

# Subconscious Stimulus Recognition and Processing During Sleep

## Abstract

*During sleep, consciousness is reduced, associated with a diminished connection of the brain to the environment. This is due to the blocking of the thalamocortical pathway by inhibitory mechanisms. This “thalamic gating” during sleep, however, is not complete, but partial. The stream of information is considerably reduced, but the brain is not fully disconnected from the environment. An inspection of the environment takes place to optimize safety during sleep. Stimuli having a meaning for the individual, or signaling danger, are recognized, and may enter into awareness, leading to a wake-up call, which allows the individual to react. This subconscious stimulus evaluation is regarded as having a guardian function for sleep. The recognition of stimuli during sleep points toward the presence of a sort of consciousness without awareness in the sleeping brain.*

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One of the most difficult psychological concepts is that of consciousness. Currently, the concept of consciousness is not clear, but according to Velmans (2000), a person is conscious if the person experiences something, and a phenomenal content is present. In this context, the presence of wakefulness is inevitable for being conscious. Sleep (sleep in this paper is exclusively slow wave sleep and not REM sleep, with its altered state of consciousness during dreaming) is, therefore, regarded as a state with a low level of consciousness. The change from alert wakefulness, associated with a high level of consciousness, to sleep, with a low level of consciousness, is mediated by reticular structures in the brainstem. During sleep, the thalamocortical system is deactivated by inhibitory processes, and this deactivation is associated with a (partial) loss of consciousness. Intriguing questions are: How great is the reduction in consciousness during sleep, and what are the cognitive capabilities of a sleeping brain? Is the brain completely unconscious during sleep or are there still cognitive processes going on which do not spark awareness?

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## **Stimulus Evaluation in Sleep**

It seems that upon falling asleep, consciousness fades away. There is certainly a decline in awareness and consciousness accompanied by a reduced interaction with the environment (Coenen and Drinkenburg, 2002). To what degree are consciousness and awareness reduced during sleep? Strong evidence exists that some processing of external information is still occurring during sleep. A sleeper will be aroused both by intense stimuli and by non-intense stimuli that contain some relevant meaning for the sleeper. From classic experiments, it is well known that the threshold for awakening is lower for a relevant stimulus than for a physically identical stimulus that has no relevance to the individual. Oswald, Taylor, & Treisman (1960) presented names to sleeping subjects, who awakened significantly faster on hearing their own names, than on hearing other names. Langford, Meddis, & Pearson (1974) showed that the latency from sleep to awakening is shorter for meaningful, than for non-meaningful, stimuli, while Zung and Wilson (1961) showed that discriminative responses can occur during sleep. Subjects, who were motivated to awake by presenting a specific stimulus, awoke easier on these stimuli than non-motivated subjects. All experiments prove that the threshold for awakening is lower for relevant, than for non-relevant, stimuli.

This phenomenon is also well known for most of us. People become more easily aroused upon hearing their names softly whispered, and a young mother may awaken at the slightest sound emanating from her new born baby. Stimuli implying a potential danger, such as the slight noise of a burglar or of a fire at home, can awaken us, even though its intensity is low. That both the physical qualities of sounds and, even more importantly, the psychological value that people grant to these sounds play a role in awakening is known from studies involving people who live close to airports. Many people regard airplane noise during the night as annoying, implying that they give a high negative value to these kinds of stimuli. The emotional coloring of these stimuli heavily modulates the awakening threshold and arouses people even at very low sound intensities. The sleeping brain is able to automatically detect these kinds of stimuli with a high impact, and these emotional stimuli may trigger a wake-up call (Griefahn, Scheuch, Jansen, & Spreng, 2004; Muzet, 2007).

