



Neuropsychological *Trends*

5
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<i>Kristian S. Hill - James L. Reilly - Margret S.H. Harris Tin Khine - John A. Sweeney</i>	
Oculomotor and neuropsychological effects of antipsychotic treatment for schizophrenia	7
<i>Ashish Desai</i>	
Digitizing the moving face: asymmetries of emotion and gender	35
<i>Stefan Winblad - Pauls Hellström - Christopher Lindberg Stefan Hansen</i>	
Facial emotion recognition in myotonic dystrophy type 1 correlates with CTG repeat expansion	43
<i>Edoardo Santucci - Michela Balconi</i>	
The multicomponential nature of movement-related cortical potentials: functional generators and psychological factors	59

The multicomponential nature of movement-related cortical potentials: functional generators and psychological factors

Edoardo Santucci - Michela Balconi

Department of Psychology, Neuropsychology Research Unit, Catholic University of Milan, Milan, Italy

edoardo.santucci@unicatt.it

ABSTRACT

Starting from a general description of the several components which form movement-related cortical potentials family, this paper aims to review the principal results coming from electrophysiological and motor neuroscience experiments. Empirical evidences of cortical and subcortical generators are analyzed, considering their mutual and simultaneous involvement for the generation of Bereitschaftspotential (BP) or Readiness Potential (RP). A specific section is dedicated to the review of the main psychological factors which influence the topography and magnitude of BP. Inside this psychological perspective another section deals with the role of motor representation for the preparation of the action, valuating the influence of motor imagery process on readiness potential.

Keywords: Bereitschaftspotential; Readiness Potential; Movement-related cortical potentials; Planning and execution; Motor representation

1. INTRODUCTION

During the last years a large body of neuropsychological and neuroimaging studies has investigated the organization and planning of voluntary movements. This research trend draws inspiration from the multiplicity of available techniques in neuroscience. For a long time functional methods

have provided a high-spatial resolution of the neural basis involved in motor processes to the detriment of a poor temporal resolution. Novel brain imaging approaches, which combine high-temporal resolution EEG with the functional MRI, have been proposed for the evaluation of brain structures involved during intentional act in human primates. In addition transcranial magnetic stimulation analysis have provided further impulse to the knowledge of human motor cortex during volitional movements.

However terms as *motor preparation*, *intentional planning* denote the impact of the *temporal dimension* prior to the actual movement which is critical in the domain of action and fairly unexplored. As a matter of fact the question of which cortical and subcortical generators standing below these processes and when they are active is far-away from a definitive answer. Sensitive to the temporal factor we here review the principal literature which deals with the relationship between volitional movements and event-related potentials (ERPs). This electrophysiological method answers for a millisecond temporal resolution assuring the prospect to dwell upon the preparation and planning of the action.

2. GENERAL PICTURE OF MOVEMENT-RELATED CORTICAL POTENTIALS

Since the original recording made by Kornhuber and Deecke in 1964, movement-related cortical potentials preceding voluntary movements in humans are subject of matter in the field of motor execution, particularly for their relations with motor cognition. The aim of the present section is to provide a theoretical review about the complexity and the several components which compound pre-motion potentials.

As a matter of fact when we consider the category *movement-related potential* we have to envisage it as divided into several subcomponents. The earliest, called *Bereitschaftspotential* (BP) or *Readiness Potential*, starts about 2000 ms before the movement onset. This slowly rising negativity is largest over the midline centro-parietal region and takes a symmetrical and wide-spread distribution despite of the laterality of the effector involved. The bilateral readiness potential is followed by a late steeper component at 400 ms before the electromyogram onset (called *Negative Slope*), which reaches its maximal amplitude over the central and parietal sites contralateral to the movement. Therefore it is possible to discern between an *early* and *late* readiness potential. As it has mentioned by Shibasaki and Hallett (2006) for a long time late BP has been worded as an indication of the movement site, while

the earliest BP as an effect of a general motor preparation process because of the wide distribution over the scalp. However this mere difference has not been accepted because the early BP seems also to be correlated to the site of movement within supplementary motor area and lateral premotor cortex. For that reason BP and NS represent a preparatory activity of the neurons in MI and the adjacent areas (Jahanshahi & Hallett, 2003).

Approximately between 100 and 50 ms before the EMG it occurs a small positive deflection, which is called *Pre-motion Positivity* (PMP). The functional role of the PMP is still matter of debate. In the original analysis of Kornhuber and Deecke (1969), which are the first to describe this positive slope, PMP had its largest amplitude over the precentral and parietal area and it was bilaterally symmetrical. They concluded that it should be reflect an intentional self-triggered movement initiation. However several studies report that PMP is not always present for all the cases analyzed and that it occurs mainly when the movement is led by external triggers, and besides when present is ipsilateral to the movement (Shibasaki et al., 1980). Another hypothesis suggested by Deecke et al. (1985) asserts that PMP reflects the reduction of activity of the supplementary motor area as soon as the timing process of movement initiation has happened. Shibasaki and Kato (1975), starting from the observation that the ipsilateral distribution of pre-motion positivity occurs barely for unilateral movements but not for bilateral ones, conclude that this deflection represents an inhibitory index of mirror movements. Namely this slope might be fundamental for the control and restraint of the opposite effector in voluntary unilateral task. Basing on the fact that epicortical recordings do not obtain any PMP, Shibasaki and Hallett (2006) conclude that this component does not have a real physiological value, and it might be a mere deflection between the negative slope (NS) and the *Motor Potential* (MP).

In the order of electromyogram onset a further abrupt negativity occurs and reaches its largest amplitude only just after the onset over the contralateral central region of the scalp; this subcomponent is called *Motor Potential* (MP). The MP reflects the activity of pyramidal neurons that project to the corticospinal tracts; it represents the final motor output to the spinal cord (Jahanshahi & Hallett, 2003).

After the movement EEG records a final positive wave called *Reafferent Potential* which reflects the somatosensory input received through the motor act and processed by the cortex.

