

Brain potential changes in voluntary and passive movements in humans: readiness potential and reafferent potentials

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Summary A method of *chronological data storage and reverse computation* is described by which bio-electrical phenomena preceding ‘spontaneous’ events within the nervous system can be analysed if these events appear repeatedly and are capable of triggering a computer.

Slow brain potentials accompanying voluntary and passive movements of the limbs were analysed by this method. These potentials were recorded from different points of the scalp from 12 healthy subjects in 94 experiments with more than 100 movements in each record. At times artifacts were superimposed upon cerebral potentials. The former were identified, and, as far as possible, eliminated.

Voluntary hand or foot movements are *preceded* by a slowly increasing *surface-negative cortical potential* of 10–15 μV , called *readiness potential*. This potential is maximal over the

contralateral precentral region, but shows bilateral spread and is larger over the frontal than over the occipital areas. The readiness potential increases with intentional engagement and is reduced by mental indifference of the subject.

Voluntary movements are *followed* by a complex potential with an early positive phase that begins 30–90 msec after the onset of movement. The late potentials following voluntary movements are similar to those after passive movements. Both resemble the late bilateral components of the evoked potentials after electrical stimulation of peripheral nerves. Some variable differences between the early components of the potentials after the onset of active and passive movements require further investigation.

No relation between the onset of voluntary movements and the phase of the alpha rhythm could be detected.

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Further applications of reverse computation are addressed. Similarities between the readiness potential and G. WALTER'S expectancy wave in conditioned reflexes, and the sources of artifacts through eye movements etc. are discussed.

Motor functions are far less studied electrophysiologically than sensory afferents. Bates [2] found a cerebral potential in humans only after, but not before the onset of a movement. He interpreted this potential as a reafferent sensory-evoked potential. Kruger and Henry [13] noticed blocking of the Rolandic beta rhythm in monkeys at the beginning or after, but not before the movement. By contrast, Caspers [4] found cortical DC voltage changes in rats that correlated with spontaneous movements and often preceded these. Jasper and Penfield [10] described a case study where the precentral beta rhythm could be blocked by merely asking the patient to prepare a hand movement. Blockage of the rare arcade rhythm of the central region shortly before the onset of voluntary movements was detected by Klass and Bickford [11] and by Chatrian and colleagues [5]. In conditioning experiments, slow cerebral potential changes between the conditional and the indicative stimuli, so before the reaction, were found by Shvets [15] in rabbits, by Rowland and Goldstone [14] in cats, and by Walter and colleagues [19] in humans. Walter [18] called this predominantly frontally occurring surface-negative brain potential the "expectancy wave."

Apart from these few suggestions from EEG studies and conditional reflex studies, there are no systematic brain electrical derivatives that demonstrate *cerebral correlations for the preparation of spontaneous action in humans*. We have therefore carried out such studies with modern computer methods of purely voluntary movements, where, in contrast to conditioning experiments, the willingness to act is independent of preceding sensory stimulation.

The aim of this work is to examine which changes in brain potential initiate and accompany voluntary movements in humans, and whether the potentials from active movements differ from those from passive movements. A secondary goal was to search for indications of changes in afference through the motor efference. For this purpose, a new method was developed [12], which also covers those bioelectrical events that *precede* the spontaneous movements. The principle is *magnetic tape storage and reverse computation*.

Methods

The EEG of 12 healthy volunteers (students) was recorded in 94 experiments on a Schwarzer-EEG-machine E 502 with extended time constant onto a multi-channel magnetic tape (MAS 24-4, Telefunken) with carrier frequency. *Voluntary movements* of the participant, reshaped into trigger pulses and saved, served to trigger the Mnemotron CAT 400 B

computer. Representing changes in cortical potential before and after the movements is possible through backward and forward analysis of the tape in large numbers of voluntary movements. The summation of the potential curve before and after the movement is facilitated by short time intervals between the curve points. An exact solution to this problem is possible through co-registration of a second, delayed trigger pulse. The interval from the beginning of muscle activity to the trigger pulse was measured by registering the electromyogram of the agonists. Selected artifact-free unpolarizable silver-silver chloride adhesive electrodes or (to reduce galvanic skin reflexes) needle electrodes were used. The overall time constant was 1.3 s. We referenced predominantly unipolarly to nose, chin, sternum and vertebra prominens, ipsilateral ear or both ears, and less frequently in bipolar longitudinal row or precentral contra- against ipsilateral. So far, spontaneous and passive hand movements and active foot movements were investigated. The study of eye movements, phonation, and higher functions is currently underway.

The influence of disturbances (galvanic skin reflexes, electrode artifacts) is to be estimated by a baseline interval, in which the summation of the curve is not triggered through a movement of the subjects but by chance. Regarding the avoidance of blink artifacts see [Results](#).

To determine the Rolandic line, we used the scheme of Taylor and Haughton [16]. For hand movements, we referenced 1 cm frontal of the middle of this line, with foot movements also from the Vertex.

The *number of movements* per experiment was between 100 and 500. Pressing a button with the index finger or palm, a rubber ball through closing the fist, or pulling a thread by flexing the wrist provided similar results. The foot movement consisted of a button press with the naked big toe or with the shoed forefoot. All movements immediately returned to the starting position. Consistency of the speed of movement during the experiment was attended to. *Passive* hand movements were executed as similar to the active ones as possible. In one part of the experiments, closure of the fist was brought about by enclosing the hands of the participant. In other experiments, passive flexion of the wrist was achieved by pulling a rope, which was stuck to the fingertips 1–3. The participant was usually instructed to *not* execute the movements *rhythmically* but in irregular intervals. In some experiments, fast rhythmic hand movements were investigated. Otherwise, pauses of at least 15 s were maintained. In some experiments, we used pauses of more than 25 s to avoid capacitor-related after-effects of potentials from the preceding movement.

