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Cortical post-movement and sensory processing disentangled by temporary deafferentation

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ABSTRACT

Motor system calibration depends crucially on the adjustment to the consequences of a movement, which often occur when the movement itself is already completed. The mechanisms by which reafferent feedback information is compared to the programmed movement remain unclear. In the current study, the hypothesis of a short term memory trace in the motor cortex which outlasts quick movements and is generated independently from reafferent feedback was challenged by temporal deafferentation.

Post-movement cortical potentials were recorded by high-resolution EEG during a reaction time task which required speeded unilateral right-hand or left-hand button presses. We analysed lateralized motor N700 (motor post-imperative negative variation), a post-movement component, under temporary deafferentation achieved through application of a blood pressure tourniquet in ten healthy adult subjects.

Motor N700 persisted under deafferentation in the absence of reafferent tactile and proprioceptive feedback input into the sensorimotor cortex, which was abolished under deafferentation. Source analysis pointed towards continuing activation in the pre-/primary motor cortex.

Thus, motor post-processing can be dissociated from reafferent sensory feedback. Motor cortex activation outlasts quick movements for about a second also in the absence of a reafferent signal. Continuing motor cortex activation could act as an internal motor model in motor learning and allow better adjustment of movements according to the evaluation of their consequences.

Introduction

Motor learning requires continuous calibration of the motor system to the consequences of movement that are recorded through reafferent input into the motor system.

However, the greater part of movement outcome feedback is only obtained after the motor command has been given. This seems to contradict the concept of long-term potentiation (Brown and Milner, 2003; Iriki et al., 1989), which claims simultaneous and synchronous stimulation as a condition for motor learning. Motor planning information could also be processed by different cortical areas than the reafferent feedback (Kaas et al., 1979; Shima and Tanji, 1998; Strick and Preston, 1982). The clarification of these temporal and organisational gaps remains crucial for the understanding of motor learning processes.

Motor N700 (motor PINV; Bender et al., 2006, 2010; Verleger et al., 1999), an early post-movement DC component over the central area contralateral to the response side, was temporally dissociated from classical postimperative negative variation (PINV; Kathmann et al., 1990), and late contingent negative variation (CNV; Bender et al., 2004a,b; Klein et al., 1996a,b, 1998). Motor N700 did not depend upon motor preparation during the Bereitschaftspotential, and motor N700 also did not reflect cortical motor activity related to muscle contraction (Bender et al., 2006). Instead, motor N700 was enhanced when subjects were instructed to memorise their completed movement (Bender et al., 2010).

The topography of motor N700 corresponded to the negative fields in MEG recordings that occurred after execution of self-paced movements. It has been proposed that these fields could at least partially originate from motor cortex activity (Cheyne and Weinberg, 1989; Kristeva et al., 1991).

The primary motor cortex has also been proposed as a possible generator location for reafferent feedback processing by a number of investigators (Abbruzzese et al., 1985; Mima et al., 1996).

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Movement-related potentials derived through a Bereitschaftspotential paradigm in a completely deafferented patient (due to polyneuropathy; Forget and Lamarre, 1987) showed that in comparison to healthy controls the "hand somatosensory potential" component (reafferent feedback; Kornhuber and Deecke, 1965; Neshige et al., 1988) was absent in the deafferented patient (Kristeva et al., 2006). This gave evidence for the claim that reafferent sensory information could be represented by components of the movement-evoked potential. Since the deafferented patient performed the movement task nearly as well as the healthy controls despite having no perceptual experience of the movement, Kristeva et al. argued that reafferent input from the periphery could be of importance for the development of movement awareness in interaction with an internal motor model (Kristeva et al., 2006).

The aim of this study was to challenge our hypothesis that motor N700 represents a motor post-processing component which does not depend upon reafferent input into the sensorimotor cortex but may rather serve to compare the programmed movement to reafferent feedback (Bender et al., 2006).

We recorded high resolution multi-channel EEG during a simple reaction time task without preceding warning stimulus, while temporary ischemic limb deafferentation was applied to the arm used for the subjects' response movement.

Short-term peripheral ischemia achieved by ischemic nerve block is a well established experimental paradigm for investigating plasticity of the human sensorimotor cortex (Brasil-Neto et al., 1993; Ziemann et al., 1998a,b). GABA-ergic inhibition appears to be underlying the rapid plastic changes in the somatosensory and motor cortices (Celnik and Cohen, 2004).

