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Фільтрація сенсорної інформації: баланс між сном і життям

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Сон – це стан мозку, який характеризується низьким рівнем пильности та приглушеною свідомістю. Уві сні реакція на зовнішні подразники та їх обробка ослаблені. Під час сну сітчасте ядро таламуса гальмує в таламусі потік сенсорної активності від органів чуття до кори головного мозку. Після надходження до аферентного шару кори головного мозку зменшений потік сенсорних відчуттів аналізується, персоналізується за шарами області кори головного мозку та передається кортикофугальною системою назад у відповідні відділи таламуса. Відділи таламуса спрямовують інформацію про відчуття у відповідні області кори головного мозку, де повідомлення можуть (під)свідомо сприйматися. За потреби людина, що спить, може прокинутися від сигналу, як-от подразника, що вказує на небезпеку чи особисто значущого подразника. Очевидно, фільтрація сенсорної інформації уві сні має дві основні функції. Перша сприяє сну, знижуючи активність головного мозку через сітчасте ядро таламуса. Друга потрібна для безпеки й добробуту людини, що спить, оскільки аналізує збережену активність про важливі й небезпечні елементи кортикофугальної системи. Ці дві функції детально проаналізовано на стадіях глибокого та швидкого сну. Попри загадкову реконструкції зовнішнього подразника в сон, у другому випадку процес фільтрації сенсорної інформації майже однаковий із тим, який відбувається у фазі глибокого сну. У випадку розширеної кортикофугальної системи зрозумілі такі феномени сну, як ефект першої ночі та виникнення станів локального сну й активності, а також сну однією півкулею мозку.

Ключові слова: сон, нейронаука, фільтрація сенсорної інформації, фаза глибокого сну, фаза швидкого сну.

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Review

Sensory gating: Balance between sleep and life

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Sleep is a state of the brain characterized by a low level of vigilance and diminished consciousness. The reaction to external stimuli and the processing of stimuli are attenuated in sleep. During sleep, the reticular thalamic nucleus inhibits at the thalamus the flow of sensory activity from the senses to the cerebral cortex. After arrival at the afferent layer of the primary cortex, the reduced sensory flow is analyzed and personalized by layers of the cortical area and transferred by the corticofugal system back to appropriate subdivisions of the thalamus. Thalamic subdivisions target the information of the senses to related areas of the cerebral cortex, where the messages can be (sub)consciously perceived. When necessary, the sleeper can be awakened by a wake-up call, either by stimuli indicating danger or by personally meaningful stimuli. Evidently, sensory gating in sleep has two main features. First, it is favorable for sleep, by reducing the cerebral brain activity through the reticular thalamic nucleus, and second, it is necessary for the sleepers' safety and well-being, by analyzing the preserved activity on essential or dangerous external elements by the corticofugal system. These two features are analyzed in detail in non-REM sleep as well as in REM sleep. In the latter type of sleep, the process of sensory gating is almost similar to non-REM sleep, despite the enigmatic reconstruction of external stimuli into the dream. With the extended corticofugal system, sleep phenomena as the first-night effect, the occurrence of local sleep and wake states, as well as the unihemispheric sleep are comprehensible.

Keywords: Sleep, Neuroscience, sensory gating, non-REM sleep, REM sleep.

Introduction

The thalamus is a station through which sensory information passes before reaching the cerebral cortex. One of the major functions of the thalamus is controlling the flow of sensory information to the cortex during sleeping and waking. The change from wakefulness to sleep is an active process controlled by reticular brainstem structures, activating the reticular thalamic nucleus. This reticular nucleus increases the inhibition of the thalamocortical relay cells from passive waking to light non-REM sleep and strengthens this further from light to deep non-REM sleep. Hence, the reticular thalamic nucleus acts as a gatekeeper by closing the thalamic gate according to the state of vigilance and decides the amount of activity in the cerebral cortex. Sensory signals ascend from the thalamus to the primary cortex and in interaction with nearby cortical layers the information is adjusted and modulated, and then bounced back to thalamic nuclei by the corticofugal system. Ultimately, the reduced and processed sensory information ascends to appropriate areas of the cerebral cortex, where the sensory information is perceived (sub)consciously. When necessary, the sleeping person can be woken up by a wake-up call. Two control nuclei are relevant in sensory gating: the reticular thalamic nucleus with its inhibition of the thalamocortical transfer, and the corticofugal system with its excitatory ability to assemble senses and

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inspect the environment of the sleeper. The process of sensory gating is studied in detail in this review.