The discriminative properties of a sleeping brain are frequently studied by measuring the electrical activity of the brain expressed in evoked potentials. This is commonly done for stimuli not awakening the subjects. Nordby, Hugdahl, Stickgold, Bronnick, & Hobson (1996), using an oddball paradigm with two tones differing in pitch and probability, found that the representation of auditory stimuli occurred in sleep just as in wakefulness. The prolonged latencies of the components of the event related potentials, however, indicate that the processing of external sensory stimuli is delayed. Karakas, Cakmak, Bekçi, & Aydin (2007) also found that the processing of auditory information is slower and takes longer in sleep. Auditory evoked potentials were recorded to frequent and deviant tones by Bastuji, García-Larrea, Franc, & Maugière (1995). During sleep, evoked potentials on frequent and deviant tones closely resembled K-complexes, but the responses to deviant tones were significantly larger than those to frequent tones. They concluded that the brain is able to detect stimulus deviances during sleep, but also that this detection is less efficient compared to the waking state.

Perrin, García-Larrea, Maugière, & Bastuji (1999) presented the subject's own name together with other names to sleeping persons while recording auditory evoked potentials.

Indeed, some late components in the evoked responses were selectively enhanced after the subject's own name. Their interpretation is that the sleeping brain is able to detect and categorize particular aspects of stimulus significance. The conclusion that the sleeping brain can detect meaningful events in auditory stimuli was underlined by Portas et al. (2000). They showed, by simultaneously recording EEG and fMRI in humans, that parts of the prefrontal cortex are more activated by stimuli having a special significance than by neutral stimuli. Data, supporting the suggestion that auditory information processing continued while persons were asleep, were also obtained by Kállai, Harsh, & Voss (2003). These authors found attention enhancing mechanisms in sleep. The large amplitude N350 component, regarded as an obvious and reliable indicator of information processing in sleep (Voss and Harsh, 1998), was considered to have an attention- preventing function. This component might counteract attentional processes in order for sleep to prevail. A competition between sleep enhancing processes and mechanisms preserving attention to stimuli seems to exist during sleep.

The conclusion of all these experiments is inevitable. Information from the external environment is processed throughout stages of sleep, although it is not always consistent with the maintenance of sleep (Colrain and Campbell, 2007). The reduction in consciousness in sleep is expressed in a shallower and less thorough stimulus processing and evaluation, but this shallower and less deep processing seems sufficient to uncover the major meaning or relevance of a particular stimulus. In their review, Atienza, Cantero, & Escera (2001) came to the conclusion that the auditory system continues to preserve essential services in order to maintain contact with the surrounding environment. The exact reduction in consciousness is, however, difficult to establish. Indeed, processing of external stimuli during sleep is important for safety and survival. Regard a hare sleeping in the open field. The environment is continuously inspected for potential predators during the vulnerable state of sleep. When there is a sign of potential danger, there is the possibility that the animal will wake up and scamper away. In order to execute a proper behavioral response, it is not necessary to become aware of all features of the stimulus, but only of information that is important enough to trigger a mechanism for an arousing stimulus. This mechanism is of crucial importance for avoiding dangerous situations during the indispensable, but vulnerable, state of sleep.

In states with complete unconsciousness, such as general anesthesia or coma, the brain is no longer able to process and evaluate any information. Alkire and Miller (2005), in a review on general anesthesia and its neural correlates, identified the thalamus as a key target of anesthetic effects. A complete deactivation and disconnection from the outside world is produced at the level of the thalamus, contributing to the anesthesia-induced unconsciousness. In a comatose state, several neurophysiological and neuroimaging studies have shown residual cortical function in patients. This cortical activation is so limited, however, that there is no further processing and integration, which are considered necessary for conscious or subconscious stimulus perception and processing (Laureys, Perrin, Schnakers, Boly, & Majerus, 2005).

### Thalamocortical Activities in Sleep

During wakefulness, thalamocortical relay cells are in a state of tonic depolarization, and neurons exhibit activity in the tonic firing mode. This implies a sustained and relatively high spontaneous activity, but with a low synchronization between cells. This activity pattern is the substrate for the low amplitude, high frequency EEG waves, which are representative of