To summarize, as reported by Shibasaki and Hallett (2006) there are various terms used in literature for the definition of movement-related cortical components; here we use the classical terminology proposed by Kornhuber and Deecke, considering that the original definition *Bereitschaftspotential* comprises at least two subcomponents (an early BP called "BP" and a late BP

called “NS”). Moreover, because the focus of the present paper is to review the pre-motion components of movement-related brain potentials, we do not consider the numerous post-movement potentials which occur after the motor act.

3. CORTICAL GENERATORS AND LATERALIZATION OF PRE-MOTION COMPONENTS

3.1. Main cortical sources

It is not yet evident *why* prior to self-paced unilateral movements the early readiness potential has a bilateral distribution over the scalp (Brunia et al., 2004). Considering the review offered by MacKinnon (2003) which analysed results coming mainly from functional methods, it seems that the principal generators of the symmetrical early readiness potential would be the *bilateral mesial frontal cortex*, which includes *rostral* and *caudal* part of the supplementary motor area (SMA), and the *cingulate motor areas*. The functional role of the *primary motor cortex* (MI) is limited to the development of the asymmetrical readiness potential, that is the Negative Slope; therefore while there is a participation of the contralateral MI, it is not possible to locate a real involvement of the ipsilateral primary motor cortex (Brunia et al., 2004).

Nevertheless Ikeda et al. (2003) dwelling upon the subject reported data of epicortical recordings which provide different conclusions (Brunia et al., 2004). As a matter of fact the symmetrical distribution of the readiness potential is widely bilateral in MI and in the caudal part of SMA. Moreover the NS is bilateral in the caudal region of SMA and contralaterally predominant in MI, even if present ipsilaterally. There is no ipsilateral distribution for MP, while it is contralaterally manifest in MI and in the caudal site of SMA.

From these first results at the cortical level it seems evident that the *supplementary motor area* acts like a common denominator for the preparation, planning and implementation of motor act. Two main hypotheses delineate its functional role. The first one ascribes a *complementary* role to the medial part of area 6 which acts in parallel to the primary sensorimotor area for the programming, starting and execution of voluntary movements. On the other hand, the second one attributes a *supramotor function* to the MII which initiates and controls the voluntary movements involved in the forming of a new motor scheme, checking the production of conventional movements as well.

In the current opinion there is a general agreement about the involvement of the medial part of area 6 during the preparation and implementa-

tion of bilateral motor acts; a few investigations, using subdural electrodes in epileptic patients before the surgery so as to identify the epileptogenic area and the way the cortex works around it, drawn attention to the fact that bilateral SMA generates pre-motion potentials during simple unilateral motor act. Further invasive researches point out that MII is implicated for the production of movement-related potentials both for simple and complex (repeated) unilateral movements. Therefore the supplementary motor area is also fundamental during the preparation of simple and complex unilateral movements. Ikeda et al. (1995) had verified the role of MII for the development of movement-related potentials and if this motor area acts prevalently during bilateral or unilateral movements in case of 3 epileptic patients.

The data were obtained through an invasive method indispensable for the evaluation of epilepsy surgery; the recording of the cortex, and specifically of SMA, is guaranteed by subdural electrodes implanted in cortex. For the first patient unilateral and bilateral foot movements were studied; for the other two patients unilateral and bilateral movement of thumb and middle finger were analysed. The scholars pointed out that the early BP and the NS at the MII evoked by bilateral and unilateral movements are nearly the same, while MP at SMA has a wider negative deflection for bilateral movements. Hence the medial part of area 6 plays a key-role during the actual execution of bilateral movements (reflected through the Motor Potential) and not only during the programming phase (BP and NS).

A high resolution EEG study proposed by Urbano et al. (1996) showed a significant cortical activity of the *contralateral sensorimotor* and supplementary motor area, during the preparation and implementation of simple and unilateral self-paced right middle finger extensions. A minimal activation was found also for ipsilateral sensorimotor cortex during the unilateral self-initiated movement. This studying strengthens the idea that MII is not involved only for the planning of voluntary complex movements, for the reproduction of new motor sequences or during the integration of sensory information for motor output, but also during the *control of simple movements*.

Other recordings from invasive methods found as principal generators of BP the bilateral sensorimotor and supplementary motor area for finger movements, while the late readiness potential (NS) is generated by contralateral MI and MII. Finally the somatosensory area and the contralateral MI generate MP. Further fMRI studies providing a higher spatial resolution of the cortical areas highlight that the rostral part of MII is involved during the motor preparation process.

Considering the time course of MII and MI prior to self-initiated movements two hypotheses stand out. The first one states that the readiness potential might be the resulting of a serial activation of MII which precedes

MI. The second hypothesis considers BP as an outcome of a co-activation of MII and MI which act in parallel; in this case the cortical activity of SMA continues until the onset of the movement (Jahanshahi & Hallett, 2003).

Since both the rostral part of SMA and premotor cortex are anatomically connected with the *prefrontal cortex*, it seems legitimate to analyse if lesions of the frontal area generate a deficit in the neural motor network and consequently would cause alterations of movement-related cortical potentials. This anatomical site has a primary role for the maintenance in the working memory of the motor program and for the timing planning of the actions too. It is believed that it has a main function during the selection between different motor responses, on the basis of the integration of sensory information, motivational and emotional factors (Umiltà, 1995).

Another function frequently ascribed to the prefrontal cortex concerns the forming of the intentions which precedes and leads the behaviour. Its role assures the ability to anticipate and appraise the actions' outcomes.

In the light of its various functions this site is essential for the programming of a general motor scheme which might be transmitted to the higher order motor areas. From these latter sites the motor plan would be processed and single motor subcomponents of the program would be determined and conveyed to MI which implement the final movements that compound the motor act (Umiltà, 1995).