Reduction of sensory information in sleep

Reduction of the stream of sensory information to the cortex during non-REM sleep was recorded by Coenen and Vendrik in 1971 and 1972 (Figure 1). They performed research on the transmission of the flow of visual information from the eye to the cortex with light flashes in a cat during active and sleeping times. Using intracellular recordings of neurons in the thalamic geniculate body of the cat, they showed that when awake, almost all incoming information is relayed to the cor-

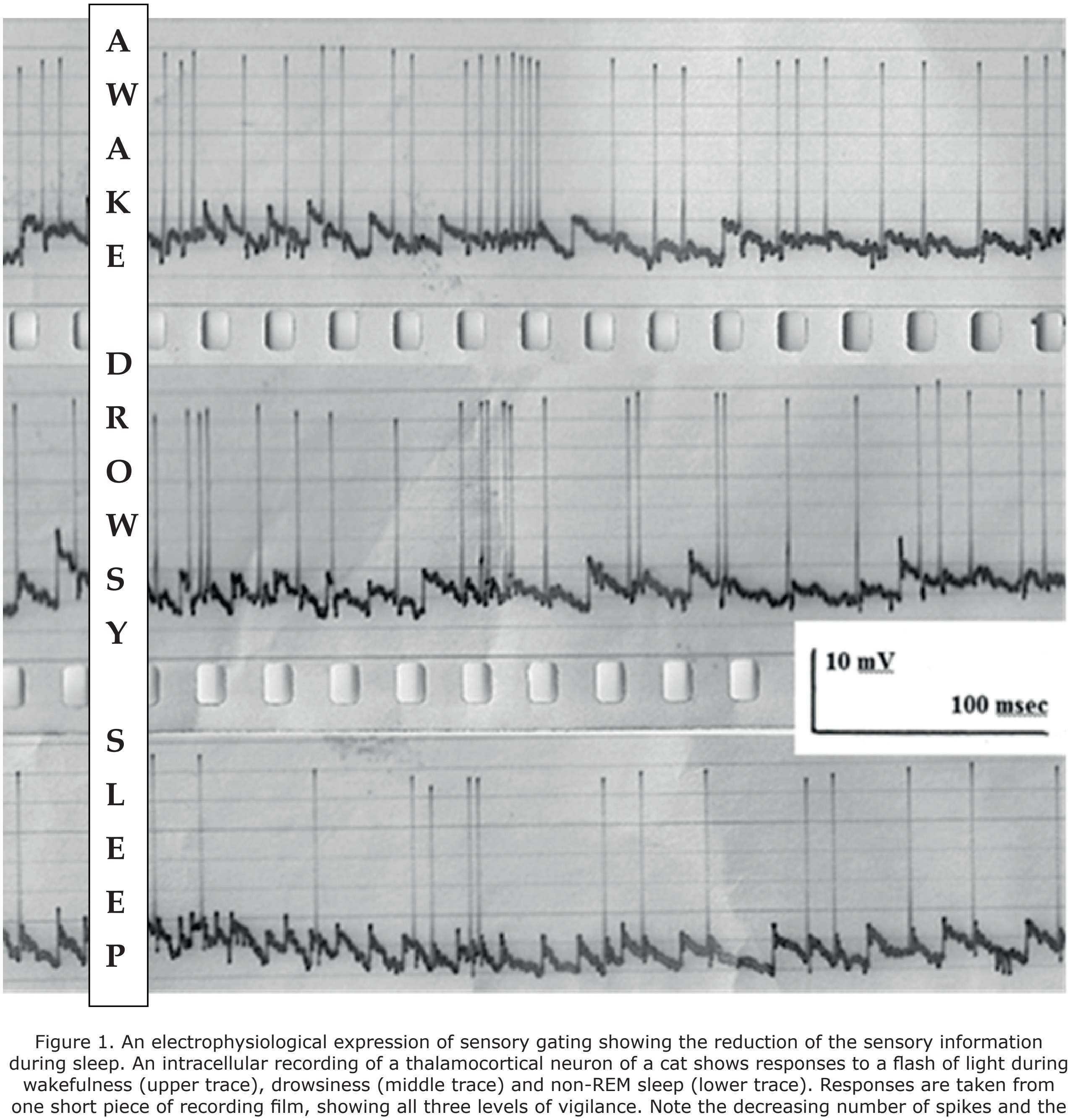

Figure 1. An electrophysiological expression of sensory gating showing the reduction of the sensory information during sleep. An intracellular recording of a thalamocortical neuron of a cat shows responses to a flash of light during wakefulness (upper trace), drowsiness (middle trace) and non-REM sleep (lower trace). Responses are taken from one short piece of recording film, showing all three levels of vigilance. Note the decreasing number of spikes and the increasing number of EPSPs during declining vigilance. The input to the recorded cell (the number of EPSPs added with the number of spikes), is equal in all states, while its output (the number of spikes) decreases sharply from the wakeful state to sleep. The transfer ratio, the output divided by input, is for waking 0.9, for drowsiness 0.7 and for sleep 0.4. Modified after Coenen and Vendrik (1972) and adapted from Coenen (2015)

tex by thalamic cells, while during non-REM sleep, only a part of the evoked information reaches cortical areas. When awake, almost all visual information arriving at the thalamus is transferred to the visual cortex, but due to the reticular thalamic blocking of the incoming series of impulses during sleep, less than half of the original information reaches the cerebral cortex. Drowsiness takes an intermediate position with an output-input ratio of about two-thirds of the original information. This implies that the transfer of information strongly depends on the state of the brain. Livingstone and Hubel (1981) replicated and extended the influence of alertness on the thalamic transfer ratio. The great majority of cortical cells showed a strong reduction in their overall firing rate during slow-wave sleep, although a minority of cells increased their firing rate.

