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Sleep and Neurophysiological Correlates of Activation of Consciousness on Awakening

E. A. Cheremushkin, N. E. Petrenko, and V. B. Dorokhov

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This article addresses contemporary concepts of the neurophysiological mechanisms of awakening from sleep and the results of our own electroencephalographic (EEG) studies of the temporospatial dynamics of activity in the cortical hemispheres using an experimental model developed by ourselves for investigation of consciousness in the sleep–waking paradigm. This model is based on continuous performance of a monotonous psychomotor test carried out lying down with the eyes closed, which in a 1-h experiment allows observation of several brief episodes of sleep with subsequent spontaneous awakening and recovery of psychomotor test performance. A necessary condition for recovery of activity after spontaneous awakening is the appearance of the EEG α rhythm, and the parameters of this rhythm determine the effectiveness of recovery of the psychomotor test and, thus, achievement of a particular level of consciousness, so this can be regarded as a neurophysiological correlate of the activation of consciousness on awakening. This experimental model for studies of consciousness may be useful for analysis of the neurophysiological mechanisms of its activation in patients with chronic impairments of consciousness and for seeking effective methods for the rehabilitation of such patients.

Keywords: spontaneous awakening, continuous discrete psychomotor test, neural correlates of activation of consciousness, EEG, α rhythm.

Studies of consciousness are a major and very difficult problem in current neuroscience and operate at the junction of various disciplines including medicine, neurobiology, psychology, and others. Recent studies in Russia have led to compilation of a list of terms for describing chronic impairments to consciousness (CIC) and the corresponding diagnostic criteria have been defined [1, 2]. The fundamental bases for medical-biological studies of consciousness were also laid down and methods for diagnosis of impairments of consciousness and searches for effective methods of restoring it were systematized.

One direction in current contemporary medicine consists of developing the methods required for detecting signs of conscious activity in patients and evaluating the retention of cognitive functions in CIC of different severities and origins [3–7]. Some authors have related impairments diagnosed in CIC to changes in cerebral activity similar to those seen during sleep in healthy subjects [8–10]. Preservation of the sleep–waking cycle depends on the severity of CIC [11–13], such that it can be used as a natural model for medical-clinical studies of consciousness [14].

The current approach to analysis of consciousness is based on the concept that each episode of consciousness has a corresponding event in the brain, i.e., its neural correlate [15, 16]. The following task arose in the framework of this concept: to identify which neurophysiological indicators correlate with different brain states and contents of consciousness. The concept of a "neural correlate" was defined by Crick and Koch [15] as "the minimal set of neuronal events and mechanisms sufficient for a specific conscious percept." It should be noted that this "minimum set" does not include all the conditions required for wakefulness or conscious experience in humans.

Most investigators hold the view that consciousness is not a complete whole and address various of its aspects. Generally, the level and content of consciousness are distinguished [17]. The level of consciousness is sometimes

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Institute of Higher Nervous Activity and Neurophysiology, Moscow, Russia; e-mail: khton@mail.ru.

used as a synonym for the level of wakefulness, while content is identified with consciousness or subjective experience [17]. There are several directions in studies of levels of consciousness: investigation of patients with CIC [18–20], during anesthesia of different depths [21, 22], and in the sleep–waking cycle [23–26].

These are based on the concept of a continuum of levels of consciousness, at one pole of which it is absent (coma, deep anesthesia, stage III sleep) and at the other it is present in healthy subjects in the state of active waking. In the same way, in our research strategy we have considered the whole of the sleep–waking cycle from the point of view of continuous changes in the level of consciousness. Contemporary reports discuss the existence of the signs of consciousness both at the REM sleep stage [27, 28] and at the second stage of slow sleep [24, 29–30]. This raises the challenge of creating a theory in which a diversity of conscious experience would extend to the largest possible number of brain states on falling asleep, awakening, and during dreams [31].

The subject of our research was the process of awakening and its associated activation of consciousness [32]. Neurophysiological investigation of awakening started in the 1970s, when it was described as a transient phenomenon interrupting the continuity of sleep [33, 34]. According to the criteria of the American Sleep Disorder Association (ASDA), they are defined as sharp shifts in the electroencephalogram (EEG) frequency, usually towards increases, of duration 3–15 sec, arising after sleep lasting at least 10 sec [35]. One view is that this phenomenon is not a pathological process but a normal component of sleep structure [36, 37].

EEG studies in two types of awakening, natural and induced by external stimulation, have shown that its power characteristics differ from the states of waking and sleep [38]. Independently of type, the bioelectrical activity of the thalamus is identical in nature and its spectral composition corresponds to an intermediate state between waking and sleep. Changes in the EEG depend on the stage of sleep, the area being recorded, and the type of awakening [38]. Schwabedal et al. [39] showed that in healthy study participants, these short-term episodes of activation interrupting nocturnal sleep, so-called wake after sleep onset periods (WASOs), are accompanied by decreases in the frequency characteristics of the α rhythm and depend on the durations of periods of waking. No such changes in frequency were seen in patients with insomnia.

Analysis of functional connections between neural networks showed that on arousal, the default-mode network and the hippocampal network retained identical levels of connectivity and spectral power as compared with the waking state prior to a period of sleep. The sensorimotor network showed a decrease in connectivity; at the same time, the connection of the thalamus with the neocortex improved. Decreases in spectral power were seen in both cases. The deeper the sleep, the greater these changes were on awakening [40].