the waking state. In this mode, nerve impulses arriving from peripheral sense organs produce excitatory postsynaptic potentials, which are able to easily pass the low-level threshold of the cells firing in the tonic mode, thereby generating outgoing nerve impulses that are transmitted to the cortical centers. This implies that entire messages, as coded by the peripheral sense organs, reach the sensory parts of the cerebral cortex in their entirety (Coenen, 1995 and 1998; McCormick and Bal, 1994; Steriade, McCormick, & Sejnowski, 1993). The large amplitude, low frequency waves associated with sleep become manifest in the EEG when thalamocortical neurons undergo considerable hyperpolarizations. Excitations in inhibitory thalamic neurons, controlled by the brainstem reticular formation, produce a powerful inhibition in thalamic relay neurons, leading to a rebound excitation (Huguenard, 1998; McCormick and Bal, 1994). The change from wakefulness to sleep is an active process originating from inhibitory mechanisms in the brainstem (Evans, 2003). Extended populations of neurons start to fire rather synchronously in bursts, which are interspersed by long silent pauses. This firing mode is called the burst firing mode, and this firing mode blocks a major part of the afferent information at the thalamic level. The incoming excitatory postsynaptic potentials cannot pass the threshold, owing to the large hyperpolarizations. Coenen and Vendrik (1972) performed direct measures in the cat visual relay nucleus of the input coming from retinal ganglion cells, as well as from the output of these thalamic relay cells. They pointed out that the input-output relation of thalamic cells was strongly dependent on the state of the brain. During waking, there was a nearly one-to-one relationship between input and output, but during sleep, the input remained constant, while the output dropped down to approximately one-third of the original activity. This increase in “transfer ratio” (Coenen and Vendrik, 1972) or the facilitation of the thalamocortical transmission, when the animal moved from slow wave sleep to wakefulness, was also established by Livingstone and Hubel (1981), by Hirsch, Fourment, & Marc, (1983) and by Fourment, Hirsch, & Marc (1988). Since that time, the thalamus is considered to be an obligatory station through which almost all sensory information must pass before reaching the sensory cortex. One of the major functions of the thalamus is the selective control of the flow of information during different states of consciousness. This function is called the “sensory gating mechanism of the thalamus” or “thalamic or sensory gating” (Coenen and Vendrik, 1972; McCormick and Bal, 1997; Steriade et al., 1993).

Most thalamic recordings are performed in the visual modality, and only some in the auditory modality. Edeline, Manunta, & Hennevin (2000) performed single unit recordings in the auditory thalamus of guinea pigs. In accordance with most visual modality studies, spontaneous activity decreased in the thalamus during sleep, despite the fact that both increases and decreases of neuronal firing could be found at a subthalamic level of the auditory system (Velluti, 1997). From the results of Edeline et al. (2000), it appeared that messages sent to the cortical neurons are attenuated during sleep. The timing of the neuronal discharges is also altered during sleep (with both longer latencies and a greater variability), which implies that the coding of information in series of nerve impulses is also affected. According to these authors, however, all changes are not sufficient to consider sleep as a totally brain-deafferented state, as was often earlier concluded. By the process of thalamic gating, the original stream of information is reduced in the thalamus, to approximately one-third of the original amount which is conveyed to, and reaches, the sensory cortices. Nevertheless, the coding of the activity seems to be preserved, the topographic maps, fundamental to sensory processing, are maintained, and the selectivity of the neurons is kept the same. These preserved capabilities of the reduced messages seem sufficient for a gross,

but rather informative, evaluation.

Peña, Pérez-Perera, Bouvier, & Velluti (1999) studied sleep-related changes in neuronal firing in the auditory cortex of the guinea pig. They found that the spontaneous and evoked activity could vary in opposite directions and that the responsiveness of the auditory system during sleep is partially preserved. With the demonstration of cortical neurons increasing their activity or showing no change in activity during sleep, this expands the results of Murata and Kameda (1963), who reported a general reduction in the activity of the auditory cortex during sleep. Recently, Issa and Wang (2008), studying marmoset monkeys during natural sleep and waking, recorded cortical unit responses to acoustic stimulation. Single units in both the primary and secondary auditory cortex decreased or increased their responses during sleep compared to wakefulness. Moreover, when the responses across neurons were averaged, sound-evoked activities in both areas were well preserved during sleep. These results may approximately demonstrate similar discharge patterns during sleep as during wakefulness, and may suggest two important features of stimulus processing. The first feature is: The thalamus functions as a gate for the flow of sensory information as was previously thought. This can be concluded given the overall decrease of activity transmitted to the primary auditory cortical neurons, which might explain the decreased responsiveness of a multitude of cortical auditory neurons. The second feature, however, is: In the complex network of the cortical layers, activation takes place gaining the thalamic input, thus enabling an evaluation of this information and eventually leading to a wake-up call (Sherman, 2001). An analogue process of gating on one hand, and gaining on the other hand was already proposed some time ago by Wróbel (2000) for the process of visual attention.