Meeren et al (1998) registered average evoked potentials of freely moving rats after light flashes. The most conspicuous difference in these potentials recorded during sleep and wakefulness is the enlargement of the mid-latency N1-P2-N3 complex, which is fully determined by the increased inhibition during slow-wave sleep (Figure 2). Apart from the enhancement of this complex, the increased inhibition does not show a significant effect on the amplitude of the primary excitation, generally indicated as N1. An early component in an evoked potential in sleep is commonly regarded as containing sensorial information, whereas the later components express more of the network features maintaining the sleep environment (Steriade et al, 1993). It is furthermore striking to note that the shape of the evoked potentials of REM sleep is almost identical to those of these potentials during wakefulness. This is consistent with the observation made by Hirsch et al (1983) and Fourment et al (1988), stating that the depolarization of cells during REM sleep is comparable to wakefulness. Evoked potentials measured during REM sleep are mostly equal to those during wakefulness, with a shape in the middle between active and passive wakefulness.

Cortical evoked potentials along with unit responses during wakefulness and sleeping have been studied in the auditory system of the freely moving cat by Karmos et al (1988). Evoked potentials produced by a click showed an early burst followed by an inhibitory phase after which firing is normalized (Figure 3). The first burst appeared relatively independent of the vigilance state, while the large, mid-latency negative wave, reflecting inhibition, is more pronounced during non-REM sleep. Inhibition is also expressed in the silent period of the PSTH of the unit response. Changes in the auditory system by the sleep-wake states are fully comparable with those of the visual system.

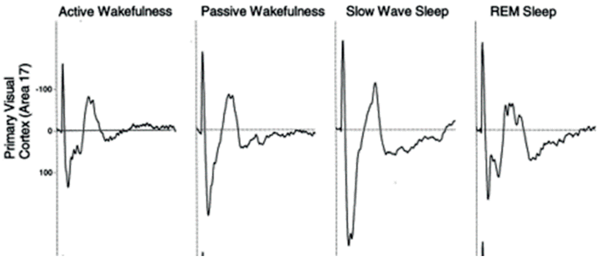

Figure 2. Grand averages of flash-evoked potentials were recorded from the rats' primary visual cortex during wakefulness, slow-wave sleep and REM sleep. Note the sharper time-locked responses during the synchronized burst firing mode of sleep compared to the smoother responses during the desynchronized tonic firing mode of wakefulness and REM sleep. The increased inhibition during slow-wave sleep is expressed in the large mid-latency N1-P2-N3 complex. The early N1 wave does not show significant changes during different states. Negativity is deflected upward. Adapted from Meeren et al, 1998

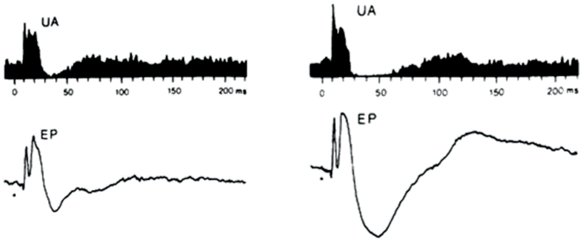

Figure 3. Auditory evoked potentials (EP) from the cortical surface along with PSTH responses of the unit activity of the neuron (UA) of the cat's middle cortical layer during wakefulness (left) and sleep (right). The long inhibitory period under sleep starting 30 ms after stimulus onset in the sleep PSTH, results in a large mid-latency complex in the sleep-evoked potential. Negativity is deflected upward. (Adapted from Karmos et al, 1988)

Edeline et al (2000) performed single-unit recordings in the auditory thalamus of guinea pigs. In accordance with most visual studies, evoked activity was generally decreased in the thalamus during non-REM sleep, despite the finding of incidental increases in neuronal firing. The original stream of information in the thalamus reaching the sensory cortex during non-REM sleep was estimated to be attenuated to approximately one-third of the original amount (Hennevin et al, 2007). Sleep-related changes in neuronal firing in the auditory system were also studied by Velluti and Pedemonte (2002) in guinea pigs. They described a general reduction in the activity of auditory neurons during non-REM sleep, although individual evoked responses in stimuli could display enhanced activities. Velluti (1997) showed that the early component N1 is rather stable during all vigilance states, while an increase of the inhibitory mid-latency complex, already starting in passive wakefulness, became even larger during non-REM sleep. This was also described by Meeren et al (2001) for rats. It is further worth noting that, just as in the visual modality, evoked responses during REM sleep are in agreement with those of the evoked potential recorded during wakefulness.

