even when studying simple single limb movements, researchers were confronted with complex cortical control signals that could only be understood in the light of the control of more complex coordinated movements. Recent interest in the control of multiple movements has also been spurred by the availability of new movement registration devices and techniques like fMRI, PET, and transcranial magnetic stimulation (TMS), enabling the study of the control of complex natural movement patterns in awake subjects. In order to understand the control processes in question,
researchers have to focus on a wide variety of information processing and control strategies. These researchers come from various scientific disciplines, with their specific methods and theories. It seems clear that definitive answers to the question of how the brain controls the coordination of multiple effectors will not be found within one discipline, but requires thorough interdisciplinary work.

In the present special issue, experts from diverse fields, like neurophysiology, psychology, psychophysics and neural modelling present new findings on the control of complex multi-limb movements. Results obtained with various methods are presented, and the importance of studying movement synergies rather than isolated movements is highlighted.

The contributions

The first three papers of this special issue focus on movement recording studies investigating the coordinative nature and underlying information processing of multi-effector movements. The final three papers focus on the role played by various brain structures in controlling multiple movements and the spatial transformations that are involved.

In a bimanual grasping study, Jackson, German and Peacock try to understand the processes underlying the simultaneous control of both hands. Their subjects were required to grasp objects of different sizes, with either one or both hands. Ocular gaze direction was manipulated in such a way that subjects had either peripheral or foveal view of the target object to be grasped. Interestingly, movement duration was always about the same for each hand, even when only one target object was foveated, whereas grip size was independently scaled for both hands. The latter finding, however, appeared to be task dependent: when both target objects were connected so that it appeared to form one object, grip apertures of both hands became interdependent, illustrating the fact that the coupling of limbs may serve functional aims in a flexible way.

In an elaborate study, Stork, Neggers and Müsseler investigate the dependence of smooth pursuit eye movements on the degree of control subjects have over the movement of the target stimuli to be tracked, and try to uncover the cortical spatial representations of the latter stimuli. It is already well known that smooth pursuit eye movements require the prediction and anticipation of future target positions in order to keep it in foveal vision. In the present study subjects had to track a target that moved along a circular trajectory with their eyes. The target movement could be stopped either by the subjects themselves or unexpectedly by the PC controlling the experiment. Subjects had to judge the position on the screen where the target disappeared, by setting a pointer, that appeared on the screen after the trial was finished and could be moved along the circular trajectory, at the estimated location. It was found that subjects were more accurate in judging the position where the target disappeared when they controlled the abortion of target motion. Also, the overshoot of smooth pursuit eye movements after the target disappeared, which is large when target movement is stopped unexpectedly by the PC, is reduced in the self-paced target
movement condition. From the latter it can be concluded that smooth pursuit eye movements are not purely stimulus driven, but rather that volitional anticipatory processes can be integrated into the smooth pursuit control process.

The study by Neggers and Bekkering focuses on the spatio-temporal coupling of saccadic eye movements and pointing movements to a target that either changed or did not change its position during the pointing movement. In previous studies these authors observed that, generally speaking, saccades to a new target appearing during reaching movements towards the original target were delayed until the hand reached its initial goal. In the present study, participants not only had to make a saccade to the new target but also had to redirect their arm movement in-flight towards the new target position. Now saccades were in fact observed during reaching, and the time of their occurrence appeared to be clearly correlated to the onset of the in-flight corrective movements of the arm, providing further evidence for a close coupling between arm and eye movements. In the discussion, a scheme for a neural model is presented to explain much of the observed behavior in eye–hand coordination in both the present and earlier studies; this model incorporates the new findings and existing models of the role of the superior colliculus in coupling ocular gaze and arm movements.

By using TMS, Van Donkelaar, Lee and Drew demonstrate specific roles for the posterior parietal cortex (PPC) and the premotor cortex (PMC) in eye–hand coordination. Under natural circumstances, the amplitude of an arm movement increases with the size of a saccade executed simultaneously with this arm movement. It is generally believed that this influence of the amplitude of the saccade on the amplitude of the pointing movement is caused by the transformation of retinal information into limb-centered coordinates, taking into account the displacement of the eyes. In a previous paper, Van Donkelaar et al. showed that the increase of arm movement amplitude with increasing saccade amplitude broke down when the PPC was stimulated by means of TMS at the right moment (a small time window of 100–200 ms after target presentation, i.e. 100–0 ms before saccade initiation, produced the clearest effects). In the present paper, an opposite effect is demonstrated by stimulating the PMC 100–200 ms after target presentation. Now the increase of the amplitude of the pointing movement with increasing saccade amplitude was even more marked than without stimulation of the PMC. These results are consistent with the suggestion that PPC codes the arm movement target in eye-centered coordinates, whereas the PMC, reflecting a later stage of sensorimotor transformations, codes it in limb-centered coordinates.

Interestingly, the study by Berndt, Franz, Bülthoff and Wascher also reports the involvement of PPC and PMC in visually guided reaching. By recording EEG potentials from the scalp above the PPC and PMC, it was observed that the event-related lateralization (ERL) increased with the amplitude of the pointing movement. When the predictability of the target position increased, the ERL of the PPC decreased, which might reflect a decreased need for sensorimotor transformations of perceived target position into movement commands. When the same movement has to be made repeatedly, the movement will get more automated, and needs less visual information, and hence less sensorimotor transformations in the PPC, than unpredictable movements. Both the study by Berndt et al. and the study by Van Donkelaar et al.
suggest that there is a specialized division of work between the PPC and the PMC in preparing goal-directed arm movements: The PPC integrates visual and eye position information into a limb-centered spatial representation, resulting in a signal that is then supplied to the PMC in order to prepare an arm movement.

Finally, an interesting theoretical report by Heck and Sultan emphasizes the important role of the cerebellum in the coordination and exact timing of multiple movement components of effectors in general (i.e. muscles of arms, legs, etc.), in fine-tuning and storing movement control signals during learning in the developing brain. It is proposed that the spatio-temporal signals related to movements, are detected by the parallel fibers and the Purkinje cells, and then sent to a motor system in order to precisely fine-tune and time the movements.

The current special issue presents a collection of state of the art research, as well as interesting ideas and theories, with regard to the mechanisms underlying complex motor behavior. The contributions to this special section reflect a growing interest in the neural processes orchestrating complex multi-limb movements in response to internal and external events.

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