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Cortical control of muscle relaxation: A lateralized readiness potential (LRP) investigation

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Abstract

Objective: We used the lateralized readiness potential (LRP) to investigate cortical mechanisms underlying the termination of muscle contraction. Active suppression and withdrawal of activation have been proposed as underlying mechanisms in isotonic and isometric relaxation.
Methods: Experiment 1 investigated isotonic wrist extension/release from extension. Experiment 2 investigated isometric activation/relaxation of a pinch grip. Tasks were performed with left and right hands and cued auditorily at variable intervals. EEG was recorded from 128 electrodes and processed to derive the LRP timelocked to the onset and offset of muscle contraction.
Results: LRPs for isotonic activation and relaxation were of identical amplitude at electrodes overlying the motor cortex, but differed at frontal locations due to higher amplitude re-afferent activity during activation. The isometric LRP was significantly smaller during relaxation than during activation, without differences in scalp distribution.
Conclusion: The LRP findings confirm differences between isotonic and isometric relaxation, which may be partly explained by the need to suppress a stretch reflex in the former condition. The presence of an LRP associated with isometric relaxation reveals active preparation in the motor cortex, indicating that muscle relaxation in the isometric task cannot be explained solely by withdrawal of activation.
Significance: High-density LRP recordings isolate different cortical mechanisms underlying the termination of muscle contraction.

Keywords: EEG; Lateralized readiness potential; Movement-related potentials; Muscle relaxation; Inhibition

1. Introduction

Normal movement requires coordinated activation and relaxation of muscles. In a variety of neurological movement disorders, inadequate relaxation of muscle contributes to the impairment of voluntary movement. In particular, this is the case in dystonia, but impaired relaxation is also thought to be relevant to the parkinsonian movement disorder. As observed by Wing (1988) and by Kunesch et al. (1995), there is not only a slow build-up of force in Parkinson's disease, but an even slower release of force. Corcos et al. (1996) have shown that dopaminergic therapy gives greater improvement of the rate of muscle relaxation than of the rate of active muscle contraction. Information concerning muscle relaxation and the control of force release has been gained from measurements following a phasic voluntary muscle contraction such as a brief squeeze (Wing, 1988; Kunesch et al., 1995). Increasingly, studies have investigated the voluntary termination of a sustained contraction. Complementary measurements of movement-related EEG potentials during the voluntary

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act of muscle relaxation have enabled a comparison between cortical mechanisms of muscle activation and relaxation (Terada et al., 1995; Rothwell et al., 1998; Yazawa et al., 1999).

To date, investigations of muscle activation and relaxation using movement-related EEG potentials have been limited to recordings of the readiness potential in self-paced tasks. For movements involving isotonic muscle contraction, the readiness potentials associated with wrist extension (muscle activation) and passive wrist flexion (muscle relaxation) have been shown to be remarkably similar (Terada et al., 1995; Yazawa et al., 1999). This result can be explained by the existence of corticomotor neurons projecting onto spinal inhibitory interneurons (Cheney and Fetz, 1985; Lemon et al., 1987; Schmidt and McIntosh, 1990). However, Rothwell et al. (1998) used a task with isometric pinch grip activation and relaxation. In this task, the terminal segment of the readiness potential, measured at lateral electrode sites and presumed to be generated by the primary motor cortex, was reduced in amplitude for muscle relaxations. Based on these different findings between tasks with isometric and isotonic contractions, the authors proposed another mechanism for force release involving the withdrawal of excitatory input to the motor cortex.

Rothwell et al. (1998) did not make strong claims as to how well isotonic and isometric tasks dissociate the two mechanisms of active inhibition and withdrawal of facilitation. One reason for caution was the recognition that with both muscle activation and relaxation, there was activity arising from frontal midline structures such as the supplementary motor area. This activity overlapped with the motor cortex activity that was of primary interest and hindered the quantification of that activity. Moreover, it was difficult to know how the strength of the midline activity might be affected by differences in task difficulty between the activation and termination of an isotonic and an isometric contraction.

Against this background, we re-addressed the mechanisms underlying voluntary muscle relaxation in two experiments, one involving wrist extension/flexion (like Terada et al., 1995) and the other involving pinch activation/relaxation (like Rothwell et al., 1998). These experiments differed from previous approaches in the following respects. First, instead of self-paced muscle activation and relaxation, we examined these acts under externally (auditorily) cued conditions. Under such conditions, the midline activation associated with self-determined timing of the movement is much reduced (Deiber et al., 1991). Second, we had subjects perform the two tasks with the left and right hand separately to enable derivation of the lateralized readiness potential (LRP). The LRP captures lateralized movement-related activity arising from the frontal convexity by means of a subtraction between homologous electrodes contralateral and ipsilateral to the side of movement (Eimer and Coles, 2003). Combining such subtractions from left and right hand movement conditions removes residual stimulus-related activity associated with the signal that instructed subjects to activate or relax. Finally, EEG was recorded with high spatial resolution, which allowed us to better evaluate whether the activity associated with muscle relaxation has the same spatial distribution as the activity associated with muscle activation.

2. Methods

Two experiments were conducted with EEG recordings during muscle activation and muscle relaxation tasks. In Experiment 1, muscle activation and relaxation were performed in an isotonic manner with wrist extension movements and subsequent release from extension. In Experiment 2, muscle activation and relaxation were performed in an isometric manner with pinch hold and release. In both experiments, surface electromyography (EMG) established muscle relaxation. The timing of activation and relaxation was derived from an accelerometer signal in Experiment 1, and from a load cell force signal in Experiment 2.

2.1. Participants

In Experiment 1, there were eight participants (seven male). Age 24–45 years. Seven participants were right-handed. In Experiment 2, there were nine male participants, aged 21–37 years, with eight of them right-handed. Two persons participated in both experiments. All participants gave informed consent after an explanation of the study. The investigations were approved by the department's Ethics Committee.

2.2. Procedures

In Experiment 1 (isotonic contractions), activation required subjects to extend the wrist briskly on hearing a high-pitched tone. In this position, the hand was held against gravity in the horizontal plane (Fig. 1). Subsequent relaxation was signalled by a low-pitched tone that instructed subjects to let the hand drop suddenly without contraction of wrist flexors. High- and low-pitched tones

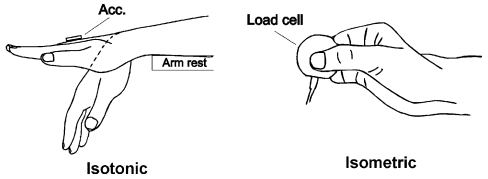

Fig. 1. In the isotonic task (left figure), the subject's hand was held extended in the horizontal plane and then released to a position with wrist flexion. In the corresponding activation condition, the hand was briskly extended to a horizontal position. An accelerometer (Acc.) attached to the dorsal surface of the hand was used to detect movement onsets. In the isometric task (right figure), the subject held a load cell between the thumb and index finger. The load cell was squeezed in the activation condition and released in the relaxation condition.