Issa and Wang (2011) measured the stream of sound information to the auditory cortex in marmoset monkeys during sleep and wakefulness. They recorded from single units of two cortical areas in the primary and secondary auditory cortex of naturally behaving monkeys. They confirmed the general finding that the overall firing rate of cortical neurons is considerably weaker during non-REM sleep compared to responses during wakefulness. They also showed that sleep alters neural responses in the auditory cortex in two ways. Sleep reduced the sensitivity of auditory neurons in such a way that quiet sounds elicited weak responses in non-REM sleep compared to wakefulness, while loud sounds evoked similar responses both during non-REM sleep and wakefulness, implying the gaining of sounds in sleep. This unusual pattern of alterations was not observed during REM sleep.

Baker (1971) recorded in two somatosensory thalamic nuclei in free-behaving cats spontaneous and evoked activity of single units, which were sensitive to the movement of hairs. They measured a high spontaneous activity during waking and low activity during sleep. The inhibition period following the early response was particularly striking in the non-REM sleep response. Identical state-dependent changes in thalamic neuronal activity in humans were described by Tsoukatos et al (1997). They measured the patterns of thalamic neuronal firing during genuine sleep and wakefulness in a patient during surgery. The extracellular single-cell activity was recorded in the thalamus of a sleeping patient. All somatosensory thalamic neurons showed bursting activity, but when the patient woke up bursting stopped and was replaced by a tonic firing pattern.

Innocuous electrical impulses were applied to the rat’s tail during sleep-wake states by Shaw et al (2006). Somatosensory evoked potentials were recorded over the primary somatosensory cortex in response to single pulses during wakefulness before sleep and during non-REM and REM sleep. The short latency component in the somatosensory evoked potential was robustly recorded during all brain states with no significant differences in amplitudes and latencies. During wakefulness and REM sleep, the middle latency component was composed of a dominant negative wave, but during light and deep sleep, this middle latency wave became longer and displayed a biphasic shape, expressing increased inhibition. Oniz et al (2015) measured somatosensory evoked potentials to non-painful tactile skin stimuli in humans. They recorded these potentials during a short period just before sleep, during passive wakefulness, during light and deep non-REM sleep, as well as during REM sleep. The early small components were almost equal in amplitude, while the late components had a significantly higher amplitude due to inhibition, during light and deep non-REM sleep, compared to passive wakefulness and REM sleep. The results of Oniz et al (2015) study on humans perfectly correspond with the data from Shaw et al (2006) obtained from rats.

Optogenetic stimulation of somatosensory cortex neurons was applied by Urbain et al (2019) in head-restrained mice during sleeping and wakefulness. Membrane potentials and neuronal firing was recorded in two somatosensory medial thalamic nuclei, along with local cortical field potentials and the EEG. The spontaneous firing of neurons, distinct between two nuclei, was generally more regular during waking and higher than during sleep when firing was more variable and locked to the cortical slow waves and spindles. The flow of somatosensory input was strongly dependent on the state of the animal and also expressed in the movements of whiskers. Fanselow and Nicolelis (1999) recorded during quiet immobility slow, large magnitude whisker responses in rats, while during behavioral activation, fast, small amplitude movements appeared. The pattern of cortical activation is markedly tied to the behavioral state.

The reduction of sensory activity is favorable for sleep

In all three main sensory systems, there is a considerable reduction in the afferent flow of sensory activity during non-REM sleep, compared to wakefulness. Until the twentieth century, the passive ‘deafferentation’ theory of sleep, which held that blocking the sensory input to the cerebral cortex caused sleep, flourished. However, when the active ‘reticular brainstem’ theory was formulated implicating that a center in the brain actively produced sleep, heavy competition among sleep scientists started. The struggle was finished when Frédéric Bremer shook hands with Giuseppe Moruzzi and Horace Magoun at the first IBRO meeting in Pisa in 1961, under the agreement that both the passive and the active theory were based on positive evidence (Finger, 1994). The brainstem reticular formation system activated by the biological clock, plays a prime role in sleep production, while the afferent sensory input takes a second role in the modulation of the sleep process. When the reticular sleep neurons are activated, sleep onsets and this process is facilitated by a reduction of the environmental sensory stimuli and relaxation of the brain, both leading to less cerebral activity and being positive for sleep onset and maintenance. The reduction of cerebral activity is strengthened by sensory gating. On the other hand, it is known that sleep is impaired by a too-high cerebral activation, both produced by strong environmental stimuli and by annoying internal stimuli such as negative thoughts before sleep as obsessive and repetitive negative thinking (‘rumination’) in sleep. When this activation is relieved by relaxation techniques or by thought-stopping techniques, sleep is improved. Also sleeping pills, working as GABA agonists and enhancing the inhibition of the afferent input by strengthening the reticular thalamic nucleus, induce sleep. Obviously, all processes inhibiting the flow of sensory input to the cerebral cortex, are favorable for sleep. Lewis et al (2015) noted that specific activation of the reticular thalamic nucleus induced the state of sleep rapidly, which is observed both in electrophysiological and behavioral respects. The conclusion is that a reduction of the flow of sensory input by thalamic inhibition facilitates sleep onset and sleep maintenance.