Wiese et al. (2004a) had verified the dysfunction of the motor system during the acute phase of prefrontal traumatic injury (within 8 weeks since the lesion) and during 3 follow-up examinations at 12, 26, 52 weeks since the trauma (2004b) comparing the patients with a control group of normal volunteers. In order to evaluate the extent of the focal lesions and the relative effect that the traumatic prefrontal injury had on movement-related cortical potentials of self-paced abductions of the right index finger, the researchers collected data coming from fMRI examinations, neuropsychological screening of the attention, and ERPs measures. Data collected from the patients group within the 8 weeks showed a significant reduction of amplitude for BP, especially at the vertex of the scalp; moreover the BP latency was delayed as to the controls. These outcomes were red in the light of the noteworthy reduction of the prefrontal projections to the rostral part of MII for the experimental group. The authors conclude that lesions in the prefrontal region do not only cause functional disabilities related to these sites, but also concern skills which are peculiar of different anatomical areas connected to the prefrontal area. In particular the results highlight that the preparation and planning phases of the motor act are damaged rather the execution level, and this is evident by the abnormal occurrence of BP. Since the supplementary motor area is one of the principal generator of the readiness potential, and consider-

ing the unusual trend of BP for traumatic prefrontal injury patients, Wiese et al. (2004a) conclude that a breaking occurs at some level of the connection between SMA and frontal lobes.

As it is mentioned in this work two main routes are well-known in literature which connect the above anatomical sites. The first one forms a cortical-striatal-pallidal-thalamic-cortical motor loop. This direct pathway connects the prefrontal cortex to the striatum, which is the receptive part of the basal ganglia, and it sends efferent projections to the medial (internal) pallidum, and then onto the substantia nigra (pars reticulata). From these structures the projections reach the ventral anterior nucleus of thalamus and finally the area 4 and 6 of the cortex. The second pathway involves a cortico-cortical route which connects pre-SMA with different prefrontal regions as for instance BA46. Damage of the fronto-subcortical loop, which is caused for the majority of the above mentioned patients by a left frontal lesion, is counterbalanced by the contribution of the right ipsilateral hemisphere, and specifically from the postrolandic area which answers for the motion. From a function level these areas guarantee an increase of attentional resources which monitor the motor execution and compensate for the reduction of planning abilities.

A significant study managed by the same authors (Wiese et al., 2004b) shows the value of longitudinal analysis for the studying of movement-related cortical potentials. As they argued these potentials are not static, but they tend to change during the recovery process which follows a traumatic brain injury (prefrontal area). For this reason it becomes essential to check if the brain plasticity, that is the functional reorganization following the lesion, leads to the recovery of the readiness potential which was reduced and delayed during the first 8 weeks. EEG analysis was performed 12, 26 and 52 weeks after the lesion, during a self-paced abduction of the right index finger. Considering the recovery of the readiness potential for the patient group after 26 and 52 weeks, mainly over the medial central area of the scalp, the researchers stated that the re-establishment of the neuronal input into SMA had occurred. As it has been asserted it is of primary importance that the routes (cortical and subcortical) to MII would be undamaged. Comparing after 52 weeks the results of the patients group with those of controls, the readiness potential for the first group increased significantly over the contralateral prerolandic hemisphere.

How to read these results? Wiese et al. (2004b) argued that in order to reach a similar performance in comparison with the healthy volunteers the prefrontal patients have to allocate more attentional resources for the execution of the action; therefore an alternative network settled during the recovery did not work in the same way as the original one and demanded conscious resources necessary for the motor execution. This is not clearly required when prefrontal lesions does not occur.

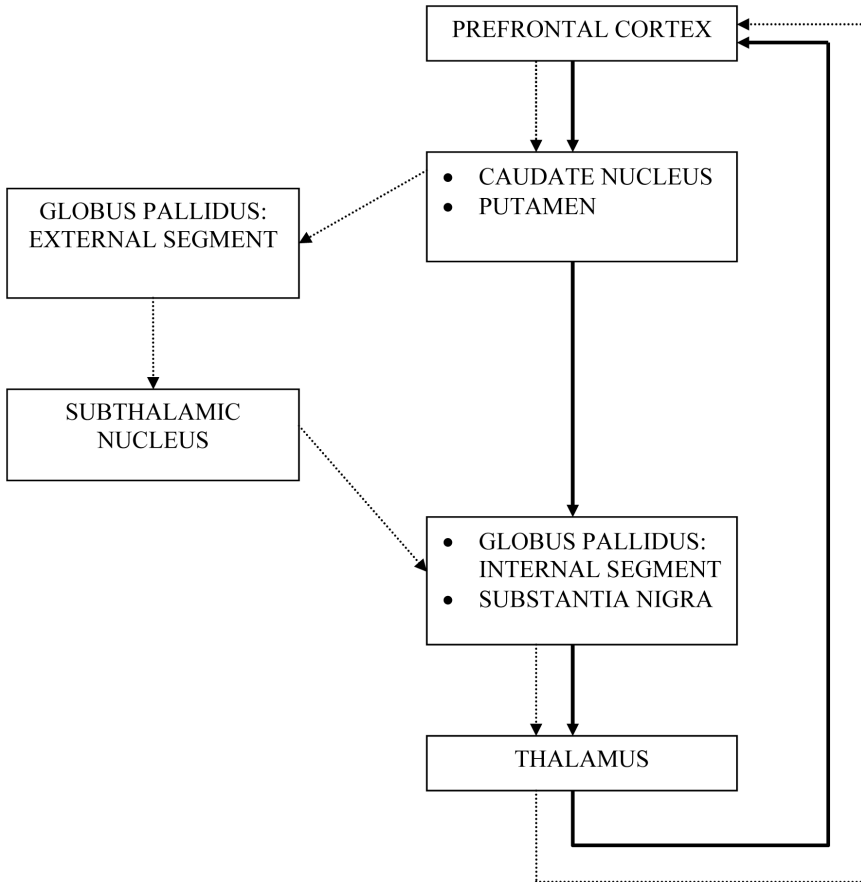


Figure 1. Scheme of fronto-subcortical pathways (modified from Grossi & Trojano, 2005)

1.2. Lateralization effect of movement-related cortical potentials and its functional value

The question of the movement-related cortical potentials lateralization assumes primary importance in the neuroscience of action, especially in view of the strict relationship between perception and action. Touzalin-Chretien and Dufor (2008) have verified the distribution of the readiness potential in healthy volunteer during a task where it was asked to press a button as

quickly as possible later than the lighting of a LED. During the reaching movement performed with the right hand subjects were instructed to fixate the act in a mirror which was placed sagittally and therefore covering the opposite non-moving hand and generating the optical illusion that the left hand was moving. Three other control conditions were used so as to compare the lateralized readiness potential: (1) direct view of the right performing hand; (2) frontal view of the right performing hand, through the frontal positioning of the mirror; (3) direct view of the left performing hand. Results show a significant activation of the readiness potential contralateral to the non-moving left hand. The observation of the image of one's own upper limb in motion generates an activation of the contralateral primary motor cortex even if the opposite limb is involved in the reaching movement. The researchers conclude that the recording of the readiness potential when the mirror is placed laterally covering the real non-moving hand, strengthens the idea that visual and motor systems are steadily correlated, above all during the preparation, planning and execution of motor acts.

