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Introduction/Editorial

Planning, preparation, execution, and imagery of volitional action

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Abstract

There are different motor sets, which a human subject can be in or act from: he or she can be in a self-initiated voluntary movement set (action) or in a response set (re-action). Also, imagery sets are available that are necessary for the acquisition and practice of skill. Most important are such imagery sets for rehearsal in theatre, dance, music, sports, combat, etc.

1. Self-initiated voluntary movement set (actions)

When a human subject performs a voluntary movement, cerebral DC-waves can be recorded that precede the movement and most probably are an expression of the brain preparing for the execution of the voluntary movement. Our group has been interested for the last 32 years now in slow potential shifts preceding such movement [28,29]. The negative shift occurring under these circumstances is called the Bereitschaftspotential (BP) or readiness potential and starts as early as 1 to 2 s prior to the onset of EMG activity in the muscle. According to theory of EEG, negativity has been related to activity of the cortical area under study, while positivity has been related to inactivity. The self-initiated voluntary movement set is experimentally realized in the Bereitschaftspotential paradigm. The BP paradigm investigates internally produced movements. Libet calls them 'endogenous' [39], although he conceives the initiation of voluntary movement differently from us. In Libet's theory, the cerebral initiation of a voluntary act starts on an unconscious level which only later leads to the appearance of conscious intention. Such thinking makes him bypass the assumption of free will in the initiation of voluntary movement. However, if we start our considerations from a basic categorical aspect, we have to conceive at least two fundamentally different categories of movement.

Movements can be internally initiated (self-initiated) or externally initiated (triggered by events from the outer world). In the first case we speak of actions, which we perform in the absence of an external cue – in our opinion out of our free will; in the latter case we speak of re-actions upon stimuli from the environment. The experimental paradigm investigating the first category of movements is, as mentioned above, the BP paradigm (self-initiated internally cued 'endogenous' volitional acts [3–5,9].

2. Externally triggered movement set (re-actions)

The experimental paradigm for the second category of movements is the CNV paradigm. Walter et al. introduced this classic reaction time experiment into slow cerebral potential research with a warning stimulus S1 and an imperative stimulus S2 after a second or so which the subject has to re-act to [50]. Grey Walter's experiment led to the discovery of another slow DC-potential shift, which he first called just the 'expectancy wave'. In the publication, he preferred the less implicating term 'contingent negative variation' (CNV). I think that Grey deliberately selected this term inviting associations with the classic pavlovian heritage of the contingent reflex in animal conditioning. Thus, the CNV paradigm is the prototype for movements that are not willful in the strict sense, since they do not require will for initiating them; the starting command comes from the outer world. To be precise, the CNV setting may also require will – e.g. in a choice reaction time experiment, the decision making process undoubtedly needs will – however, will in decision, not in initiation. Will in initiation, so to say 'will in the time domain', is required in the BP paradigm. In the CNV paradigm, the individual does not need to care about 'when to do' (i.e. about the right moment to start the movement), the stimulus from the outer world gives this

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command. The 'when to do' is the last of three questions, and we will now explain, why we attribute this question to the supplementary motor area (SMA, [6]).

3. What to do? How to do? When to do?

In more detail, our experimental data so far suggest that the frontal cortex has important functions in central voluntary movement physiology, in particular the mesial frontal surface including the SMA – maybe 'supplementary' is more important than 'primary' (MI) – these include: (3.1) decision about the right moment to initiate a voluntary act, when to do; (3.2) temporal coordination of movements, sequences of movements, bimanual and other interlimb coordination [11,33,36]; (3.3) participation in motor learning [34], also cf. lesion of an SMA [1,10,34].

3.1. Decision about the right moment to initiate a voluntary movement

If we are dealing with actions (BP) – as opposed to re-actions (CNV) –, which a subject initiates out of his or her own will, then we have to postulate a center in the brain that – in the absence of a trigger from the outer world – starts the movement. Our real volitional actions, self-initiated, endogenous, performed at our free will, must have a 'pacemaker', trigger, go-signal, motor command, starting sign or however we name the initiation mechanism that launches the movement. Kornhuber and we suggest that it is the SMA that fulfils this priming function (cf. [6,8,12,30]). Kornhuber has put forward the hypothesis that a voluntary action needs three questions to be answered: (1) What to do, (2) How to do, and (3) When to do. All three strategic decisions are thaught to be carried out by the frontal cortex – Eccles' neo-neocortex – since they are abandoned by frontal lesions, albeit in different frontal regions [15,16].