Preserved sensory activity during sleep

Although the incoming sensory information is firmly reduced in sleep, an intriguing point is what the brain can do with the preserved incoming sensory activity. For example, a question that is often heard is whether it is possible to learn a foreign language by playing this language during sleep. In their work with the incoming activity of light flashes during sleep in cats, Coenen and Vendrik (1972) estimated the preserved activity during non-REM sleep to be less than half of the original generated activity. This is presumably what Edeline et al (2000) also suggest by measuring average auditory evoked potentials. Bastuji et al (2002) explored in humans the possibility of whether the brain can extract information from external stimuli during sleep. They found that event-related potentials during sleep could discriminate between the subject’s own name relative to neutral names. Moreover, they described that a shallow semantic analysis of auditory stimuli remains possible in the sleeping brain, but could not elucidate the extent and limits of these capabilities. This made the interpretation complex and prevented drastic conclusions. In behavioral studies, Coenen and Drinkenburg (2002) pointed out that some simple learning as involved in habituation and associative learning seems possible during sleep, although it is limited compared to the waking state. They came to the conviction that complex forms of processing are hardly possible during sleep, also implying that learning a foreign language while asleep seems an illusion. The limited information of original messages hiding in the spike activities of the burst-silent firing pattern during sleep seems insufficient for higher forms of processing. This does not exclude that the preserved sensory activity seems sufficient for a superficial analysis of external information during sleep, and may therefore fulfill a relevant role in the necessary monitoring of the environment during sleep (Coenen, 1995).

The corticofugal system

The sleep-reduced sensory information of external stimuli ascends from the thalamus to layer 4 of the primary sensory cortex, and in interaction with layers 5 and 6, plays a leading role in stimulus processing (Usrey and Sherman, 2019) (Figure 4). A sharper perception of complex external stimuli by 'egocentric selection', implying extra gaining of relevant stimuli and extra suppression of irrelevant stimuli, is obtained here. Moreover, it colors the information according to the actual state of the brain, with respect to vigilance, attention, emotions and memory representations (Ferguson and Cardin, 2020). Axons of cortical layers 5 and 6 form the corticofugal pathway and this pathway projects the adjusted and modulated stream of information back to several subdivisions of the thalamus, mostly directly or sometimes indirectly via the reticular thalamic nucleus (Usrey and Sherman, 2019). The complexity of this corticofugal circuit of sensory gating can be expressed in the overwhelming number of non-sensory modulatory inputs to the thalamic cells. The modulatory system to the control nuclei of the thalamus consists of about ninety percent of all inputs, whereas the sensory input to the thalamic relay cells, the driving input, is estimated at no more than one-tenth of all inputs (Sherman, 2001a). The corticothalamic loop is implicated in the generation of several rhythmic sleep activities such as spindles, slow-wave oscillations and 40-Hz oscillations, as well in the synchronization of these activities in various relay stations (Contreras et al, 1996; Nuñez-Molina and Amzica, 2004). This synchronization improves sensory processing greatly. Corticofugal projections targeting the thalamocortical relay cells of the thalamic subdivisions mainly cause excitations, but also inhibitions via the reticular nucleus. The ultimate stations are the related parts of the sensory cortices, where the information comes into the (sub)consciousness of sleep. The complex thalamo-corticothalamic circuit connects the environment via the thalamus with the cerebral cortex. The primary cortex forms the heart of sensory processing, receiving and adjusting the external information and providing cortical areas of the extensive corticofugal system with the information of all senses, integrated into a sensory imagination, necessary for a functional contribution to processing and behavior.

