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Cortical motor areas are activated early in a characteristic sequence during *post*-movement processing

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During motor learning in goal-directed reactions, a specific movement has to be associated with feedback about the movement's success. Such feedback often follows when the movement is already over. We investigated the time-course of *post*-movement cortical motor processing by high-resolution analysis of lateralized post-movement potentials in forewarned and simple reaction time tasks. In both paradigms we could separate a post-movement component (motor postimperative negative variation-mPINV) peaking about 500 ms *after* the button press (confirmed by electromyogram and accelerometer). mPINV could not be sufficiently explained by motor cortex activity related to EMG output and/or by sensory feedback. mPINV was enhanced by long intertrial intervals and its lateralization changed with response movement side. Its scalp potential distribution resembled (pre-)motor cortex activity during preceding movement stages and differed from the frontal motor potential peak (proprioceptive and somatosensory reafferent feedback); suggesting post-movement activation of pre-/primary motor cortex. Dipole source analysis yielded a single radial source near premotor cortex which explained lateralized mPINV almost completely. mPINV was present in simple reaction time tasks, indicating that mPINV is an independent component and does not represent delayed resolution of pre-movement negativity. An equivalent of "classical" PINV (cPINV) occurred later over prefrontal and anterior temporal sites in simple and forewarned reaction time tasks. Our results suggest that high-resolution analysis of lateralized movement-related potentials allows to image post-movement motor cortex activity and might provide insights into basic mechanisms of motor learning: A characteristic sequence might involve motor cortex activation (mPINV) before "higher order associative areas" come into play (cPINV).

Keywords: Postimperative negative variation; Movement-related cortical potentials; Current source density; Lateralized readiness potential; Motor systems

Introduction

Understanding motor processing after a movement is crucial to understand the cortical mechanisms involved in movement evaluation and motor learning. We need to comprehend how feedback about movement success or reinforcers is linked to specific motor programs at cortical level. Movement execution often terminates *before* feedback is obtained, while long-term potentiation, one of the basic mechanisms of associative learning, requires neurons to be activated simultaneously (Brown and Milner, 2003; Shanks, 1993). The bridging of such time gaps remains to be explained in many aspects. Multichannel EEG/event-related potential research with its excellent time resolution constitutes an adequate method to examine the time course how implicated cortical areas play together to accomplish this task in human subjects.

Recently, we could show that an auditory forewarned reaction time (contingent negative variation-CNV) task evokes a prominent lateralized post-movement negativity over the central area contralateral to the required unilateral response (dominant right hand) in adolescents, which peaked about 800 ms after the imperative stimulus (i.e., about 500–600 ms after the button press response) (Bender et al., 2004). The topography of this post-movement component, which we refer to as mPINV (motor postimperative negative variation), pointed towards post-movement motor cortex activation and may correspond to a small post-movement negative field which has been described over primary sensory-motor areas in MEG-recordings of self-paced movements (Kristeva et al., 1991). Moreover, its latency correlated with reaction time. Most important, mPINV topography differed from the topography of late CNV, indicating an independent post-movement component instead of "delayed CNV resolution" (Rockstroh et al., 1989). This differentiation had been a major problem in earlier adult studies (Klein et al., 1998) but was easy to establish in our large sample of children and adolescents, because mPINV and late CNV showed different maturational trajectories: A prominent mPINV was found in 6- to 11-year-old children, while they were still missing significant negativity over motor areas during late CNV (Bender et al., 2005). mPINV

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preceded the peak of longer-lasting contralateral central beta event-related synchronization (ERS), which has been proposed to reflect an “idling” state of motor cortex (Chen et al., 1998; Leocani et al., 2001; Pfurtscheller, 1992) or processes related to sensory feedback (Cassim et al., 2001). Though contralateral central beta ERS and mPINV showed a parallel sharp increase, mPINV rather coincided temporally with beta ERS over SMA (Bender et al., 2004). Thus both evoked activity (mPINV) as well as movement-induced EEG rhythms point towards prolonged movement-related changes in motor cortex beyond movement execution (Pfurtscheller et al., 1998; Stancak and Pfurtscheller, 1996).

mPINV peaked before an equivalent of “classical” PINV (cPINV), a negative shift involving lateral fronto-temporal areas and developing in healthy adult subjects especially when control over an aversive imperative stimulus is lost or gained (Kathmann et al., 1990; Klein et al., 1998). cPINV therefore is thought to reflect contingency reappraisal and/or response uncertainty (Kathmann et al., 1990; Klein et al., 1998; Klein et al., 1996a,b). In agreement with previous suggestions (Verleger et al., 1999), a topographic PINV model integrating motor *and* cognitive components of movement evaluation processes may enable to understand increased central PINV amplitudes in different patient populations, e.g., in young migraineurs (Besken et al., 1993; Cherniak et al., 2001) or adult schizophrenic patients (Rockstroh et al., 1999; Wagner et al., 1996). Moreover, mPINV could represent a general post-movement evaluation process (of the executed movement or changes in body position) and might provide new insights into the cortical mechanisms of motor learning and conditioning.