The issue of lateralization and cortical generator has to contemplate the role of motor potential (MP) which assumes different features depending on the ability/disability to carry out movements. Castro, Diaz and van Boxtel (2007) analyzed the movement-related cortical potentials in *spinal cord injured patients* unable to move their toes and compared the results with those collected by two control groups. The experimental group was composed of 8 paraplegic and 2 tetraplegic patients. The task required an active preparation and execution of a motor act (flexion and extension of the toes) as soon as an acoustic stimulus was heard (experimental group and first control group) or a motor preparation of the same movement without physical implementation (second experimental group). Lesions of the segments of spinal cord were intervened between 2 and 5 months before the studying; this time interval was chosen so as to analyse the brain reorganization following the first lesion's phase. Core results pointed out that the amplitude of the readiness potential for spinal cord injured patients was not unlike as regards to the "movement" and "no-movement" control groups, assuming an intermediate value between the controls.

The topographic distribution of the readiness potential was similar for experimental and movement control group, assuming a maximum amplitude in centro-parietal sites, while for non-movement control group the largest amplitude was recorded in the parietal area. In the patients group and movement control group the increase of the readiness potential over the central region was greater at the midline than in either the hemispheres. Lack of inter-hemispheric lateralization effect suggests the importance of the effector; that is in this case the use of lower limbs rather than the upper ones.

How to explain this data? This is referable to the participation of both the controlateral primary motor cortex and the bilateral supplementary motor areas.

The recording of the readiness potential has been done also for stroke patients during the recovery of the affected hand. A larger amplitude of the late readiness potential occurred at the central area ipsilateral to the paretic hand; this suggests that the ipsilateral motor cortex leads the motor recovery of the affected upper limb when the other hemisphere (controlateral) is damaged (Honda, 1997).

As we argued a fundamental role for the corticospinal activity which triggers the motion is carried out by the controlateral primary motor cortex (BA4) which is reflected through the motor potential (MP). It is common knowledge that the electrical stimulation of the brain cortex areas of corticospinal pathway cause muscular contractions of the controlateral half of the body (Umiltà, 1995). Many studies had explained that MI is very sensible to the electrical stimulation. As a matter of fact the stimulation of specific sites of MI caused the repetitive contraction of groups of muscles; this shows that BA4 has a somatotopic organization of the whole controlateral motor periphery (Umiltà, 1995). As regards to MP, no overall differences were found between the frontal and central areas both for spinal cord injury patients and no-movement control. Nevertheless for movement control group the distribution of MP was greater for the central site than for the frontal area. This means that for those who performed the movement the amplitude of MP is greater close to MI.

Moreover for the experimental and no-movement control group the amplitude values of MP recorded for both the inferior limbs were not correlated with the laterality condition. On the other hand for those who performed the movement, MP in the left hemisphere was greater when the movement was performed with the ipsilateral foot and not with the controlateral one; an analogous outcome was also noticed over the opposite hemisphere. This research makes clear that in case of spinal cord lesions the movement-related cortical potentials do not disappear, and the readiness potential is almost the same as to the healthy subjects which prepare and perform the action. On the other hand this analogy fails for the motor potential, where this component is more similar between patients and no-movement control group. The authors concluded that in case of diseases of spinal cord or peripheral nerves the MP and not only BP are useful markers for the evaluation of the functional reorganization of the brain (Castro et al., 2007).

The physiological significance of MP as an index which reflects the corticospinal activity involving the primary motor cortex controlateral to the voluntary movement becomes more clear through the analysis of Mayer et

al. (1995). In this study movement-related cortical potentials were recorded in 6 mirror movements patients compared with 7 healthy subjects. A mirror movement could be defined as an automatic and involuntary reflex of the opposite side of the body during the intentional movement of the other contralateral effector. Generally these involuntary movements concern the upper extremities of the body. Aim of the researchers was to analyse pre-motor potentials and lateralization of the cortical activity during the preparation and execution of self-initiated voluntary extensions of the middle finger of both hands. As a significant involuntary muscle activity of the opposite limb appears during the motor performance of mirror movements patients, the researchers were interested to evaluate the lateralization of MP. Data showed similar components related to the preparation phase for controls and patients: there were no significant differences between the groups for the readiness potential and the negative slope too. On the other hand MP was bilaterally distributed over the left and right MI for mirror movements patients, while for the controls was clearly lateralized to the contralateral MI. Therefore a large cortical activity of the ipsilateral hemisphere occurs for the patients, and this supplementary cortical activity around the EMG is able to balance, at least to a certain degree, an atypical connection between the cortical motor system and the spinal motoneurons (corticospinal pathway).

4. KEY SUBCORTICAL SYSTEMS AS GENERATORS FOR MOVEMENT-RELATED CORTICAL POTENTIALS

We have seen that the expression *Bereitschaftspotential* indicates a sequence of electrophysiological subcomponents which are also called “movement-related cortical potentials”.

This latter term makes clear that a variety of generators are localised in the cortex. However other generators come from *subcortical structures*. Even though it might be difficult to explain and quantify the participation's level of subcortical generators, there are several evidences which back the involvement of these systems. The results come chiefly from intracerebral recordings of patients candidates for epilepsy surgery or with intractable chronic pain.