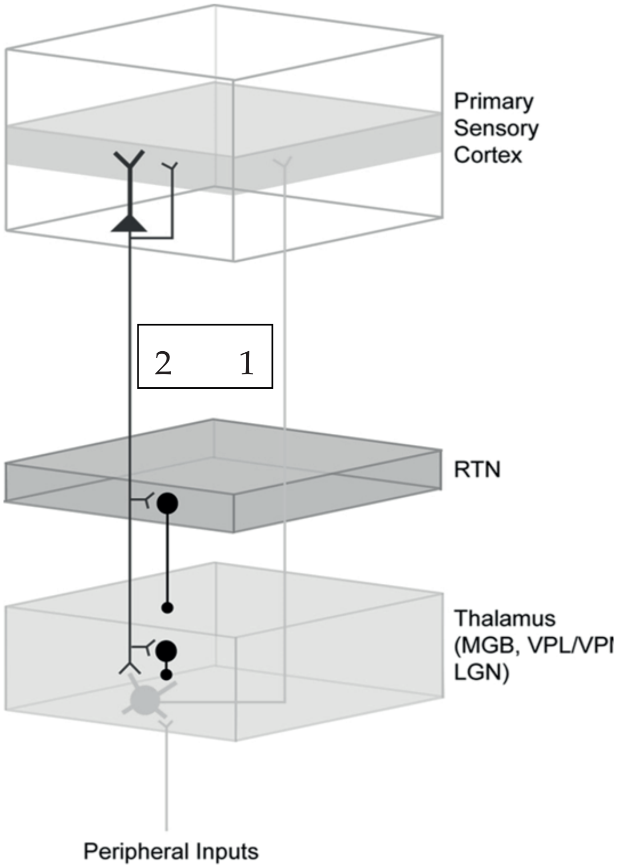

Figure 4. Schematic diagram of thalamic-corticothalamic circuitry. Thalamocortical neurons (1) receive peripheral inputs and project axons to layer 4 of the primary sensory cortex. Corticofugal neurons (2) receive local input from thalamocortical recipient layers 4 and 5 and provide output to the thalamus. Corticofugal projections also supply inhibition to thalamic neurons via reticular neurons. Adapted from Briggs and Usrey, 2008

Together with the thalamic reticular nucleus, the complex corticofugal system plays a pivotal role in the control of sensory information. The brain continues maintaining essential contact of the sleeper with the surrounding environment, by monitoring and analyzing the sleep environment. On the one hand, the partial decoupling between the brain and environment facilitates sleep by relaxing the cortex, but on the other hand, protects the sleeper by analyzing the environment. This way, sensory gating creates a 'vigilant sleeper' (Andrillon and Kouider, 2020). It is interesting to note that Voss and Harsh (1998) described in their work with human auditory evoked potentials an attention-enhancing component, the evoked 40-Hz oscillations, as well an attention-reducing component, N350. These components with opposite mechanisms suggest a competition between sleep-enhancing and life-protecting processes, underlining the fragile balance between sleep maintenance and life well-being. A game between the advantages and disadvantages for sleep is to a lesser extent delivered by earplugs. Wearing earplugs is useful in a situation where noise stimuli disturb sleeping, but has a downside by blocking sound stimuli indicating a risky situation.

Gating and Gaining in Sleep

Livingstone and Hubel (1981) described that besides a general decrease in the spiking of most cortical visual cells during non-REM sleep, a minor amount of cells increased their firing rate. A general inhibitory gating is produced by the reticular thalamic nucleus increasing its obstruction on the thalamus from passive wakefulness to light and further to deep non-REM sleep. However, another part of the reticular thalamic nucleus weakens its inhibition to the thalamic nucleus at the transition from light to deep non-REM sleep, and this might explain the gaining of a part of cortical cells (Sysoev et al, 2021). Velluti and Pedemonte (2002) have noticed that during non-REM sleep the spontaneous and evoked activity in the auditory system of the guinea pig could vary in opposite directions. Despite a general reduction in the activity of neurons in the auditory cortex, the responsiveness of these neurons was partially preserved and could even show excitations. The authors hinted with these findings on a more complex role of the cerebral cortex with its extensive corticofugal projections in gaining specific areas. Issa and Wang (2011) reasoned, in the same way, to clarify their findings in marmoset monkeys that loud sounds, always having a tone of emotion and danger, evoke similar responses in non-REM sleep compared to wakefulness (Figure 5). Extra gaining has terminated the normal loudness reduction of these sounds during non-REM sleep by gating.