## Conclusion

It is suggested, here, that the thalamocortical inhibition, which takes place during sleep and is expressed in hyperpolarizations and subsequent neuronal bursting, is the neuronal substrate for the decrease in consciousness. The partial loss in consciousness seems necessary for the induction and maintenance of sleep. How large is this loss of consciousness? When we consider the original concept of consciousness, it first appears that conscious awareness of stimuli is lacking, but in actuality, some sensory, attentional, and mnemonic processes are still (partially) intact. This leads to some uncovering of the meaning of stimuli during sleep. Merikle (2007) notes that during full wakefulness, some sort of subconscious or preconscious stimulus processing also takes place. It may be that this preconscious stimulus processing is similar to subconscious stimulus processing during sleep. Both the wakeful-preconscious and sleep-subconscious processing seem autonomic processes or some form of covert consciousness without phenomenal awareness.

Despite the fact that parts of the cortex remain active during sleep, consciousness is largely reduced. Indeed, that the cortex serves as an exclusive seat of consciousness is a view that has to be abandoned, and it must be replaced by the view that integrated activities of cortical, thalamic, and brainstem structures form the neural basis for consciousness (Newman, 1995). This view reminds us of the integrated information theory of consciousness, implying that consciousness is the result of the ability of a system to integrate information. This integration is reduced or breaks down during sleep (Tononi and Massimini, 2008).

Sleep is a necessary process for life, although it is still not convincingly clear what function(s) it plays: Perhaps it is for brain or body restoration, for memory consolidation, or for both. That sleep is a life-protecting process is suggested by the lethal effects of long-term deprivation of sleep. But sleep is also a vulnerable process. Both humans and animals lay immobile, often unprotected, while dangers may be lurking in the environment. What can protect this vulnerable state and make it safer? It is proposed, here, that sleep allows for the continuous processing and evaluation of incoming information, which in turn protects both man and animals from the risky nature of sleep. This subconscious information processing and evaluation has a guardian function in sleep. The shallow processing of the reduced flow of information to filter out relevant messages is made possible by active circuits in the cortex that receive such reduced information. This process seems necessary for life safety and survival, and it forms a compromise between sleep and safety. Sleep has undergone an evolutionary process for obvious reasons but must be protected. This is performed by stimulus evaluation that is continual and occurs subconsciously. Although this evaluation is less intensive than during wakefulness, it is strong enough to detect gross stimulus relevance, and when necessary, provides a wake-up call to allow one to perform a proper behavioral reaction. In sleep, a sort of consciousness is present with some ongoing cognitive processes, but the outcome of these processes only leads to awareness when it is necessary.

## References

- Atienza, M., Cantero, J.L. & Escera, C. (2001). Auditory information processing during human sleep as revealed by event-related brain potentials. *Clinical Neurophysiology*, *112*, 2031-2045.
- Alkire, M.T. & Miller, J. (2005). General anesthesia and the neural correlates of consciousness. *Progress in Brain Research*, *150*, 229-244.
- Bastuji, H., García-Larrea, L., Franc, C. & Maugière, F. (1995). Brain processing of stimulus deviance during slow-wave and paradoxical sleep: a study of human auditory evoked responses using the oddball paradigm. *Clinical Neurophysiology*, *12*, 155-167.
- Brualla, J., Romero, M.F., Serrano, M. & Valdizán, J.R. (1998). Auditory event-related potentials by semantic priming during sleep. *Electroencephalography and Clinical Neurophysiology*, *108*, 283-290.
- Coenen, A.M.L. (1995). Neuronal activities underlying the electroencephalogram and evoked potentials of sleeping and waking: implications for information processing. *Neuroscience and Biobehavioral Reviews*, *19*, 447-463.
- Coenen, A.M.L. (1998). Neuronal phenomena associated with vigilance and consciousness: from cellular mechanisms to electroencephalographic patterns. *Consciousness and Cognition*, *7*, 42-53.
- Coenen, A.M.L. & Vendrik, A.J.H. (1972). Determination of the transfer ratio of cat's geniculate neurons through quasi-intracellular recordings and the relation with the level of alertness. *Experimental Brain Research*, *14*, 227-242.
- Coenen, A.M.L. & Drinkenburg, W.H.I.M. (2002). Animal models for information processing during sleep. *International Journal of Psychophysiology*, *46*, 163-175.
- Colrain, I.M. & Campbell, K.B. (2007). The use of evoked potentials in sleep research. *Sleep Medicine Reviews*,