The planning and the execution of an action entail a control phase which is fulfilled by the activity of the cerebellum and the basal ganglia. These structures have connections with the corticospinal pathway and other descending cortical tracts.

The *cerebellum* has a primary role for the regulation of skilled action (Gazzaniga, 2004). The more recent structure in the phylogeny process,

that is the *neocerebellum*, is responsible for the monitoring and planning of intentional acts. Lesions to the posterior lobe of the cerebellum cause lack of motor coordination, especially when the action required the timing of more than one effector. Looking at the question of its functional role Gazzaniga (2004) reports at least two principal hypotheses:

- a. The cerebellum is responsible for the *timing of the movements*. As soon as the selection of the limbs occurs (process carried out by the cortex), the cerebellum answers for the muscular synchronization required for the activation of the different limbs involved in the motor sequence.
- b. The cerebellum enables an *advance sensory outcome of the action*. As soon as the lateral cerebellum receives a go-signal to move it sends to its turn a feedback signal to MI defining force, direction and timing of the effectors involved for the action's execution. The cerebellum provides these parameters on the basis of anticipations about the sensory consequences of the action. This ability is based on the previous experience of the subject.

A deep lateral cerebellar nucleus, called *dentate nucleus*, seems to be essential for the planning of the action while the other nuclei have a share in the motor control. Thach and colleagues (1992) had shown that the dentate neurons fired before the onset of the voluntary movements and their inactivation postponed the initiation of the intentional acts. Some studies mentioned in the article of Brunia et al. (2004) report that lesions of the deep lateral cerebellar nucleus correlate with the lack of the readiness potential (Shibasaki, 1978; Ikeda, 1994). However other works do not reach the same conclusions and emphasize that lesions of the dentate nucleus cause the lack of BP just over MI but not over the premotor cortex (Gemba et al., 1980).

Also the *thalamic nuclei* share in the development of BP. Intracerebral recordings obtained from patients with intractable chronic pain drawn the attention to the contralateral nucleus posterolateralis (Rektor, 2003). *Posterior thalamus*, *midline thalamic nuclei* and *motor thalamic nuclei* are subcortical structures where it is possible to find out generators of BP.

During the last years the use of *deep brain stimulation* for extreme cases of Parkinson's disease or Essential Tremor has pointed out the function of the *subthalamic nucleus of Lewis (basal ganglia)* and the *ventral intermediate nucleus of the thalamus* which projections reach the cortex (Brunia et al., 2004). Clinical cases with Parkinson's disease assert the importance of the *striatopallidonigral system* for the development of the readiness potential. As a matter of fact a significant reduction of amplitude in this potential is evident for Parkinson's disease sufferer. This depends on the reduction of activity of *dopaminergic neurons of the substantia nigra*. Pars reticulata of the substantia nigra and internal pallidum are the efferent connections of the basal ganglia and these project to the ventroanterior nucleus of thalamus. The efferences

of this latter nucleus reach the area 4 and 6 of the cortex. From this point of view the direct pathway formed of the internal pallidum and thalamus has as target structures the primary motor cortex, premotor cortex and the supplementary motor area. It is interesting to remember that a first hypothesis which comprised the role of subcortical systems for self-paced movements was already worked out by Deecke, Grözinger and Kornhuber (1976).

The striatopallidonigral system has a primary function for the facilitation and inhibition of the movements. The cortical selection process among possible motor plans is favoured by the basal ganglia. The inhibitory activity of the subcortical system allows the monitoring of the motor system and the answering for the selection of a range of motor programs in competition, without the muscular response which produces an actual movement. As soon as an action plan prevails against the others the inhibitory signal decreased while the facilitation one raised up (Gazzaniga, 2004).

It is not clear if the basal ganglia are involved for the production of motor sequences. Parkinson's disease sufferers for instance make more mistakes during movements which require different gesticulations and they become bradykinetics (Gazzaniga, 2004).

Another hypothesis states that the difficulty for Parkinsonian patients to trigger the movement, giving the sensation of "freezing" subjects, depends on a deeper disability to change "cognitive coordinates" which interact with the motor level (Gazzaniga, 2004). This hypothesis looks basic so as to build a motor cognition theory, where the striatopallidonigral system carries out a key-role for the action and the cognitive processes too. If it is true the basal ganglia back the activity of the cortex, answering for the dynamism and the fluency of the motor sequences.

To conclude the discussion of generators implied in the development of movement-related cortical potentials associated to voluntary self-paced movements, it is most likely that the *Bereitschaftspotential* might be the outcome of more than a few cortical and subcortical structures, and not a mere cortical event (Rektor, 2003). This is not surprising because the motor system of the brain is wide. Without any pretension of order it includes the rostral and caudal part of SMA, primary motor cortex, premotor cortex, dorsolateral prefrontal cortex, frontal eye fields, posterior parietal cortex, cingulate cortex and structures as the cerebellum, basal ganglia, thalamus and the overwhelming majority of the spinal cord (Pocket et al., 2006). The exact definition of how much depends on cortical or subcortical generators still remains subject for discussion, even if it is possible to assert that the share of the cortex is essential and fundamental.

Table 2. Main cortical and subcortical generators of movement-related cortical potentials

CORTICAL GENERATORS		
POTENTIAL	AREA	LATERALIZATION
<i>Early BP</i>	MII (rostral and caudal area)	Bilateral
	MI	Bilateral
<i>Negative Slope (NS)</i>	MII (caudal area)	Controlateral
	MI	Controlateral
	Prefrontal cortex	Controlateral
<i>Motor Potential (MP)</i>	MI	Controlateral
SUBCORTICAL GENERATORS OF BEREITSCHAFTSPOTENTIAL		
CEREBELLUM	BASAL GANGLIA	THALAMIC NUCLEI
		Posterior thalamus
Dentate nucleus	Subthalamic nucleus	Midline thalamic nuclei
		Motor thalamic nuclei

5. PSYCHOLOGICAL FACTORS AND MOVEMENT-RELATED CORTICAL POTENTIALS

There are different factors which could influence the amplitude and topography of BP (for a complete review Jahanshahi & Hallett, 2003; Shibasaki & Hallett, 2006). This section aims to summarize, starting from the above mentioned works, some psychological features which correlate with the changing observed in BP.

