



Review article

Beyond the “Bereitschaftspotential”: Action preparation behind cognitive functions

F. Di Russo^{a,b,*}, M. Berchicci^a, C. Bozzacchi^{a,c}, R.L. Perri^a, S. Pitzalis^{a,b}, D. Spinelli^{a,b}^a Department of Movement, Human and Health Sciences, University of Rome “Foro Italico”, Piazza Lauro de Bosis, 15, Rome, 00135, Italy^b Santa Lucia Foundation, IRCCS, Via Ardeatina 306, Rome, 00179, Italy^c Netherlands Institute for Neuroscience, A Research Institute of the Royal Netherlands Academy of Arts and Sciences, Meibergdreef 47, 1105BA, Amsterdam, The Netherlands

ARTICLE INFO

Keywords:

MRCP

ERP

Cognitive action control

Pre-motor cognition

EEG

BP

pN

ABSTRACT

Research on preparatory brain processes taking place before acting shows unexpected connections with cognitive processing. From 50 years, we know that motor-related brain activity can be measured by electrocortical recordings 1–3 s before voluntary actions. This readiness potential has been associated with increasing excitability of premotor and motor areas and directly linked to the kinematic of the upcoming action. Now we know that the mere motor preparation is only one function of a more complex preparatory activity. Recent research shows that before any action many cognitive processes may occur depending on various aspects of the action, such as complexity, meaning, emotional valence, fatigue and consequences of the action itself. In addition to studies on self-paced action, the review considers also studies on externally-triggered paradigms showing differences in preparation processes related to age, physical exercise, and task instructions. Evidences from electrophysiological and neuroimaging recording indicate that in addition to the motor areas, the prefrontal, parietal and sensory cortices may be active during action preparation to anticipate future events and calibrate responses.

1. Introduction

The “Bereitschaftspotential” (BP), firstly described more than 50 years ago by Kornhuber and Deecke (1965), identifies the slow rising negative electrocortical activity preceding motor acts, also known as readiness potential (RP; Vaughan et al., 1968). This response-locked activity is currently termed as motor-related potential (MRP) or, more frequently, motor-related cortical potential (MRCP¹). The MRCP has been typically studied for simple self-initiated movements such as fingers or hand flexion and extension. These movements are usually triggered by individual volition in the absence of external cues. For simple movements, the earliest MRCP component, the BP, initiates 1–2 s before the movement onset over the frontal-central areas of the scalp: it reflects the slow increasing cortical excitability and preconscious readiness for the forthcoming movement. Starting 400–500 ms before movement onset, the excitability of premotor areas increases more rapidly showing a steeper negative slope (NS’ or late BP component), that reflects the stage of movement preparation often associated with conscious decision of movement. The preconscious

interpretation of the BP has been recently challenged by Schmidt et al. (2016). They proposed that the BP (or early RP) could represent a correlate of the upcoming voluntary action, but not as a necessary causal factor. The BP could mostly reflect negative deflections from unspecific slow-cortical potentials and could be the result of an unequal ratio of negative and positive slow potential preceding self-initiated movement.

Concomitantly with the movement initiation, the negative ramp reaches its peak that is called motor potential (MP) component. Following the MP, the activity rapidly returns to positive amplitude forming a peak at about 200–300 ms after movement onset. This positive activity has been labeled re-afferent potential (RAP) and has been associated with afferent somatosensory inputs due to the peripheral touch, as in case of an object reaching movement. The MRCP is modulated by the effector that will be used for the motor response and it is typically influenced by factors such as movement complexity and timing. The BP originates from the supplementary and cingulate motor areas, while the premotor and motor areas are the main sources of the NS’. The MP is mainly produced by the primary motor area (M1) and

* Corresponding author at: Department of Movement, Human and Health Sciences, University of Rome “Foro Italico”, Piazza Lauro de Bosis, 15, Rome, 00135, Italy.

E-mail address: francesco.dirusso@uniroma4.it (F. Di Russo).¹ The term MRCP is used to distinguish this cortical potential from the motor-evoked potential (MEP), which is the muscle activity induced by the transcranial magnetic stimulation (TMS) over the motor cortex.

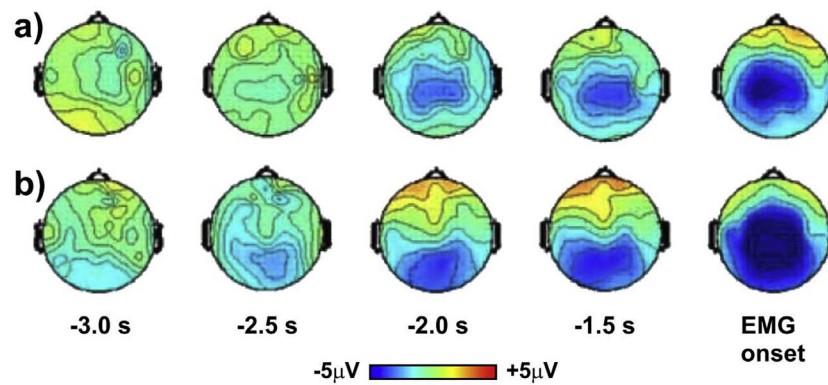


Fig. 1. MRCP for simple movement (a) and pantomimed tool use movement (b) where was visible the parietal negative activity (modified from Wheaton et al., 2005a).

the RAP has been associated with activity from the primary somato-sensorial area (S1).