Results

Voluntary movements The typical cortical potential fluctuations (Figs. 1, 2, 3, 4, and 5) are sometimes seen (at least

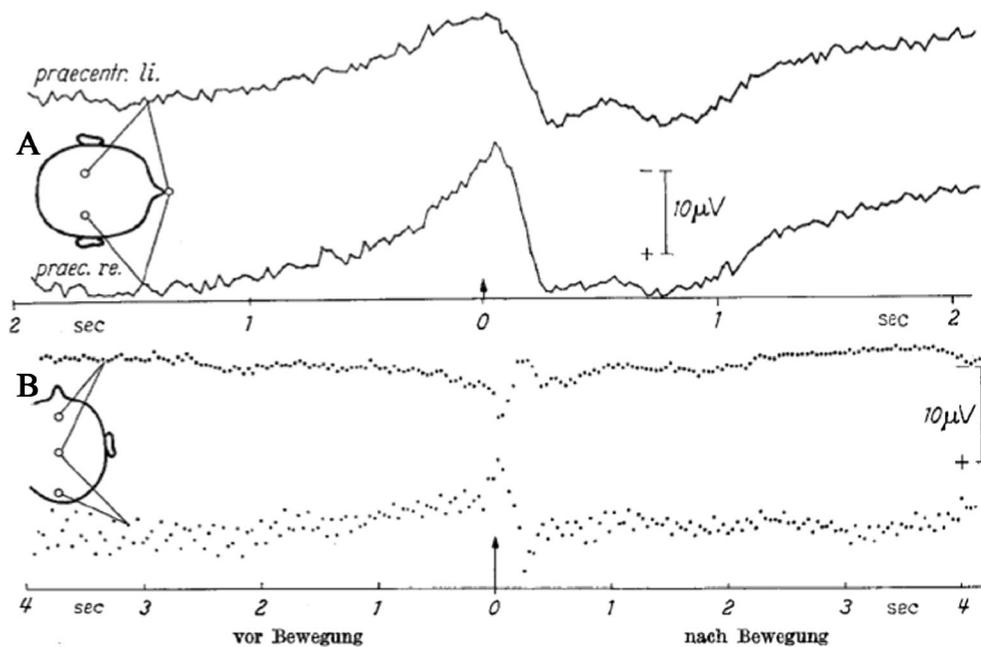


Fig. 1 **A** Brain potential changes in voluntary movements of the left hand. The *arrow* indicates the onset of movement in all figures. Negative potential with readiness, positive potential after the action with larger amplitude above the *contralateral* (*right*) hemisphere. Unipolar measurements of the precentral region against the nose. Average of 512 movements. Negativity upwards. Left of 0 = time before the onset of the movement in the electromyogram. Participant G.F. **B** The bipolar serial measurement with sagittal electrodes in

voluntary movements of the right hand shows a reverse of phase around the precentral electrode: the *premotor negativity* and the *postmotor positivity* are *strongest above the precentral region*. In the frontal-precentral measurements, the negativity of the precentral electrode is downwards, in the precentral-occipital upwards. Average of 400 movements. Participant B.C. Note: “praecentr.” = precentrally; “li.” = left; “re” = right; “vor Bewegung” = before movement; “nach Bewegung” = after movement

suggestively) after only 20 voluntary movements. One often finds a sufficiently smooth baseline interval-trial and a usable curve only after more than 100 movements. Voluntary movements of the hand or foot are regularly preceded by a slow increasing surface-negative potential that starts on average (with large dispersion) 1–1.5 s before the muscle activity and reaches an average amplitude of about 10 to 15 μV . This slowly rising negative wave preceding the movement is hereafter also referred to as the “readiness potential.” The interval from the start of the negative potential to the voluntary movement is smaller at short intervals between the movements. In different experiments, intervals between 0.4 and 4 s from the beginning of the potential change until the onset of movement were found. The readiness potential reaches its peak in the contralateral central region 30–90 ms (usually around 50 ms) *after* the onset of movement (in the electromyogram), followed by descent to postmotor positivity. The rhythmical cerebral potential changes of approximately rhythmic voluntary movements can be made visible through a longer duration of analysis (Fig. 2B).

The premotor negative potential in the precentral region is usually larger on the hemisphere that is *contralateral* to the moving hand than on the ipsilateral hemisphere, irrespective of whether the right or left hand is moved. The ipsilateral potential is on average only 75 % of the contralateral potential.

In addition, the contralateral potential often shows a strong increase at the onset of the movement, while the ipsilateral increases only little or already begins to decrease (Fig. 1A).

The negative potential before the movement usually extends over the entire cerebral convexity from frontal to occipital (Fig. 2A) but has its largest amplitude in the central region. This can be seen both in unipolar and in bipolar serial readings. In these, phase reversal will take place at the precentral electrode (Fig. 1B). The readiness potential is usually greater frontally than occipitally; it may be absent occipitally (Fig. 6A).