Arousal is not a uniform process. Voss [41] took the view that there are two stages in awakening, i.e., cognitive and behavioral. People initially have the opportunity to react to external stimuli but no opportunity to mount a conscious behavioral response, this appearing later [41]. Another point of view is that waking leads to rapid restoration of consciousness with a subsequent relatively slow recovery of alertness [42]. The onset of consciousness on awakening is linked with processes of hyperpolarization, i.e., depolarization of neuron membranes. It can be suggested that a particular level of neuron depolarization is a prerequisite for the function of consciousness on awakening. The alternation of hyperpolarization and depolarization (the so-called bistable state of neurons) seen in the slow-wave sleep stage may be a sign that it is absent [23, 25, 26]. This bistability is seen as impairing the synchronous interaction of cortical areas of the brain required for the functioning of consciousness.

On the basis of qualitative analysis of the EEG in studies of spontaneous awakening after daytime sleep and subsequent recovery of the performance of a continuous discrete psychomotor test, Dorokhov [43] identified two types of phasic activatory EEG patterns preceding awakening: α-spindles accompanied by high-frequency EEG components and K complexes. The type of pattern depended on the sleep stage from which awakening occurred [43]. Later studies in this model using functional MRI brain scans showed that activation of various areas of the brain occurs at the moment of awakening: the right thalamus, the left cuneus, the cerebellar areas, and the stem structures of the brain [32].

Investigations of spectral EEG characteristics before awakening, determined in terms of recovery of performance of the psychomotor test after short-term episodes of sleep (microsleeps), found increases in spectral power characteristics in the δ and α ranges [44]. We link this result with pre-awakening K complexes of different extents with superimposition of low-frequency α oscillations [44]. This EEG pattern (K complexes with subsequent α activity) may be linked with the actions of a universal thalamocortical activatory mechanism, which can be regarded as a neural correlate of the activation of sequential levels of consciousness needed for performance of the psychomotor task.

We regard this continuous-discrete psychomotor test [32, 43] as an effective experimental model for studies of the activation of consciousness on awakening. The test performance procedure was as follows. During a period of 1 h, the subject, lying in bed with the eyes closed, carries out two sequential alternating tasks: the first is to count from 1 to 10 sotto voce, with accompanying synchronous pressing of a button with the right hand ("count and press") and the second is to count sotto voce alone, without pressing. The monotonous nature of the test promotes rapid decreases in the level of arousal with subsequent alternation of episodes of microsleep and spontaneous awakening. The subject is given the instruction: "start doing the test again when you wake up, starting with the first task – button-pressing."

It can be suggested that spontaneous restoration of button-pressing is triggered by cerebral processes linked with extraction of the hypothetical instruction from memory – “count and press the button,” whose performance requires activation of consciousness. The occurrence of several episodes of microsleep and awakenings during a single experiment allows influences of differences in the power levels of different rhythms on the results to be avoided and provides for assessment of episodes of waking with different levels of recovery of psychomotor activity.

In analyzing the data, we considered complete and partial recovery of performance of the psychomotor test on spontaneous awakening from sleep stage II [45]. Recovery was regarded as full when the subject correctly performed the first task, i.e., pressed the button 10 times and, after a time interval commensurate with the duration of the second task (10 sec count without pressing), pressed the button at least once (repetition of the first task). Episodes in which the wait for the next press was >1 min were taken as cases of partial recovery of the instruction “count and press” (incomplete or complete).

Previous studies based on visual observations demonstrated the need for recovery of the α rhythm for renewal of activity on awakening [43]. Quantitative analysis of EEG data in subsequent investigations confirmed these results [44–46]. The existence of a link between the characteristics of α oscillations and the effectiveness of psychomotor test performance during spontaneous awakenings was demonstrated. On partial recovery in situations with small (2–5) and relatively large (6–10) numbers of button presses, α-rhythm spectral power was greater in the situation with longer periods of observed behavioral activity. Termination of pressing returned measures of α activity to those obtained before awakening [46]. On full recovery of test performance, this EEG characteristic was significantly greater than in cases of partial recovery [45].

It should be noted that in the time segment preceding the moment of recovery of psychomotor activity, α-rhythm spectral power was greater when there were more button presses. This was seen in the anterior areas of the brain 5–6 sec before the start of pressing in the low-frequency α range (8–10.5 Hz) and 3–4 sec before in the high-frequency range (11–13.5 Hz). Activation of the α rhythm in the anterotemporal and ventrolateral prefrontal cortex on awakening, anticipating the onset of activity, may reflect processes linked with extraction from working memory of the instruction on which basis further actions are planned [44, 46].

We suggest that the effectiveness of recovery of the psychomotor test after awakening is determined by the level of activation of consciousness controlling the functioning of cognitive processes supporting verbal counting and synchronous button-pressing effector activity. Working from this suggestion, the situations considered above, with incomplete and complete numbers of presses, are associated with different levels of activation of consciousness in the transition from sleep to waking.

Thus, different temporospatial, amplitude, and frequency characteristics of the α rhythm are regarded as neural correlates of the activation of sequential neural levels of consciousness on awakening from sleep.

It is interesting to note that from the experimental point of view, the unconscious state is often defined as loss of the ability to respond to external stimuli [47]. The authors took the view that conscious experience before and after the unconscious state may be radically different. Although a person may be in the state to press the button or clench the fist in response to a command both before and after a period of general anesthesia, the level of content of consciousness immediately after recovery from anesthesia is probably weakened as compared with the baseline preconscious state. A number of subjects in our studies self-reporting use of the psychomotor test mentioned awakenings in which they were unable to press the button (unpublished data).

The use of transitional states in the sleep–waking cycle in medical-biological practice deepens our understanding of changes in the functional activity of the cerebral cortex; studies of neurophysiological events correlating with the appearance and disappearance of consciousness bring us towards an understanding of its natural bases, this expanding the scope of the search for effective methods of rehabilitating patients with chronic impairments of consciousness.

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