A tripartition of the frontal cortex has been suggested regarding these three fundamental questions of volition [8]. The frontoorbital cortex is probably primarily involved in deciding 'what to do.' At least lesions of these structures render the patient unable to decide what to do, particularly what is right to do, what is appropriate to do [27]. The 'How question' is primarily dealt with by the frontolateral cortex with its strong corticocortical connections with the sensory association areas of the parietal lobes. Quick decisions regarding the tactics, the 'how' (i.e. what is the best way) to achieve the goal requires always the newest information about the sensory situation. These areas include the prefrontal and premotor areas of the frontal convexity.

After the 'what to do' and the 'how to do' questions are solved, all what is left to be decided is the 'when to do', i.e. to decide about the right moment to start the action. This is the task of the frontomesial cortex, including the SMA. The 'when to do' is the final question in the motivational chain and is as close to the start of the movement – and time-locked to it – that it can be recorded by the BP paradigm, while the other 2 decisions 'what to do' and 'how to do' cannot be directly investigated by our experimental paradigm.

It was one of our early observations that the BP is composed of two components [4,5,32]. The early component (BP1) has a vertex maximum, is bilateral, almost bilaterally-symmetrical, and its slope is usually of a low to moderate steepness. The late component (BP2) has a C1 or C3 maximum (with right-sided actions), is asymmetric (contralaterally dominant), and its slope usually has a higher steepness. These characteristic differences in topography made us suggest that the symmetric BP1 is principally generated by the frontocentral midline including the SMA (with always the two SMAs being active even preceding unilateral actions), while the asymmetric BP2 is principally generated by the MI.

In the MEG (magnetoencephalography), the two components can be seen as well (Bereitschaftsfeld (BF) 1 and 2, [7,14]). In order to overcome the problem of cancellation of the opposing SMA dipoles, experiments were carried out in a patient having a lesion in his right SMA due to anterior cerebral artery infarction [37]. The results clearly show (with right-sided movements) that the only remaining left SMA creates a well-defined dipole during the early BF period (BF1, 1200 to 600 ms prior to the onset of movement), while during the late period (BF2, 200 to 0 ms prior to the onset of movement) the principal generator is a dipole in the left MI (area 4 hand area). This is one of the experimental supports for our hypothesis that SMA leads MI in time in the final motivational cascade prior to the execution of the motor act. Other supports are that in our BP experiments it is always the SMA (midline) that shows the earliest activity prior to starting the motor act. Only later comes the MI activity into play [36].

Thus, we think that in the pre-movement motivational cascade when it comes to intention or the channeling of motivation into execution of movement, it is the frontocentral mesial cortex including the SMA that is involved in this function. Our critics often say that we are attributing a 'supramotor' function to the SMA, but that is not true. We attribute a premotor function to the SMA, and this, indeed, is the SMA's essential function: SMA is pre-motor with respect to the motor cortex, i.e. it is upstream of MI in the final pathway. Or in other words, we extend the premotor nature the SMA undisputedly has in brain topography, cytoarchitecture, hodology and developmental systematics also to physiology: it is pre-motor also in time. In this respect it might be interesting to note that cooling the SMA in monkey abolishes the execution of a motor task requiring a premovement selection process [46,47]. In all our measurements of the onset time of the BP, its earliest onset time is always in recordings from the vertex (Cz) or slightly before the vertex (FCz, [3–5,9]).