The potential curve *after* hand movements is polyphasic and depends on the speed of the individual movements. It also shows individual differences. At *medium speed of movement* (duration of muscle activity in the electromyogram of the flexors around 250 ms) and coarse resolution in the computer (point interval = 40 ms) a typical potential sequence is as follows (Figs. 1A, 3A, 4A): The first peak of the positivity for finger and hand movements occurs with an average of about 330 ms after the onset of movement. Then, it follows a small negative peak with a maximum at about 500 ms, then a second positive maximum at approximately 690 ms. This is often followed by a flat negative wave. At *rapid* execution of the individual movements and more detailed resolution (point interval of 10 ms), there are more peaks, and the potential changes are more frequent (Fig. 7C): After the negativity,

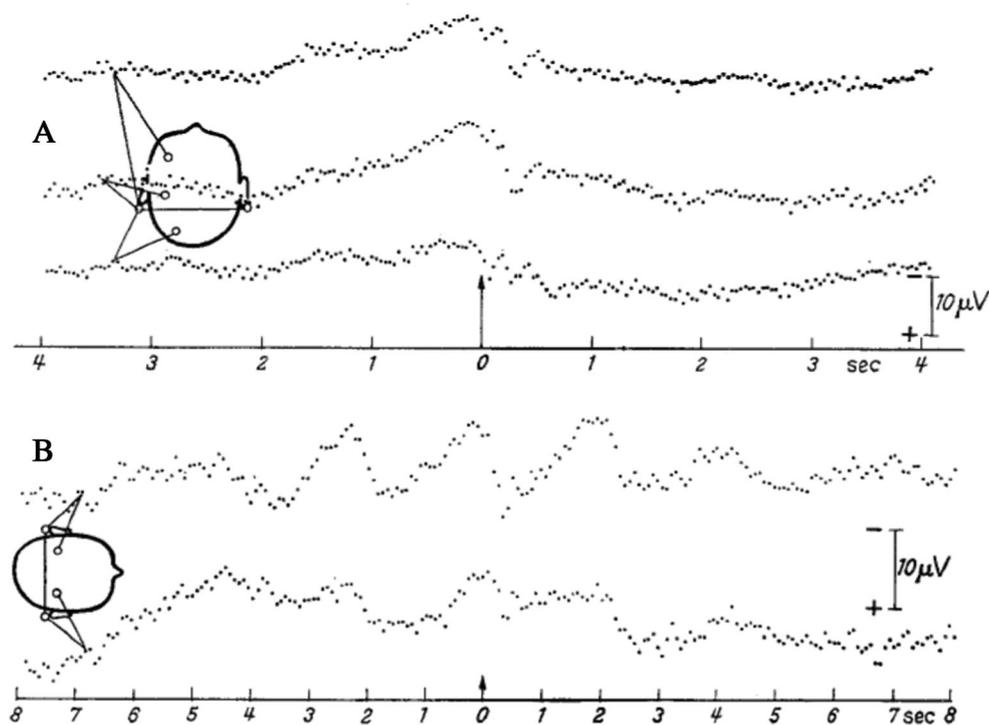


Fig. 2 **A** Wide spread of the readiness potential before voluntary movements and the refferent potentials after the movement of the contralateral hand over the brain convexity with similar course frontally, precentrally, and occipitally. Occipitally, there was a smaller amplitude of the readiness potential. Referenced to both ears. Average of 256 movements. Participant B.C. **B** Brain potentials in approximately

rhythmic button press with the right hand about 0.45/s. With increasing distance of the summation process in the computer, the brain potentials become blurred, because the movements are not followed rhythmically precise. Brain potentials larger above the contralateral (*left*) hemisphere. Referenced to both ears. Average of 170 movements. Participant B.C

which begins before the movement, has reached its peak 30–80 ms after the onset of the movement, four positive peaks appear on the contralateral central region with latencies of about 120, 290, 400, and 550 ms, and three negative peaks at about 200, 330, and 480 ms, then flat negativity. Shape and latency of late peaks are more variable than those of early peaks. The first peak after the movement often shows a greater amplitude above the contralateral hemisphere than above the ipsilateral. The late waves are bilaterally more or less symmetrical. The first peak after the movement often shows strong differences over different brain regions from frontal to occipital, while the later peaks on different brain regions are similar to each other (see Fig. 7).

The peak of the negativity, which begins before the movement, and the first part of the potential after the movement are sometimes superimposed by an *eye movement artifact*, which often occurs coordinated with the hand movement (Fig. 3). This positive artifact of unipolar measurements from the skull convexity though is strongest above the frontal region and reaches its peak already 80–160 ms after the onset of the hand movement and is thus to be distinguished from the strongest cerebral positivity after the movement. We obtained

eyeblick-free measurements through EEG registrations with frequent short pauses between which the subject suppressed the eyelid and fixated a fixation point.

The premotor negativity is similar for *hand and foot movements* (Fig. 4). The potential curve is also largely similar postmotorically, although there are some subtle differences, which is to be expected from refferent-evoked potentials [1].

For the same kind of movement, there is within-participant variability of the size of the brain potentials before and after the movement, depending on conditions, which were described by the participant on the one side as focus, attention, conscientiousness, curiosity, and on the other side, as fatigue or indifference. Other things being equal, the potential is greater at higher *intentional engagement* in the execution of the movements (Fig. 5). The absence or presence of *habituation* apparently also depends on the intentional engagement: as long as the participant is excited about the success of the experiment, the cerebral potentials before and after the movement usually show no decrease with an increasing number of movements. By contrast, the potentials progressively decrease with increasing length of the experiment if the intentional engagement decreases (Fig. 5).