In the current study we further examined mPINV and the sequence mPINV/cPINV in order to elucidate the conditions under which mPINV is evoked. We intended to confirm our model of two different PINV subcomponents (motor and “classical cognitive” PINV) in healthy young adults. Moreover we aimed to discard alternative explications for mPINV apart from post-movement motor processing:

By experimental variation of response movement side we challenged our assumption (derived from our previous topographical analyses) that mPINV was related to cortical *sensorimotor* processing. Hypothesis 1: Lateralization of mPINV but not cPINV should vary with response movement side.

Second, we characterized the relationship between finger movement (acceleration), electromyographic activity (EMG) and mPINV time-course and topography. Hypothesis 2: mPINV is not sufficiently explained by reafferent sensory feedback (mPINV occurs after the movement and differs in its topography from proprioceptive and somatosensory potentials) or cortical activity directly related to EMG output (no EMG activity paralleling mPINV will be found in the target muscle) but reflects additional cortical post-movement processes.

Third, we examined simple reaction time tasks without a preceding warning stimulus in order to find out whether mPINV constitutes a rather general mechanism of post-movement processing and is independent from previous preparation and CNV resolution in adults: Hypothesis 3: mPINV still occurs when no warning stimulus precedes a goal-directed reaction movement.

Fourth, by comparing long and short intertrial intervals we tested whether long intertrial intervals were necessary for mPINV to appear: Hypothesis 4: mPINV occurs only when long intertrial intervals are used. The role of the length of intertrial intervals (ITI) seems important in order to explain why a PINV has been described so far mainly in CNV-like experiments (Bender et al., 2005; Klein et al., 1996; Verleger et al., 1999) but, e.g., not in oddball P300 paradigms, where short ITI are used (Salisbury et al., 2001). This fact had led to the interpretation that delayed CNV resolution (e.g., due to glial cell depolarization by preceding sustained negativity; Caspers et al., 1980; Rockstroh et al., 1989) is responsible for PINV generation. Moreover, the influence of ITI on mPINV could explain how short delays between subsequent trials in motor training can elevate the efficacy of this training.

Therefore, we applied multi-channel high resolution EEG analysis of mPINV during forewarned and simple reaction time tasks and varied response movement side. The analysis of externally triggered movements in simple reaction time tasks allowed us to differentiate in adults, whether mPINV would occur only after preceding sustained negativity (such as the Bereitschaftspotential in self-paced movements or late CNV) or if it would occur as an independent separate component, whenever intertrial intervals were sufficiently long. We applied the lateralized “readiness” potential (LRP) rationale (see methods below), a subtraction procedure which takes advantage of the fact that only movement-related activity changes its lateralization together with response movement side, in order to eliminate activity related to the imperative stimulus. We applied the LRP rationale not only to pre- but also to post-movement stages. We intended to prove that movement-related motor cortex activation occurs after movement execution (as indicated by EMG and accelerometer) in visual CNV as well as auditory simple reaction time tasks (independent from stimulus modality): We expected a contralateral post-movement central negativity during mPINV, reflecting (pre-) motor cortex activity (Gerloff et al., 1998); similar to the topography of the preceding negative slope (NS), initial slope (isMP) or parietal peak of the motor potential (ppMP) (Nagamine et al., 1994; Tarkka and Hallett, 1991). We expected mPINV topography to differ from the topography of the frontal peak of the motor potential (fpMP; reafferent sensory input) (Botzel et al., 1997; Seiss et al., 2002; Shibasaki et al., 1980a,b; Tarkka et al., 1991). We used dipole source analysis (automated RAP-MUSIC algorithm) in order to test whether a single cortical source near (pre-)motor areas might be able to explain mPINV. Finally, we looked for a later occurring equivalent of “classical” PINV in the simple reaction time tasks in order to find out whether the sequence of mPINV and cPINV could represent a general pattern for post-movement evaluation.

Materials and methods

Subjects

We analyzed 18 healthy right-handed (Edinburgh Handedness Inventory, Oldfield, 1971) young adults aged 24 to 34 years (14 male, 4 female, mean age 28.2 ± 2.3 years, mean values are given ± standard deviation, SD). No subject took any psychoactive medication or suffered from neurological or psychiatric symptoms. We screened for visual (corrected visus ≥ 0.8) and clinical hearing impairments. The study was approved by the local ethics committee and all subjects provided written informed consent according to the Declaration of Helsinki.