3.2. Temporal coordination of movements, sequences of movements, bimanual and other interlimb coordination

Lang et al. [35] found an activation of the SMA in sequential motor tasks. The sequences were comprised of different flexions or extensions of the two index fingers and hands. At variance were the combinations how the above elements had to be composed to sequences by the subject. The DC recordings of the movement-related potentials showed 'phasic' components immediately prior to and after the onset of every single movement element of the sequence. These, however, were superimposed upon 'tonic' DC potential shifts (BP prior to and negativity of performance 'N–P' during the movement). This tonic component (shift of the cortical steady potential) – referred to baseline before the onset of the movement sequence – can be positive or negative. The level of negativity (which is activity) describes the 'activation background' out of which the single elements of the sequence evolve. This negative DC background varied to a large extent with type and complexity of the sequence and the coordinative demands of the task, being significantly more negative over the frontocentral midline in the complex task as compared to the simple task. More precisely, it was over the frontocentral midline (SMA) that in the complex task as compared to the simple one both the negativity and the regional density of the inward-directed current flow (Current Source Density, CSD, [40]) significantly increased, while over the MI hand area of both sides, there was no difference regarding task complexity. The side of the performing hand influenced negativity and CSD of the MI areas significantly but not the frontocentral midline (SMA). This double dissociation clearly shows the existence of two spatially separate neuronal systems with different functionality. This is important to note because it renders Bötzel et al.'s [2] assertion unlikely, who failed to find any SMA contribution to the BP, when applying spatio-temporal dipole source analysis (STDSA) techniques. These authors along with Toro et al. [48] thus created a discrepancy not only with our findings but also with Ikeda et al. [26] and with Rektor et al. [45], who both – using intracranial (the latter even intracerebral) recordings – proved an SMA contribution to the BP. The explanation is that STDSA is not sufficient to resolve the two principal BP sources (SMA and MI) so that they are lumped together in Bötzel et al.'s [2] analysis (cf. [43]).

It is of interest to investigate the cerebral potentials accompanying the performance of voluntary movement sequences over a longer period. Lang et al. [38] investigated changes of cortical activity when executing learned motor sequences over an epoch of 20 s. The quality of performance remained constant over the epoch and the duration of the entire experiment. However, the topographies of the DC potentials changed considerably: in parietal recordings the potential remained stable over the 20 s epoch, over the contralateral MI it declined only slighly. However, over the frontocentral midline (SMA) it declined significanty, reaching baseline at the end of the epoch. This may have to do with a transition from consciously-controlled to more automatic movement execution and it appears that the SMA activity is not immediately associated with processes such as the programming and execution of movement but rather with a supervising control of these processes. Thus, SMA activity is not only necessary for the intention and initiation of the voluntary movement (cf. above) but also for its supervising control during execution – if necessary, i.e. mainly during the acquisition of novel tasks. Once the task, albeit temporally complicated, has been learned to the extent that performance is more automatic, SMA participation seems to be less and less required. This again shows that SMA is not simply a 'performer' but rather a 'supervisor'. Regarding a hierarchy in control for movement, SMA seems to range over MI also in this respect. However, some authors think that the proof of this hierarchical concept is still lacking (cf. [51]). Although also Wiesendanger admits that "in the region of the medial-frontal cortex there is a gradual change from caudal to rostral with the posterior portion being more 'motor', the anterior more 'complex'". We think this is in good agreement with our thinking and would mean that our interpretation of SMA function would mainly pertain to the anterior SMA or pre-SMA of Rizzolatti [41]. In Wiesendanger's intracortical motor stimulation experiments, the anterior SMA was 'clearly less excitable, although more sluggish responses may be obtained, dependent on whether the animal is about to move.' Also the cortico-cortical connections were more widespread in the anterior SMA [25,51]. Luppino et al. [41] in a detailed hodological analysis also described fundamental differences in connectivity between the two SMA portions. Again it would be rather the pre-SMA that has the properties which we attribute to the SMA on the basis of our experiments. However, not enough is known yet about the cingulate motor area (CMA). The CMA is located in the upper bank of the cingulate sulcus, its activation would produce a radial electrical dipole. Such a dipole is well visible in the EEG but not in the MEG.

3.3. Participation in motor learning

This SMA function is also well documented by the experiments of Lang et al. [34]. The SMA is not the only area engaged in motor learning, the premotor cortex of the convexity is also (electrodes F3 and F4 of the EEG) as well as the middle frontal gyrus of both sides in SPECT. Basal ganglia and cerebellum are also involved [13].