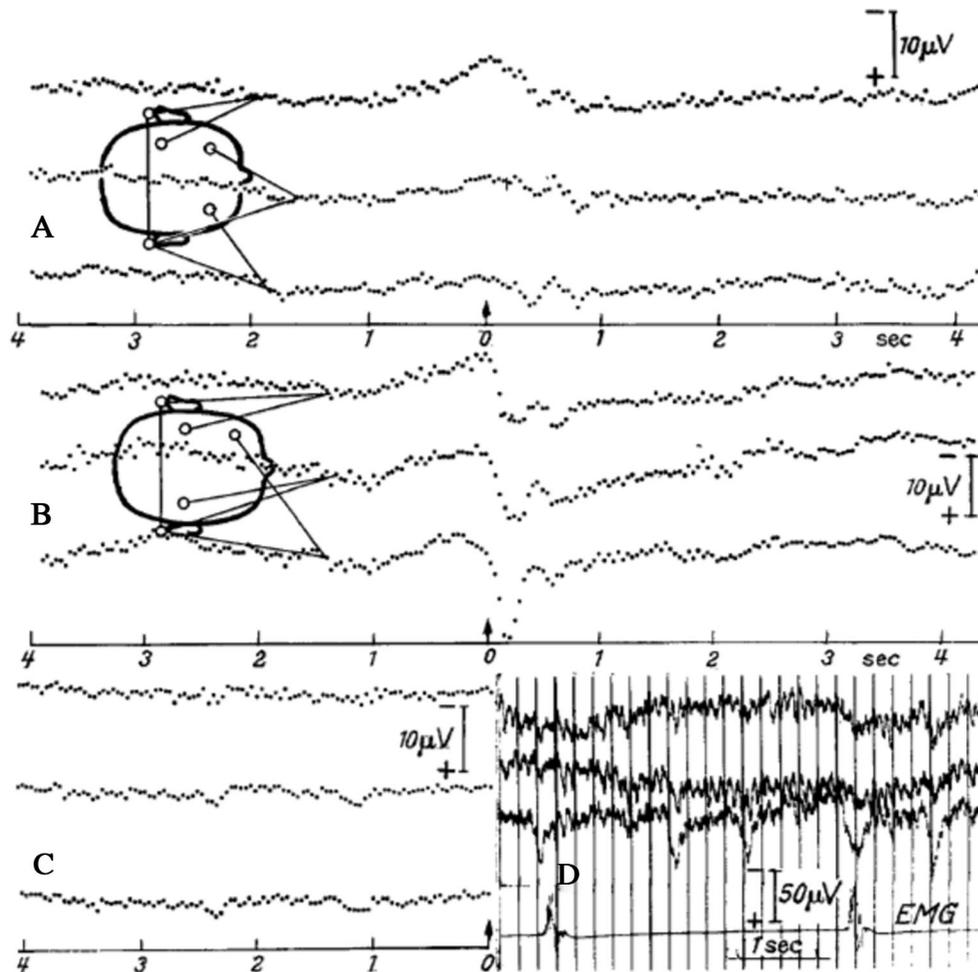


Fig. 3 A–D The coordination of hand movements and eyeblink causes a superimposition of the brain potentials with the eye potential. **A** Brain potentials without eye potentials. The participant fixates a fixed point (visually) and suppresses eye blinks during the hand movement. Precentrally a larger readiness potential than frontally. Referenced to both ears. Average of 280 movements. Participant P.S. **B** The brain potentials of the same participant in hand movements (balloon press) are superimposed (when the eyes are closed) by a positive eye movement artifact due to eye blinks, which starts with the hand movement and is frontally larger than precentrally. Average of 256

Voluntary movements and spontaneous brain potentials (alpha rhythm) Four of our 12 subjects also had precentrally and frontally a well-defined alpha rhythm, which was partially blocked by voluntary movements. A precise relationship of the alpha phase at the beginning of the voluntary movement was found neither precentrally nor occipitally in unipolar measurements. Of course, the summation of movement-coupled curved sections showed an alpha modulation, but with amplitudes that do not significantly differ from the expected value

$$A_N = A_0 \sqrt{N} \frac{\sqrt{\pi}}{2} \left(\text{standard deviation } A_0 \sqrt{N} \frac{\sqrt{4-\pi}}{2} \right)$$

(D. Morgenstern, personal communication) at a summation of a sine wave of constant frequency with random phase shifts

movements. Referenced to both ears. The slow negative-positive potential prior to the readiness potential is a capacitor-related after-effect of brain potentials of previous movements. **C** Null-trial with the magnetic tape storage of the experiment shown in **A**. **D** The simultaneous registration of EEG and electromyogram of the flexors of the lower arms shows their co-occurrence on the eye movements (eye blink at closed eyes) with the hand movements (balloon pressing). EEG curve piece of the measurements from **B**. The eye artifact is positive at the skull convexity and the largest frontally

(Fig. 6). The same was found experimentally in the baseline interval and in the summation of technical sinusoidal oscillations with random phase shifts. A seeming increase in the occipital alpha amplitude with movement sometimes occurred as a result of alpha blocking before movement and reappearance of occipital alpha spindles during movement (Fig. 6).

Passive hand movements Before the onset of passive hand movements, there are usually no cerebral potential changes except the spontaneous rhythms. In rhythmic movement sequences and intentional engagement of the participant, however, a gradually increasing negativity, similar to the readiness potential, can appear before the onset of a movement.