11, 277-293.

- Drinkenburg, W.H.I.M., Schuurmans, M.L.E.J., Coenen, A.M.L., Vossen, J.M.H. & van Luijtelaaar, E.L.J.M. (2003). Ictal stimulus processing during spike-wave discharges in genetic epileptic rats. *Behavioural Brain Research, 143*, 141-146.
- Edeline, J.-M., Manunta, Y. & Hennevin, E. (2000). Auditory thalamus neurons during sleep: changes in frequency selectivity, threshold, and receptive field size. *Journal of Neurophysiology, 84*, 934-952.
- Evans, B.M. (2003). Sleep, consciousness and the spontaneous and evoked electrical activity of the brain. Is there a cortical integrating mechanism? *Clinical Neurophysiology, 33*, 1-10.
- Fanselow, E.E., Sameshima, K., Baccala, L.A. & Nicolelis, M.A.L. (2001). Thalamic bursting in rats during different awake behavioral states. *Proceedings of the National Academy of Sciences, 98*, 15330-15335.
- Fourment, A., Hirsch, J.C. & Marc, M.E. (1988). Reticular control of thalamic transmission during behavioural states: a study in dorsal lateral geniculate relay neurons of the cat. *Experimental Neurology, 100*, 305-321.
- Griefahn, B., Scheuch, K., Jansen, G. & Spreng, M. (2004). Protection goals for residents in the vicinity of civil airports. *Noise and Health, 6*, 51-62.
- Hirsch, J.C., Fourment, A. & Marc, M.E. (1983). Sleep-related variations of membrane potential in the lateral geniculate body relay neurons of the cat. *Brain Research, 259*, 308-312.
- Huguenard, J.R. (1998). Anatomical and physiological considerations in thalamic rhythm generation. *Journal of Sleep Research, 7 S1*, 24-29.
- Inoue, M., Duysens, J., Vossen, J.M.H. & Coenen, A.M.L. (1993). Thalamic multiple unit activity underlying spike-wave discharges in anesthetized rats. *Brain Research, 612*, 35-40.
- Issa, E.I. & Wang, X. (2008). Sensory responses during sleep in primate primary and secondary auditory cortex. *The Journal of Neuroscience, 28*, 14467-14480.
- Kállai, I., Harsh, J. & Voss, U. (2003). Attention to external stimuli during wakefulness and sleep: evoked 40-Hz response and N350. *Psychophysiology, 40*, 955-966.
- Karakas, S., Cakmak, E.D., Bekçi, B. & Aydin, H. (2007). Oscillatory responses representing differential auditory processing in sleep. *International Journal of Psychophysiology, 65*, 40-50.
- Langford, G.W., Meddis, R. & Pearson, A.J.D. (1974). Awakening latency from sleep for meaningful and nonmeaningful stimuli. *Psychophysiology, 11*, 1-5.
- Laureys, S., Perrin, F., Schnakers, C., Boly, M. & Majerus, S. (2005). Residual cognitive function in comatose, vegetative and minimally conscious states. *Current Opinion in Neurology, 18*, 726-733.
- Livingstone M.S. & Hubel, D.H. (1981). Effects of sleep and arousal on the processing of visual information in the cat. *Nature, 291*, 554-561.
- McCormick, D.A. & Bal, Th. (1994). Sensory gating mechanisms of the thalamus. *Current Opinion in Neurobiology, 4*, 550-556.
- McCormick, D. & Bal, Th. (1997). Sleep and arousal: thalamocortical mechanisms. *Annual Review of Neuroscience, 20*, 185-215.
- Murata, K., & Kameda, K. (1963). The activity of single cortical neurones of unrestrained cats during sleep and wakefulness *Archives Italiennes de Biologie, 101*, 306-331.