It is obviously not easy to define the function of the SMA. Neither lesion studies in man and monkey nor DC-potential studies in EEG and MEG in man, nor Emission-CT studies in man nor single unit recordings in monkeys nor direct cortical recordings in epileptic patients have yielded really unequivocal results. The reason is that the function of the SMA is so extremely task dependent. On the other hand, our hypothesis that SMA – as a prime function in voluntary self-initiated movement or action – has to do with intention (for review see [30]) has never been falsified. On the contrary, piece by piece direct cortical recordings by the Lüders group [26,42] and others [45] have rather confirmed our notion: while earlier, pre-movement activity in the SMA had not been found in intracranial recordings, presently this method – if we accept it as the 'gold standard' – has definitely proven that a BP can in fact be recorded in the SMA [26,45]. Remains the question as to whether SMA activity leads in time before MI activity. On the basis of our data this is so in most cases. Let us see whether also this notion will be confirmed some day.

4. Motor imagery set (mental representation of motor acts)

The 'visualisation' of a motor act, i.e. to internally envisage a motor act without that it actually takes place is the topic of the present special issue, based on the satellite symposium 'Mental representations of motor acts' on the ENA – European Neurosciences Association 17th Annual Congress Vienna 4–8 September 1994. This also is a set, a human subject is capable of – we can see something in our mind's eye – although the imaginative power of individuals may be different. This is thought in psychology or sensory physiology to be an intrinsic personality feature – that persons are more 'eidetic' or less so. In our experiments, we distinguished 'high imagery individuals from low imagery individuals [24]. Psychological considerations have led to two major hypotheses concerning the neurological basis of mental imagery. On the one hand it has been said "that a subject is imaging whenever he employs the same cognitive processes that he would use in perceiving, but when the stimulus input that would normally give rise to such a perception is absent" (Neisser, cited by Eysenck [18]). From this it seems likely that imagery activates the same areas of the brain that are activated by actual perception. This hypothesis is corroborated by numerous case studies that describe a loss of e.g. visual imagery in conjunction with visuoperceptive impairment (for review cf. [19]). On the other hand, imagery has been understood as a non-verbal mode of information processing that is opposed to verbal processing [44]. Since verbal abilities are lateralized to the left hemisphere, it has been concluded that imagery should be a domain of the right hemisphere. However, little empirical support has been found for this hypothesis (for review cf. [17]), and recently even the opposite claim of a left hemisphere superiority for imagery has been made [20,31]. Goldenberg et al. [21–23] found rCBF patterns in SPECT for visual imagery in the left inferior occipital lobe. In episodic memory tasks, they found rCBF increase in lateral inferior temporal regions, whereas in semantic memory tasks, the left inferior parietal lobe was included.

In a SPECT study investigating imagining of colours, faces and a map, we found that 12 out of 30 subjects reported the spontaneous occurrence of mental visual images [22,23]. In these subjects flow in both frontoorbital regions was higher than in those subjects who had not experienced spontaneous imagery. Voluntary imagery led to an increase of regional flow indices in basal temporal regions of both hemispheres and to a rightwards shift of global hemispheric asymmetry. The local changes were distinctly more marked with faces than with colours or the map. Imagining faces was also the only condition that led to an increase of activity in the left inferior occipital region, which has been suggested by previous studies to be a crucial area for visual imagery. In a companion study using negative cortical DC-shifts [49] imagery of colours, faces and a map resulted in sustained negative DC-shifts at temporal, parietal and especially at occipital sites. The topographic distribution of such DC-shifts was modulated as a function of whether spatial or visual imagery was performed. During imagining the spatial map, a parietal maximum was observed, as opposed to a distribution in favour of temporal and occipital sites during imagining faces and colours. The results suggested a neuroanatomical dissociation between visual and spatial imagery. Since a similar visual-spatial dichotomy exists in perception, the finding was interpreted as further evidence of a shared cerebral substrate for images and percepts.

The following papers of the satellite symposium 'Mental representations of motor acts' compiled in this special issue are all dealing with the fact that we can imagine objects, sounds (music), and deliberately motor acts in our mind's eye. It is hoped that the present endeavor of an interdisplinary approach will contribute to our understanding of the important issue of imagery and particularly motor imagery.

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