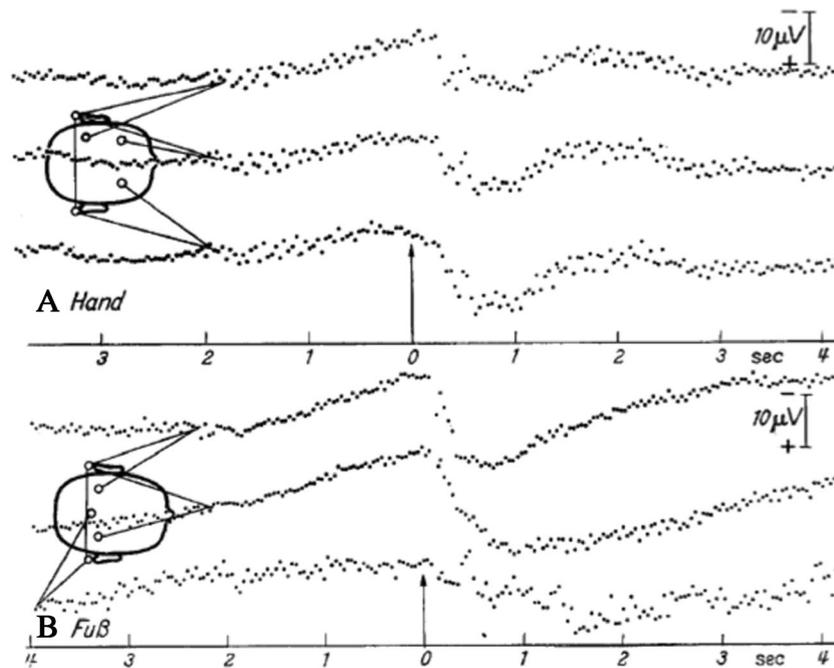


Fig. 4 The comparison of hand movements (**A**) and foot movements (**B**) shows similar changes in potential above the cerebral convexity. Referenced to both ears. Average of 256 movements each. Participant

B.C. **A** Pressing a balloon with the right hand. Eyes closed. Needle electrodes. **B** Button press with the big right toe. Eyes closed. Adhesive electrodes. Note: “Fuß” = foot

The brain potentials occurring during and after passive movements are generally similar to the potentials in active voluntary movements (Fig. 7). In particular, an early negativity with a peak at about 50 ms after the onset of a movement is often present, although not as reliably as in active movements. If a precentral alpha rhythm is present, it is usually largely blocked during the passive movement.

The latencies of the individual positive and negative peaks from the onset of the movement (which, for passive movements, was equated to the start of the activity in the

electromyogram of the experimenter) were on average about 30 ms shorter for passive movements than for voluntary movements. In rapid passive hand movements the positive peaks occurred on average at 90, 240, 390, and 500 ms, negative peaks at 40, 190, 280, and 470 ms. While the late components of the complex above the precentral region ipsilateral and contralateral usually showed no continuous differences in amplitude, the first positive peak at 90–100 ms, if one is available, is usually larger contralaterally; its amplitude ipsilaterally is on average only two thirds of the contralateral amplitude.

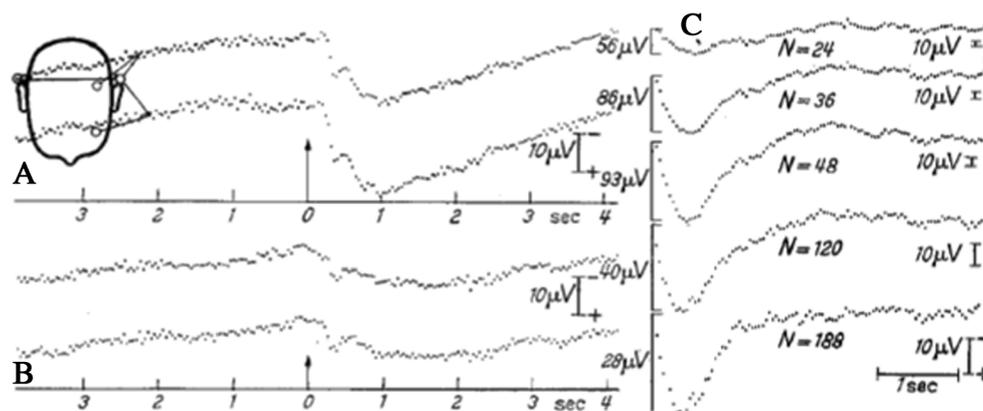


Fig. 5 **A–C** Influence of intentional engagement on the size of the brain potentials in voluntary movements. Experiments that immediately followed each other in the same participant (B.C.). Referenced to both ears. Same amount of movements in **A** and **B** ($N=256$ each). **A** Strong. **B** Weak intentional engagement. **C** Influence of psychological anticipation on the absence or presence of habituation of the brain potentials after voluntary movements of the right hand (only the postmotor part of the

curve is shown). Referenced to the nose. Averaging of the first 24, 36, 48, 120, and 188 movements of a continuous experiment. Naïve, initially very curious participant (A.H.). Unusually large potentials, which initially even increase. After 50 movements, an explanation of the experiment was provided, upon which the intentional engagement and the amplitudes of the brain potentials reduced