The *intention to act* constitutes the basis for the motion. We might define “intentionality” as the will to move so as to achieve an overt state oriented towards a changing in our environment.

Usually this change in the external world is indispensable for reaching goals or needs. The intentional involvement might be conceived as the final stage of a neuro-psycho-physiological process which includes a sequence of motor information and the respective instructions in order to produce a goal-directed movement. It is tightly correlated with the motivational level, but these dimensions are not superimposed.

The motor system model proposed by Pocket and colleagues (2006) devises two intentional levels. *Willed intentions* form the first dimension: they cause a general plan where goals and types of movements are defined. The dorsolateral prefrontal cortex and the rostral area of MII represent the foremost cortical generators of willed intentions. On the other hand *sensori-motor intentions* answer for the integration of sensory information into the previous plan, adapting the motor commands to the external event. Posterior parietal cortex supports this level.

Initiation of the act forms the next step of the motor system model. The researchers assert that it is quite difficult to locate an exact neural starting mechanism. As a matter of fact some movements are triggered in response to external cues while others are self-initiated. This division involves the parallel activation of different brain regions as dorsolateral prefrontal cortex, SMA, striatopallidonigral system and primary sensorimotor cortex. With reference to the temporal activation of these regions it is probable that the cortical activity flows from rostral to caudal direction and then conclude in MI (Pocket et al., 2006).

The *ongoing monitoring* and the *adjustment* of the act are critical features for the achievement of goals. This constant control could be carried out using somatosensory information both in unconscious or conscious modality. The former is certainly mediated by the cerebellum (cerebrocerebellum) while the latter by the activity of the frontal cortex (Pocket et al., 2006).

As Jahanshahi and Hallett (2003) stated in their book, *movements performed in an automatic and stereotyped way* cause a reduction of BP amplitude. In view of the fact that the overwhelming majority of the researches work with experimental designs where it is required the repetitive performing of self-initiated elementary movements (as for instance move a finger or a toe) there is a low level of motor freedom because the act is rather prearranged and also the same. In this case the planning of the action (for each movement) does not coincide with the sequence of different motor orders directed towards the forming of a complex movement, but rather to the timing selection of "when to move" a certain muscular group.

Motor intentionality means the evaluation of the action's awareness and the estimation of the automatic demands in habitual situations. A range of studies have drawn the attention to the reduction of amplitude of movement-

related cortical potentials during the *long-standing execution of identical and recurring movements*. The decrease of BP has been ascribed to an increase of the *fatigue level* and indirectly to a reduction of the intentional involvement dimension (Freude, 1987).

Others believe that this drop in amplitude depends on a *motor learning process* which required less attentional resources (Taylor, 1978). An interesting work of Dirnberger and coworkers (2004) emphasizes that the amplitude's reduction is significant for the *right hemisphere* independently of the side of the moving effector. In this study 33 healthy volunteers were enrolled for a simple task requiring the repetitive pressing of a button, at first with an hand and then continuously with the opposite one. This means that some of the right-hemispheric functions are less involved and fundamental during the repetition of recurring movements. The reduced activation of BP over the frontal and parietal area of the right hemisphere might be interpreted through automatic mechanisms which balance the decrease of the attentional demands.

Fixed repetitive movements correlate with lower BP amplitude compared with *freely movements* (Jahanshahi & Hallett, 2003). An increase of BP during the freely movements of a joystick (Praamstra et al., 1995) is evident in the supplementary motor area which "reflects the higher demands of planning before the execution of freely selected random movements" (Lang, 2003).

Another factor which influences BP is the *complexity of the movement*. Lang (2003) reports the experiment of Benecke et al. (1985) which compared the readiness potential before (a) single movements; (b) sequential complex movements; (c) simultaneous complex movements. The results showed that the amplitude of BP was larger for complex movements in comparison with single movements. Same results were obtained through the work of Simonetta and coworkers (1991). Here the volunteers had to perform a simple flexion of the index finger and then the same movement followed by a more composite act (the use of a button). Even in this case the complex sequence evoked a larger and earlier BP as to the simple movement. The scholars highlighted the difficulty to disentangle the above results because first it is not clear if the complexity of the action implies an exclusive regional activation of MII or a wider distribution activity of MI and MII simultaneously.

In the second place the manipulation of the task's complexity has to faced with intervening potential variables as the degree of novelty, motivation and intentionality which influence the amplitude and topography of BP.

Other factors which play a key-role for the distribution and amplitude of the movement-related cortical potentials are *force*, *inertial load* and *speed of the action* (Lang, 2003). Also the *part of the body* involved in the intentional action is decisive (Lang, 2003).