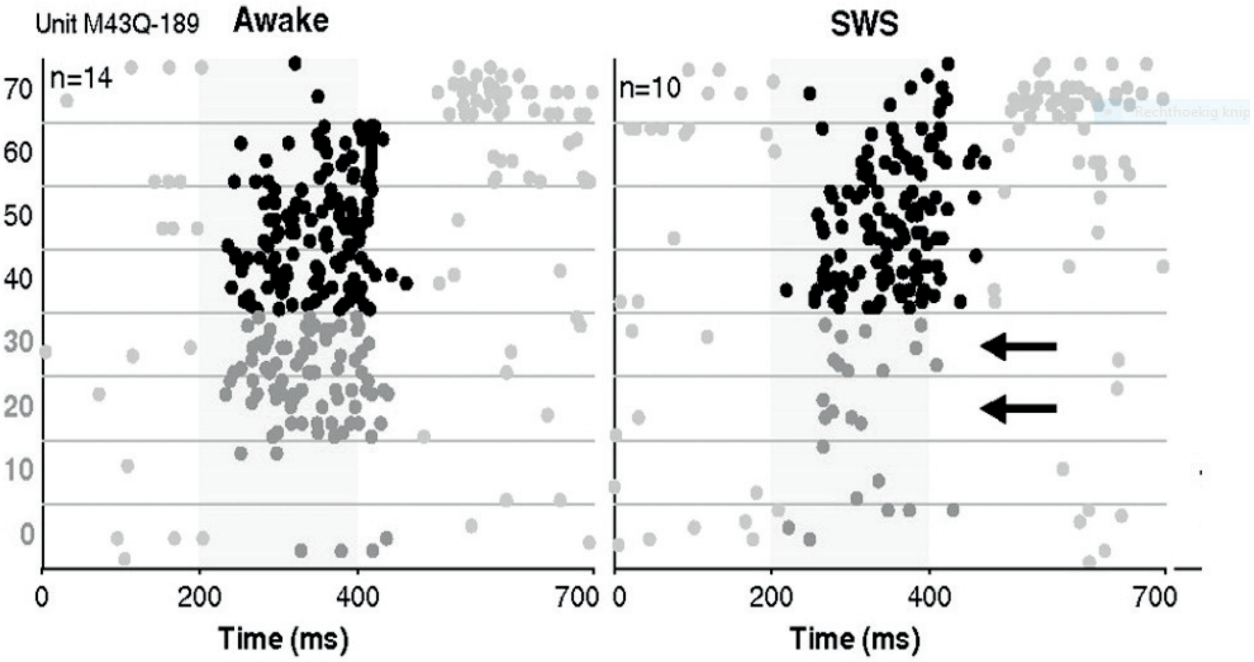

Figure 5. Selective loss of responses to quiet sounds of a neuron collected from the primary auditory cortex of a marmoset during slow-wave sleep. The response of this neuron to quiet sounds disappeared during sleep (black arrows), even though a robust response of this neuron to loud sounds remained. The stimulus was a 780 Hz pure tone and sound intensities in dB are indicated on the vertical axis. Adapted from Issa and Wang, 2011

Urbain et al (2019) described a strong phase locking between oscillations at the somatosensory cortex and neuronal firing of two thalamic nuclei (the ventral posterior media nucleus and the posterior media nucleus). During non-REM sleep, a different activity in these two thalamic nuclei, reflecting cortical slow waves and oscillations, was uncovered. Strong correlations between spiking, cortical spindles and slow waves were found in the ventral posterior media nucleus, while a weaker correlation between spiking and the cortical slow waves was found in the posterior media nucleus. The temporal firing of thalamic cells reflected that these slow waves during non-REM sleep were generated at the level of the primary cerebral cortex, where the cortex seems to be in the lead. Eighty percent of the ventral posterior media nucleus cells and sixty percent of the posterior media nucleus cells exhibited spike firing at specific phases of the cortical slow-wave cycles. This difference reveals a distinct modulation of the ventral posterior nucleus and the posterior medial nucleus throughout non-REM sleep episodes. This ultimately leads to differential activities at the appropriate somatosensory cortical areas, expressed in distinct whisker movements in sleep. These differences in whisker movements in adjacent cortical areas probably mean precise sensing of the exact body position during sleep.

Presumably, the corticofugal system in humans ensures that they never fall off the bed during sleep. Due to touch receptors in the skin, sleepers know ‘subconsciously’ their position in bed. The somatosensory system of the sleeper is significant because it indicates not only a safe position in bed but also the time to move and turn in bed to prevent insufficient blood circulation expressed in numbed arms and stiff muscles (Coenen et al, 2009). Moreover, it may awaken a person when the urge to urinate is strong. Overall, the corticofugal system assures the sleeper that he/she will get through the long night with a good quality of sleep in a proper, healthy and safe way!

Wake-up call, local sleep-wake patterns and unihemispheric sleep

Sleep is indispensable for the mind and body, but takes place in a rather vulnerable situation. Both humans and animals sleep immobile and unprotected, while events in the environment might require a fast awakening from sleep. It is indeed well-known that a sleeping person can be awakened not only by intense stimuli but also by soft stimuli, which have a meaning for the sleeper. Dangerous signals in the environment, voices from care-seeking persons, and a cry of a newborn baby (Figure 6) are all examples of stimuli that easily awaken people. Even when such stimuli are rather gentle, awakening follows. This implies that the meaning of these stimuli has to be recognized and a wake-up call may follow (Atienza et al, 2001; Coenen, 2010).