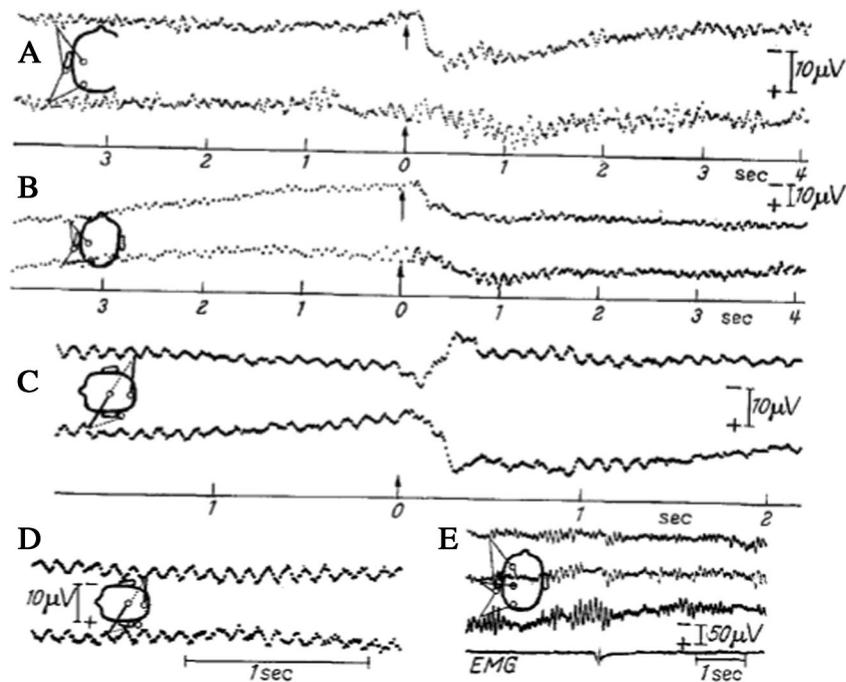


Fig. 6 A–E. Spontaneous hand movements and spontaneous brain rhythms (alpha waves). **A** Blocking of the alpha rhythm in the contralateral precentral region during the voluntary movement. Occipitally, however, short alpha blocking before the movement at the start of the precentral readiness potential, which is missing in this case. During and after the movement a large alpha rhythm occipitally. The amplitude of alpha in the EEG 1 s before the movement on average $55 \mu\text{V}$ occipitally, after the here presented averaging of 200 movements $3.6 \mu\text{V}$ (expectation: $3.4 \mu\text{V}$). **B** Occipital alpha blocking during the readiness potential before voluntary movements of the right hand.

Reappearance of occipital alpha spindles 250 ms before the movement (seeming increase of the alpha amplitude with movement). **C** Similarly, no correlation with the onset of voluntary movements with a fixed phase of the alpha rhythm could be detected with bipolar derivatives. **D** The baseline interval with summation of random curve-parts of the experiment shown in **C** results in the same alpha amplitudes. **E** Excerpt of the EEG curve of the experiment shown in **B**: shortly before and during the hand movement a complete blocking of the alpha, whereas there is a reappearance of the alpha rhythm occipitally. Only small alpha blocking with movement frontally

Differences between active and passive movements are not always recognisable in the late post-motor brain potentials. The total potential difference (between the largest positive and negative peaks) is in some experiments larger for passive, in other experiments larger with active movements, the latter especially when the active movement is preceded by a strong readiness potential, for which apparently the intentional engagement of the participant is important.

By contrast (with rapid movement where the results are most accurately comparable) the *first* potential peak after the movement in active and passive movements is often quite different (Fig. 7). Especially some participants show a strong positivity for passive movement with peaks at 80–90 ms, without any preceding negativity, and this positive potential is often much greater than the corresponding potential in active movements. This early large positive peak at passive movements can be found especially on the central region, while frontally at that time in some participants—this seems to be an individual peculiarity—a negative peak occurs. Sometimes, however, there is initially a stronger negativity on passive movement with peaks of 50 ms, while only a slight negativity occurs at this moment in active movements. One participant showed a strong negative peak in passive

movements at 230 ms, with a much smaller corresponding peak for active movements.

Discussion of the results

Our method of *reverse computation* of a *chronologically stored* sequence of events opens a new field of investigation. It allows the representation of the temporal and spatial distribution of potentials in the nervous system that accompany or precede volitional, affective, gnostic, or motor processes, provided that these processes are repeatable and can be used to trigger processing operations in a computer, either directly or indirectly. Repeatability is required when the magnitude of the occurring signals lies below the noise level: e.g., the readiness potential before movements (in the overall time constant of 1.3 s that we used) is about 10 to $15 \mu\text{V}$, the alpha rhythm of the cortex, however, is often fivefold. The method of reverse computation of chronologically stored biological data is of course also applicable outside of neurophysiology. Its use is always to consider if the origin of seemingly spontaneously occurring events is supposed to be singled out from “noise” by averaging.

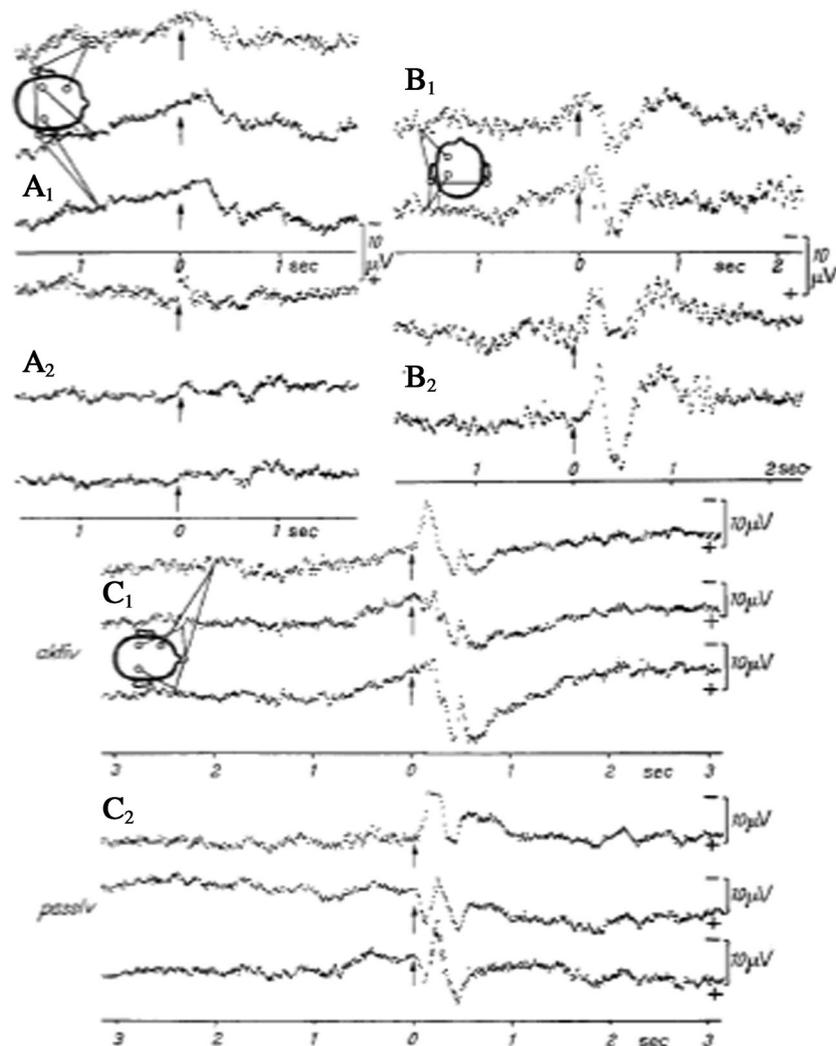


Fig. 7 A comparison of brain potentials with passive and similar voluntary movements of the right hand in three different participants. In **A** to **C** always the top (1) voluntary movements, below (2) passive movements with measurements from identical locations. **A** and **B**