The first 40 years of the MRCP research are reviewed by Shibasaki and Hallett (2006) and the present review aims at updating the MRCP literature, presenting results of the last 10 years of studies investigating the motor preparation in a variety of complex movements that were not considered before. Considering the variety of brain processes involved in the action planning, this review aims to overcome the description of the mere preparation in the motor areas (as reflected by the BP), describing the set of electrophysiological activities associated with the more complex neurocognitive aspects of the action preparation.

To this aim, here we review past and recent literature on the pre-motor, anticipatory brain process taking place before the execution of complex actions, as self-initiated praxic actions, virtual actions, fatiguing or incompatible movements, and movements aimed at self-administering emotional pictures.

In addition to studies on self-initiated actions, the review includes also studies on the movement preparation to external stimuli. The latter laboratory condition mimics a frequent day-life condition in which we have to choose the appropriate action depending on the external events. The review takes also into account the motor preparation by means of group differences, such as children, elderly, physically fit people, and adult subjects with an individual tendency to respond very quickly or very slowly. The speed and/or the accuracy of response are the behavioral variables mainly considered in these studies.

The final part of this review addresses the cerebral localization of the MRCP components during eye or arm movements. We delineated a network of regions located in the prefrontal, frontal, parietal and insular cortices differently involved in the action planning depending to several movement-related factors (such as complexity, meaning or awareness of the action).

2. Praxic actions

The MRCP has been widely studied for simple self-paced movements, such as pressing a button; however, little was known about the activity preceding more complex and praxic actions (i.e., movements implying interaction with an object) until the last decades. From the beginning of the 21st century, the research on motor preparation started to investigate movements such as grasping and reaching, i.e. actions through which humans and primates normally interact with the surrounding environment. These actions imply high-level cognitive processes and visuo-motor transformations, from the perception and recognition of the object to the achievement of the final action goal. In this section, we present a series of works that have extended the study of the MRCP to this complex class of movements. In particular, we will refer here to pantomime, grasping and reaching movements. These findings improve our knowledge on the cognitive processes taking place well before the action unfolds, as indicated by the preparatory activity

recorded with MRCP.

2.1. Pantomime

Pantomime of tool use is a widely-used task for experimental and clinical purposes. It is based on the demonstration (gesturing) of transitive actions involving the use of specific tools as if the objects were physically present and held by the hand. The task does not entail any visuomotor transformation (being the object absent) and requires a skilled mental representation (praxic and semantic) of the object and the action (De Renzi and Lucchelli, 1988).

Although the tool is physically absent, the execution of pantomime movements involves the same cortical structures as object-oriented actions, including frontal and parietal cortices (Rizzolatti et al., 1998; Luppino and Rizzolatti, 2000). This is likely induced by the strong connection between tools and action representation. Neuroimaging studies have allowed the localization of the areas directly related to the programming and the execution of the gestures. However, although functional magnetic resonance (fMRI) experiments provided evidences of the connections between these areas, there are still limits in describing the actual temporal sequence of activations by neuroimaging. The low temporal resolution of the technique left open many questions about the mechanisms underpinning motor preparation, and MRCP recording is a valuable tool to answer some of these questions.

In a pioneering experiment, Wheaton et al. (2005a) studied the motor preparation for praxic movements by electroencephalography (EEG) recording. They compared two types of self-paced pantomime (i.e. pantomime of tool-use and communicative gestures) to evaluate the temporal activation sequence of the cortical areas in the parietal-frontal network. With respect to previous research on simple motor sequences, the preparation of these meaningful actions started much earlier, up to three seconds before the movement onset. Interestingly, the earliest activity originated in parietal regions (Fig. 1). For both types of actions, transitive and intransitive, the authors reported a similar pattern of preparatory activity, which originated in the superior parietal lobe (SPL), shifted towards the inferior parietal lobe (IPL) and reached the more anterior sensorimotor areas about 2 s before movement initiation. For the first time, the authors reported an earlier component of the MRCP originating in the left parietal cortex that they attributed to the increased cognitive demands of these actions (see also Andersen and Buneo, 2002).

In a follow-up study, Wheaton et al. (2005b) verified whether this early posterior activity, preceding the well-known BP component, was specifically associated with praxic movements or it was a not previously explored part of the motor preparation. Therefore, they compared pantomime of tool use with simpler, meaningless movements (i.e. thumb adduction). Results confirmed the specific involvement of parietal structures only in case of complex and praxic actions (Wheaton et al., 2005b). The studies by Wheaton and collaborators

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