- Muzet, A. (2007). Environmental noise, sleep and health. *Sleep Medicine Reviews, 11*, 135-142.
- Newman, J. (1995). Thalamic contributions to attention and consciousness. *Consciousness and Cognition, 4*, 172-193.
- Nordby, H., Hugdahl, K., Stickgold, R., Bronnick, K. & Hobson, J.A. (1996). Event-related potentials (ERPs) to deviant auditory stimuli during sleep and waking. *NeuroReport, 7*, 1082-1086.
- Oswald, I., Taylor, A.M. & Treisman, M. (1960). Discriminative responses to stimulation during human sleep. *Brain, 83*, 440-453.
- Peña, J.L., Pérez-Perera, L., Bouvier, M. & Velluti, R.A. (1999). Sleep and wakefulness modulation of the neuronal firing in the auditory cortex of the guinea pig. *Brain Research, 816*, 463-470.
- Perrin, F., García-Larrea, L., Maugière, F. & Bastuji, H. (1999). A differential brain response to the subject's own name persists during sleep. *Clinical Neurophysiology, 110*, 2153-2164.
- Portas, Ch., Krakow, K., Allen, Ph., Josephs, O., Armony, J.L. & Frith, Chr. (2000). Auditory processing across the sleep-wake cycle: simultaneous EEG and fMRI monitoring in humans, *Neuron, 28*, 991-999.
- Pratt, H., Berlad, I. & Lavie, P. (1999). 'Oddball' event-related potentials and information processing during REM and non-REM sleep. *Clinical Neurophysiology, 110*, 53-61.
- Rivadulla, C., Martinez, L., Grieve, K.L. & Cudiero, J. (2003). Receptive field structure of burst and tonic firing in feline lateral geniculate nucleus. *The Journal of Physiology, 553*, 601-610.
- Sherman, S.M. (2001). A wake-up call from the thalamus. *Nature Neuroscience, 4*, 344-346.
- Snyder, F. (1971). The physiology of dreaming. *Behavioral Sciences, 16*, 31-44.
- Staines, W.R., Black, S.E., Graham, S.J. & McIlroy, W.E. (2002). Somatosensory gating and recovery from stroke involving the thalamus. *Stroke, 33*, 2642-2651.
- Steriade, M., McCormick, D.A. & Sejnowski, T.J. (1993). Thalamocortical oscillations in the sleeping and aroused brain. *Science, 262*, 685-697.
- Swadlow, H.A. & Gusev, A.G. (2001). The impact of bursting thalamic impulses at a neocortical synapse. *Nature Neuroscience, 4*, 402-408.
- Tononi, G. & Massimi, M. (2008). Why does consciousness fade in early sleep? *Annals of the New York Academy of Sciences, 1129*, 330-334.
- Velluti, R.A. (1997). Interactions between sleep and sensory physiology. *Journal of Sleep Research, 6*, 61-77.
- Voss, U. & Harsh, J. (1998). Information processing and coping style during the wake/sleep transition. *Journal of Sleep Research, 7*, 225-232.
- Weyand, Th., Boudreaux, M. & Guido, W. (2001). Burst and tonic modes in thalamic neurons during sleep and wakefulness. *Journal of Neurophysiology, 85*, 1107-1118.
- Weyand, Th. (2007). Retinogeniculate transmission in wakefulness. *Journal of Neurophysiology, 98*, 769-785.
- Wróbel, A. (2000). Beta activity: a carrier for visual attention. *Acta Neurobiologiae Experimentalis, 60*, 247-260.
- Zung, W.W.K. & Wilson, W.P. (1961). Response to auditory stimulation during sleep. *Archives of General Psychiatry, 4*, 548-552.