adhesive electrodes, **C** needle electrodes. Missing of readiness potential before passive movements. Stronger overall difference in **A** after voluntary movements, in **B** after passive movements. In **C** different curve of potential after passive and voluntary movements

DC measurements of the scalp, which would be preferable because of the slowness of the occurring potential changes, were not applied because we have not yet managed to stabilise a sufficiently sensitive DC gain over sufficiently long time. One can probably use a lower number of movements at DC, because it shows the slow potential changes in their true size. Of course, the form of slower potential changes is altered by capacitor coupling.

One must be especially careful in the interpretation of summation results. Smallest *artifacts* that do not stand out in the EEG can increase through summation if they occur in a reasonably reliably timed relation to those events that trigger the summation process. We currently see the following three kinds of possible artifacts in the study of hand and foot movements:

1. Artifacts due to *co-movements* of the eyes or muscles at the head and neck. While the slowly increasing readiness potential before the movement cannot be caused by such, the

potential changes during the movement are superimposed by *ocular artifacts*, if eye movement during the movement of the hand is not suppressed by a fixation point. Myogenic artifacts of the neck muscles, as they were found by Bickford and colleagues [3] in acoustic and somatosensory-evoked potentials, are at most relevant as a small component for potentials in limb movements, which occur the greatest precentrally and frontally. In our experiments, the EEG showed no evidence for a correlation of hand movements in the musculus temporalis.

2. We were initially fooled by artifacts caused by *shaking or vibrating the electrodes or cables*. The slow negative readiness potential cannot be caused by these, but a superposition of the waves during and after the movements by such artifacts is possible. Although the consistency of the major features of the postmotor potential curve with its positivity during different head positions and at different

fixations of head, electrodes, and wires speaks against shaking artifacts, but so far one cannot exclude (the possibility) that some peculiarities of the potential flow after the onset of the movement in individual trials as well as differences between the waves in active and passive movements can be retraced to such artifacts.

3. The *galvanic skin response*. An association of the galvanic skin reflex with active or passive movements is conceivable per se, but our previous experiences speak against this, at least with regard to the galvanic skin response, which is readily visible in the EEG: it shows no apparent correlation with the studied movements; derivatives with visible galvanic skin reflexes have strong curve fluctuations in the baseline interval, that do not occur in good experiments. And the current knowledge of the process of the galvanic skin reflex does not match the potentials in voluntary movements with their uniform slow increase before and rapid fall short latency after the movement. In particular though, we have identical findings from readings with adhesive electrodes and needle electrodes, which reduce the influences of the galvanic skin reflex. Further evidence against the galvanic skin reflex as the origin of the readiness potential comes from similarly slowly increasing negative potentials in epidural and epicortical derivatives in conditioning experiments [14, 15, 19] and in freely moving rats [4].

The two *main results* of this study are the surface-negative *readiness potential* preceding voluntary movements and the *broad similarity of later potential changes after active and passive movements*.

That the *readiness potential* remained undiscovered in Bates' [2] careful investigation despite special study with a long time constant was probably due to the inadequate photographic method, compared to today's computer technology. Agreement exists between the readiness potential and the negativity of the DC voltage registered in rats, which often occurs before orientation movements (Caspers [4]). A positivity, as Caspers observed them during cleaning movements, we could not identify before the start of the movement in humans. The positivity prior to the action, which we reported in our first experiments [12], we hereby revoked.

Agreement exists also between the readiness potential before voluntary movements and Walters' [18] negative "expectancy wave" between the conditional and the indicative stimulus in the conditioning of reactions in humans. Both are frontally stronger than occipitally, both bilaterally strongly formed, and both depend on the intentional engagement. Presumably, we are dealing with a similar neural process. Walter assumes that the expectation wave originates from the superficial layers of the cortex. Differences exist perhaps in the fact that the readiness wave is precentrally greater than frontally, and contralaterally to

the moving limb larger than ipsilaterally, but the expectancy wave must be examined in more detail in this regard. Similar slow, surface-negative brain potential changes were already found earlier in conditioning experiments on rabbits and cats by Shvets [15] as well as Rowland and Goldstone [14]. However, the last authors also noted partly negative and partly positive potential changes in the same time period between conditioned stimulus and conditioned response, often from the same discharge point. This though may have been because their indifferent electrode in the sinus frontalis in reality was a different electrode.

Regarding the terminology, we cannot understand the expectancy wave as the negative potential prior to voluntary actions, because nothing is expected; rather the bio-electrical process seems to belong to those brain processes that appear as *readiness to act* in consciousness/conscious awareness. Perhaps the term "readiness" would also be more appropriate than "expectancy" in the conditioning situation, which was studied by Walter and colleagues, as the wave only appears, if the participant is supposed *to act* on the indicative (second) stimulus, and its appearance is associated with a shortening of the motor response time.