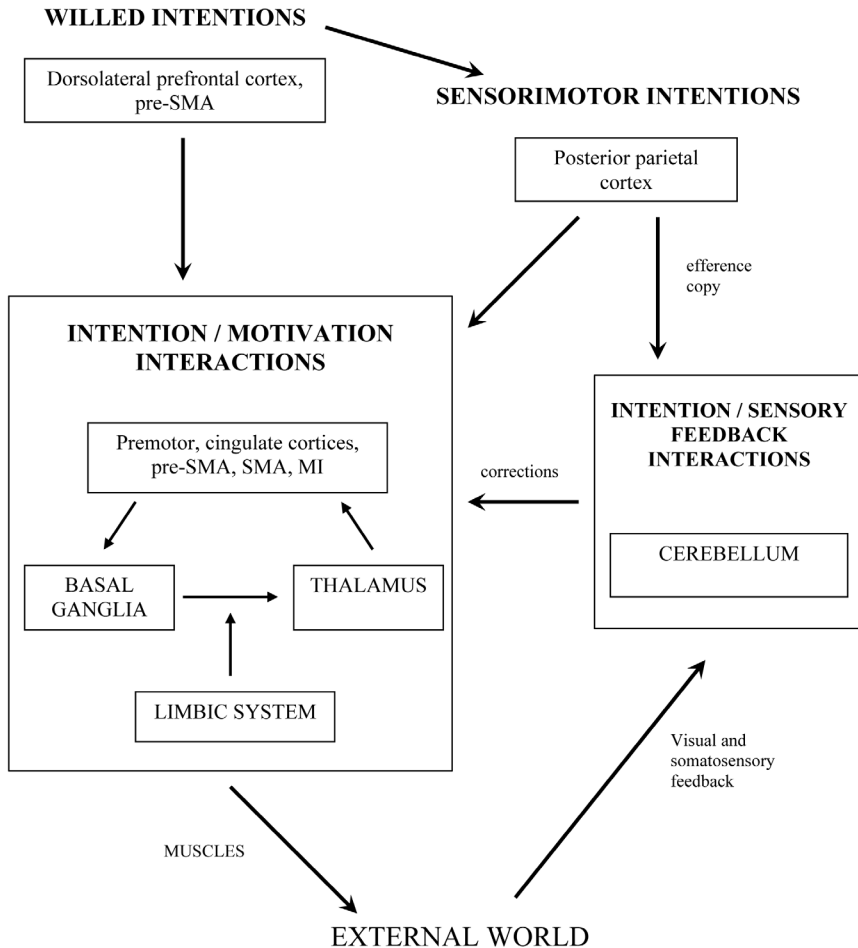


Figure 2. Scheme of the motor system model proposed by Pocket (modified from Pocket et al., 2006)

5.1. Motor representation and movement-related cortical potentials

Although the factors quoted in the previous section usually are implemented automatically in the motor commands, it is possible to make them explicit through the use of a *motor imagery* paradigm.

Motor imagery is defined as an internal rehearsal of a movement without any overt physical movement (Jeannerod, 1994). It belongs to the same category as those involved in motor preparation and programming differentiating for the fact that the cortico-spinal output is blocked for the former (Decety, 1996). Motor imagery process involves part of the neural structures which are necessary for the control, monitoring and planning of actual movement. Two perspectives qualify this cognitive experience. A *first person* or internal perspective highlights motor-kinaesthetic information, while *third* or external imagery emphasizes visuo-spatial information of the action (Decety, 1996).

According to Jeannerod thought (1994, 1997) every movement we perform daily is led by a representational level which defines goals and ways to reach them. Our representative capability is central for action: it may be built from the interaction between environment and our cerebral organization. Even the simplest movement that the nervous system generates is planned purposefully. In fact CNS organizes our muscles in such a way as to the total synergistic muscular activities turn out a regular and planned act. The representational level processes the acts in a *pragmatic way* which comes out difficult to put it into words: in fact motor representations are not objects of contemplation, they are normally rapidly transformed into movements. In this sense “motor imagery is a key-process for the comprehension of motor representations because it renders them available to the consciousness. Motor imagery represents the result of conscious access to the content of the intention. Motor preparation is an entirely non-conscious process, which escapes the subject’s awareness. Only the final result is under the subject’s judgement, so that the action, once executed, can be recognized by him to correspond (or not) to his intent. By contrast, the content of motor images can be accessed consciously by the imager”. “Conscious” (imagined) and “non-conscious” (prepared in view of execution) actions share common mechanisms and show functional equivalence” (Jeannerod, 1994). Motor imagery represents the result of conscious access to the content of the intention of a movement, which is usually performed unconsciously during movement preparation. Taking in mind this perspective, conscious motor imagery and unconscious motor preparation share common mechanisms and are functionally equivalent (Lotze & Halsband, 2006).

Carrillo-de-la-Peña and colleagues (2008) verified the functional role of MI during the actual execution of finger’s motor sequences compared with the imagination of the same movements. This study aimed to record the lateralized readiness potential (LRP) during the exposure of a preliminary cue (two arrows pointing to the right vs to the left determining the selection of the effector) followed by a numerical stimulus (1, 2, 3) which fixes one out of the three motor sequences previously learned and now actually performed or

imagined. The results showed two specific phases of the lateralized readiness potential. During the first stage of LRP no significant differences stood out between the experimental conditions (actual vs simulated movement); this means that the preliminary cue causes an early LRP which reflects a planning process oriented to the selection of the suitable limb, and this is true for both conditions (physical execution vs simulated execution).

On the opposite side the presentation of the target stimulus directed towards the settlement of the motor sequence causes a lateralized readiness potential which is largest for the actual execution as regards to the motor imagery task. From this viewpoint it might be possible that the second phase of LRP reflects the enhancement of the planning process which aims to comprise all the action's parameters as force, direction, motor sequence and actual implementation.

In addition to the ERPs analysis they used low resolution tomography so as to determine which areas of the motor system were mainly activated during the tasks. Data drawn the attention to the primary involvement of posterior cingulate gyrus (BA31 and BA23), the anterior cingulate gyrus (BA24) and insula (BA13) during the actual execution of the motor sequence. In conclusion this work points out the cortical activation of BA4 during the imagination and execution of the action. These results argue against the original idea of a hierarchical organization of the motor system where BA4 has only an executive function, and support the idea of a functional equivalence between imagery and execution. Besides it becomes comprehensible that MI has high-level motor properties. However the analysis of the different periods of the lateralized readiness potential reveals considerable differences between the processes which come the researchers to state that "equivalence" does not mean "equality" (Carrillo-de-la-Peña et al., 2008).

Moving in the view of MI involvement the same authors (2004) had once examined the rate of LRP during the simulation and actual execution of the thumb so as to give support to the idea of a primary activity of BA4 during the mental rehearsal of an action. Volunteers had to press (first condition) or imagine to press (second condition) a button of a keypad according to the target stimuli (two arrows pointing left or right indicating which hand should be used). Before the latter precues stimuli consisting of two arrows pointed in the same way of the target (congruent condition) or in opposite direction (incongruent condition) occurred. Control condition scheduled the occurrence of a circle, which had to inhibit the performance. The simulation of the action generated a lateralized readiness potential which had the same distribution and latency of that obtained through the actual movement. Besides for both the conditions LRP was largest for the incongruent trial as to the congruent one. These results strengthen the idea of a contribution of MI

during motor imagery process. However the amplitude of LRP is lower for imagined movements compared with the actual ones. This difference should be interpreted as a reduction of the main parameters codified for motor imagery process; not all the kinematics features has to be processed during this mental state, but only a small part of them (for instance the limb selection and movement direction). Moreover this analysis makes clear that the sensory information are continuously updated during the implementation phase: in fact LRP is larger and delayed for the incongruent condition as to the congruent one. Lateralized readiness potential reflects both a preparatory stage shared between actual execution and mental rehearsal and an effective implementation level exclusive for the action. For both cases primary motor cortex carries out a significant function.