Material and methods

Subjects

A routine thrombophilia screening, which was evaluated by a senior haematologist, was performed in order to avoid complications by the ischemic nerve block. Ten subjects aged 21 to 25 years (seven female, mean age 24.0 ± 1.0 years; mean values are given ± standard deviation SD) participated in the study. All subjects were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971). No subject was on any psychoactive medication, suffered from neurological or psychiatric symptoms or had a history of illness in this field. All subjects were screened for a past medical history of cardiovascular and thromboembolic diseases and for visual impairment (corrected visus ≥ 0.8). Arterial hypertension (≥ 160 mmHg) was defined as an exclusion criterion.

The study was approved by the local ethics committee. All subjects provided written informed consent according to the Declaration of Helsinki before entering the study.

Tasks and procedures

The experimental sessions took place in an electrically shielded, dimly illuminated room, where subjects were seated facing a standard computer screen at 1 m distance. The subjects' head was resting on a chin rest and their hands were placed next to a STIM response pad (Neuroscan Inc., TX, USA).

A button press on the response pad by flexion movements of the left or right thumb was required when the visual imperative stimulus, a stylised hand figure, appeared on the screen at the position of the fixation cross. This visual stimulus was the only cue given. Between responses, the thumbs rested on the response pad buttons. The button was pressed about 2 mm in downwards direction (comparable to a mouse click), immediately followed by an equally small passive return movement. Speed and accuracy of the button press responses were equally emphasised by the task instructions. Subjects were instructed to perform the fast response movement, even if this would be confined under deafferentation conditions. Interstimulus intervals (ISI) varied pseudorandomly from 7 to 11 s. The visual stimulus was presented for 100 ms and no visual feedback about the outcome was given. The sequence of stimulus presentation was programmed and controlled using the Gentask module of the STIM software package (Neuroscan Inc., TX, USA).

Two trial blocks of 40 trials each were recorded separately for right and left hand responses in session 1 (T1). For ethical reasons we decided to apply temporary deafferentation only to subjects who showed a clearly distinguishable motor N700. However, as motor N700 was clearly present in all subjects, no subject had to be excluded. In session 2 (T2), the baseline motor N700 recording was repeated.

Temporary deafferentation was achieved through a commercial blood pressure cuff that was applied around the subject's upper arm just above the elbow and inflated 50 mmHg above the systolic blood pressure.

The temporary deafferentation session was subdivided into blocks of 30 trials followed by an intermission of 1 min, where subjects rated tactile sensitivity and proprioception on rating scales from 0 to 10 (10 meaning condition fully intact, 0 condition vanished).

A final trial block was recorded after the subject had rated tactile sensitivity as vanished. We refrained from applying longer ischemia, because subjects described the temporary ischemia and deafferentation to become unpleasant at this point. It was ensured by a clinical examination that sharp–blunt and two-point discrimination had indeed disappeared at the end of the final block. After full subjective recovery, the temporary deafferentation trial was performed for the other hand. At the end of T2, two further post-ischemia trial blocks (40 trials) were recorded, one for each response movement side, to allow a comparison with pre-deafferentation ('baseline') values.

Whether subjects started with the right or with the left hand was counterbalanced across the sample for all conditions.

Recordings and measurements

A QuickAmp amplifier (Brain Products GmbH, Munich, Germany) was used to record continuous 64-channel EEG at a sampling rate of 500 Hz. The recorded band-pass was DC to 140 Hz. 64 sintered Ag–AgCl electrodes were used with an electrode cap (Easycap, FMS, Herrsching, Germany) with equidistant electrode positions. The channels were named according to the equivalent positions in an extended international 10–20 system [small deviations are indicated by '].

Vertical and horizontal electrooculogram (VEOG and HEOG) were recorded from electrodes placed 1 cm above and below the left eye and bilateral to the outer canthi. Surface EMG activity was recorded from Ag–AgCl electrodes for the thenar muscles (abductor pollicis brevis muscle and opponens pollicis muscle) against a reference over the distal radius bone (Davey et al., 1998). A 20 Hz high-pass filter was used for the EMG data.

Impedances were kept below 5 kΩ for EEG and below 10 kΩ for EMG electrodes. EEG was recorded against an average reference.

Data preprocessing

Data preprocessing was conducted offline with the BrainVision Analyzer software (Brain Products, Munich, Germany). The raw EEG was segmented on the imperative visual stimulus (stimulus-locked) and on the onset of the EMG-response (response-locked). The advantage of the dual segmentation was that no loss of information occurred: The last few trials under deafferentation were only available for the stimulus-locked data because the EMG signal also vanished when deafferentation was completed. However, the EMG-response-locked data carry more precise information about the timing of the motor command and the reafferent sensory signals. The stimulus-locked segments had a length of 8 s, starting 1 s before the visual imperative stimulus until 7 s afterwards in stimulus-locked trials. For