When comparing the brain potentials that occur during and after *voluntary movements* with the corresponding brain signals in similar *passive movements*, the similarities are far more impressive than the differences. The differences mainly relate to the first potentials after movement onset. They are considerable in individual experiments, but diverse and irregular on the whole. We therefore suspect that they could be based on small differences in the execution of the movements or even on artifacts. (We had no objective registration of the motion sequence except for the electromyogram.) Bates' [2] interpretation of the potentials that occur after the start of movement as refferent is therefore at least partially correct. A manipulation of the refferent events in the cortex by the motoric neuronal excitation process or the consequences thereof (roughly in the sense of the "efference copy" by von Holst and Mittelstaedt [9]) can be neither proved nor disproved by the current findings. The differences between early brain potentials after active and passive movements require further investigation with a larger temporal resolution in the computer.

The question remains, whether the cortical events of passive movements really are completely passive. It is conceivable that an active yielding was involved in the passive movements in our experiments, in which cortical processes may play a role. This suspicion is at least reasonable in rhythmic succession of passive movements; because a small readiness potential might occur before the movement. However, a comparison with the evoked potentials after electrical stimulation of the median nerve [6–8, 17] shows a sufficient overlap of the cerebral

potentials after passive hand movements with the late bilateral potentials after median nerve stimulation. The early, almost only contralateral potentials at approximately 20 and 50 ms on median nerve stimulation might indeed not be recognisable with passive hand movements in our precentral measurements, but this is to be explained by their short duration (approximately 10 ms) and small amplitude and by the, in comparison to the electrical stimulus, low synchronisation of afferent excitation with hand movements. From this comparison, one can therefore not conclude on active cortical components in the brain potentials after passive hand movements.

We could not determine a *fixed relationship of the phase of the alpha rhythm at the start of the voluntary movements*, as Bates [2] saw in a part of his experiments. It would have had to show itself with our methods as an increase in the amplitude of alpha at the onset of a movement to approximately A_0N when we call the average alpha amplitude A_0 in the EEG and the number of the summed movement-coupled curves N . Since Bates superimposed only 20 curves, observed the phase concordance in only one fifth of his attempts, and did not define the time period of simultaneity quantitatively, the possibility of random creation of his findings cannot be excluded. The apparent relation of the alpha phase to voluntary movements, which was found in some of our tests by blocking alpha before the movement and as a reoccurrence of occipital alpha spindles during the movement, perhaps indicates an effect of movement readiness on the occipital lobes and occipital relaxation already during movement, whereas alpha blocking still prevails during the movement in the precentral region (Fig. 6).

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References

- Allison T (1962) Recovery functions of somatosensory evoked responses in man. *Electroencephalogr Clin Neurophysiol* 14:331
- Bates JAV (1951) Electrical activity of the cortex accompanying movement. *J Physiol Lond* 113:240
- Bickford RG, Jacobson JL, Cody DTR (1964) Nature of average evoked potentials to sound and other stimuli in man. *Ann N Y Acad Sci* 112:204
- Caspers H (1961) Changes of cortical D.C. potentials in the sleep-wakefulness cycle. In: the nature of sleep. Churchill, London
- Chatrian GE, Petersen MC, Lazarte JA (1959) The blocking of the Rolandic wicket rhythm and some central changes related to movement. *Electroencephalogr Clin Neurophysiol* 11:497
- Dawson GD (1947) Cerebral responses to electrical stimulation of peripheral nerve in man. *J Neurol Psychopathol* 10:137
- Giblin DR (1964) Somatosensory evoked potentials in healthy subjects and in patients with lesions of the nervous system. *Ann N Y Acad Sci* 112:93
- Goff WR, Rosner BS, Allison T (1962) Distribution of cerebral somatosensory evoked responses in normal man. *Electroencephalogr Clin Neurophysiol* 14:697
- Holst von E, Mittelstaedt H (1950) Das Reafferenzprinzip. *Naturwissenschaften* 37:464
- Jasper H, Penfield W (1949) Electrocorticograms in man: effect of voluntary movement upon the electrical activity of the precentral gyrus. *Arch Psychiat Nervenkr* 183:163
- Klass DW, Bickford RG (1957) Observations on the Rolandic arceau rhythm. *Electroencephalogr Clin Neurophysiol* 9:570
- Kornhuber HH, Deecke L (1964) Hirnpotentialänderungen beim Menschen vor und nach Willkürbewegungen, dargestellt mit Magnetbandspeicherung und Rückwärtsanalyse. *Pflügers Arch Ges Physiol* 281:52
- Kruger L, Henry C (1957) Electrical activity of Rolandic region in unanesthetized monkey. *Neurology (Minneapolis)* 7(490)
- Rowland V, Goldstone M (1963) Appetitively conditioned and drive-related bioelectric baseline shift in cat cortex. *Electroencephalogr Clin Neurophysiol* 15:474
- Shvets TB (1960) (**Moscow Colloquium**) Conference on electrophysiology of higher nervous activity. Abstracts, Moscow 1958, p. 138. Cited after V. S. RUSINOV: general and localized alterations in the electroencephalogram during the formation of conditioned reflexes in man. *Electroencephalogr Clin Neurophysiol Suppl* 13:309
- Taylor EH, Haughton WS (1900) Some recent researches on the topography of the convolutions and fissures of the brain. *Trans Roy Acad Med Ireland* 18:511
- Uttal WR, Cookl L (1964) Systematics of the evoked somatosensory cortical potential: a psychophysical-electrophysiological comparison. *Ann N Y Acad Sci* 112:60
- Walter WG (1964) Slow potential waves in the human brain associated with expectancy, attention and decision. *Arch Psychiat Nervenkr* 206:309
- Walter WG, Cooper R, Aldridge VJ, McCallum WC, Winter AL (1964) Contingent negative variation: an electric sign of sensorimotor association and expectancy in the human brain. *Nature (London)* 203(380)