Using the same paradigm a recent analysis of Carrillo-de-la-Peña and coworkers (2008) tried to record the lateralized readiness potential; in this case equivalent experimental conditions were submitted adding two new responses to the target stimuli: (a) actual flexion of the matching toe; (b) imagined flexion of the equivalent toe. Motor imagery generated a lateralized readiness potential with the same properties (latency and waveform) of those obtained during the physical execution, even if the amplitude was lower for imagined movements. Therefore the occurrence of LRP during the mental simulation proves that a cortical activity oriented to the action preparation, and specifically to the selection of the limb, takes place even if the participants prepare an act which will not be performed later. It is noteworthy that for both the conditions (motor imagery and physical execution) the polarity of LRP was reversed during the preparation response of the foot.

This inversion of polarity becomes one of the principal arguments in favour of the contribution of BA4 during the motor imagery process (Carrillo-de-la-Peña et al., 2008). Only the somatotopic representations of different parts of the body explicate the inversion of polarity of LRP between the conditions (*ibidem*). And as they argued this inversion gives reason for leaving out other cortical generators as the lateral and medial part of area 6. Because LRP is generated in MI it is possible to extend its functional role beyond the mere transmission of motor command, and considering it as involved in the action preparatory process.

The research of Jankelowitz and Colebatch (2002) offers a complementary perspective in order to compare and analyse the relation of the movement-related cortical potentials for tasks requiring the execution of self-initiated, cued and imagined finger and shoulder movements.

Fourteen subjects were instructed to perform different tasks with their right effectors: (a) self-paced movements (abduction of the index finger, flexion of all fingers, elbow flexion and shoulder abduction); (b) rapid finger

and shoulder abduction in response to a time interval prearranged acoustic stimulus; (c) imagination of the same movements performed in b condition after the presentation of the acoustic stimulus, using a first person perspective; (d) just for half of the participants rapid finger and shoulder abduction in response to an acoustic stimulus presented randomly; (e) for the other seven subjects a new recording (with the adding of electrodes) of self-paced abduction of the shoulder and the actual and simulated abduction of the index finger and shoulder. Movement-related cortical potentials occurred for all the conditions (self-paced, cued and imagined movements). Even so the amplitude of the pre-motor potential prior to the imagined movement was lower than the self-initiated and cued movements. The maximal amplitude was present over Cz, and it is largest for shoulder condition as to the finger one. An interesting data comes from the analysis of C3 electrode. The latter recorded an higher amplitude for self-paced and cued movements as regards to the simulated arm movements. This means that for the motor imagery condition no lateralization effect occurred. The occurrence of a maximal peak at the vertex of the scalp leads to the investigation of the cortical generators involved in motor imagery. The area below Cz comprises a part of the supplementary motor area and more deeply the cingulate motor areas; therefore the pre-motor potential should reflect the activity of both the areas. The incidental activation of the motor cortex seems insignificant, and therefore they did not find an involvement of BA4. Indeed results showed a symmetric distribution of the readiness potential at Cz, where the NS did not occur for imagined movements.

The above records call attention to the functional difference between *conscious* and *unconscious* motor preparation. In this wake Castro and coll. (2005) tried to analyze and compare pre-movement potentials between participants who were instructed to prepare and then realize toe movements and people who were told to prepare the same movements but without the final execution. The preparation phase for the execution of a repetitive motor sequence was higher when people performed the movement compared with no-moving condition. A larger amplitude of RP were recorded over the central area when the movements start. For non-moving condition RP was maximal over the parietal region. It is worth mentioning that the readiness potential was largest for moving condition as to the non-moving level. In addition no significant differences were found for the subsequent potentials (PMP and MP) between the experimental conditions. This is remarkable because suggests that as soon as the movement is prepared (reflected through the activity of RP) the amplitude of the pre-motion potentials correlated with the execution phase (PMP and MP) does not depend on whether the act is performed (Castro et al., 2005).

6. CONCLUSION

This paper starts with a general description of *movement-related cortical potentials*. The picture obtained is rather articulated.

First of all, the overwhelming majority of researchers make use of different terms in order to refer to the same general phenomena. This taxonomy accounts for various components partible in two main categories: *pre-movement* potentials and *post-movement* potentials. Here we have envisaged barely the pre-motion category.

The description of *cortical* and *subcortical generators* for self-paced movements clarifies a mutual involvement of both sources, particularly when the movement takes place. Therefore readiness potential recorded on the scalp might be an outcome of summated potentials which are generated at the same time from cortical and subcortical structures (Rektor, 2002). In this sense decreasing of BP in motor imagery process might depend on a transitory and partial activity of the cortical motor areas specifically involved during the actual execution. A reduced and partial involvement of subcortical structures might represent an additional explanation for the data coming from motor imagery researches. “Transitory and partial” does not mean “absent”, therefore MI, basal ganglia and cerebellum have a functional role for high-level motor processes as motor imagery and motor representation too.

Several factors, as already reported by Shibusaki and Hallett (2006) and Hallett and Jahanshahi (2003), influence the topography and magnitude of BP. Here we have emphasized, starting from these reviews, the importance of some *psychological variables* like *intentionality*, *movement complexity* and *attentional demands*.

Finally when we assume terms as “preparatory and executive stage of the action” we have to consider an *action representation* dimension which is in most cases automatic and unconscious.

Make this level conscious (through a mental motor image) means to reconsider the functional value of the readiness potential: namely the event that the electrophysiological features of BP would be different during the simulation of the action as to its real implementation. As a matter of fact *sharing of brain structures does not stand for a full overlapping of them*.

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