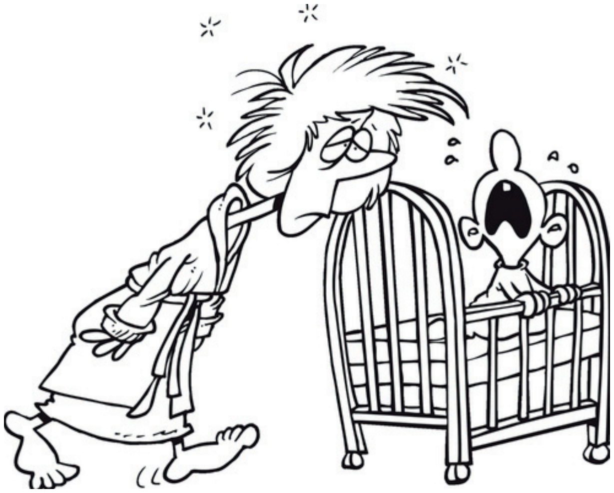

Figure 6. A cry of a newborn baby is a wake-up call for parents. Although sleep-related infant death is still an issue, a baby’s cry in a vast majority of cases does not mean that there is something wrong. Nevertheless, it is the advice to caregivers to listen carefully to whether there are no deviations from normal crying. A wake-up call is a warning signal for eventually dangerous situations and forms a crucial part of the sensory gating system

The amygdala is the center involved in decoding attentional, emotional and threatening stimuli and together with the medial prefrontal cortex plays a key role in the analysis and processing of deviant stimuli (Marek et al, 2013). The amygdala serves as the detection system of unusual stimuli, connecting the information via the reticular thalamic nucleus to the thalamic relay cells. These neurons are creating powerful excitations to the neurons of the prefrontal cortex, eventually producing a wake-up call (Sherman, 2001b). Although the wake-up call delivers not the precise nature of stimuli causing the awakening, the vigilance at awakening prepares the individual for an adequate behavioral response.

Generally, sleep is regarded as a global brain phenomenon, although Koella already suggested in 1984 that sleep could occur in a specific, local situation. This reflects the vision of Evans (2003) regarding the existence of a double thalamocortical network in the brain: a global one involving all cortical areas with non-specific thalamic nuclei, and a second one related to cortical and thalamic areas with specific functions. Indeed, a locally awakened state was recently isolated in the brain of sleep-walking patients by Terzaghi et al (2009), while a regional sleep stage was identified in awake rats by Vyazovskiy et al (2011). Moreover, intracerebral EEG studies in humans have shown a coexistence of wakefulness and sleep patterns in cortical areas (Nobili et al, 2012), while Vantomme et al (2019) concluded that the appearance of sleep in the brain is not global and uniform, but that local awakenings could exist during genuine sleep.

The first-night effect, the phenomenon of troubled sleep in a new environment, is a manifestation of the regional interhemispheric asymmetry of sleep depth. The hemisphere with reduced sleep depth has areas with awakened vigilance and acts as a night watch to detect unfamiliar surroundings. The more vigilant hemisphere shows enhanced evoked brain responses to deviant external stimuli and these stimuli may cause more awakenings and faster behavioral responses than those detected by the other hemisphere (Tamaki et al., 2016). Further development of the night watch during sleep is manifested in the so-called unihemispheric sleep, during which mammals, such as whales and dolphins, or birds, such as common swifts and house sparrows, sleep with one hemisphere being asleep while the other is awake. Studies have shown that unihemispheric sleep is indeed genuine sleep, because one hemisphere has a high-amplitude slow-wave activity, while the other has a desynchronized EEG pattern. The phenomenon of unihemispheric sleep extensively supports the idea of local sleep and local wakefulness states (Konadhode et al, 2016). For sea mammals, unihemispheric sleep is the only way to sleep in the sea, while for migrating birds it enables non-stop long-lasting flights. All phenomena, from wake-up calls to asymmetric sleep-wake patterns in hemispheres, are permitted by the corticofugal system using extra inhibitory gating and extra excitatory gaining.

External stimuli during REM sleep

In all three sensory modalities, the average evoked potentials recorded during REM sleep are similar to those recorded during wakefulness, and at variance to those recorded during non-REM sleep. The REM sleep event-related potentials are lying between those of active and passive waking. This corresponds well with the opinion of Laureys (2005), who estimated the level of consciousness of REM sleep based on vigilance and awareness and on that of the consciousness of moderate wakefulness. The identical shape of average potentials during REM sleep and wakefulness implies that the cortical brain activity during REM sleep is relatively comparable to waking and more comparable to non-REM sleep. Sensory gating is scarcely investigated during REM sleep, but its resemblance with wakefulness suggests that the sensory gate stands relatively open. Indeed, the fact that external sensory stimuli can be incorporated into a dream, a phenomenon highly associated with REM sleep, suggests that stimuli can pass the gate. This was confirmed by the 'recall' technique introduced by Dement and Wolpert in 1958, showing that it was relatively easy to study the incorporation of external stimuli, such as a spray of water, into ongoing dreams. Nonetheless, in subsequent experiments, it turned out that it was rather difficult to influence the dream content with external stimuli. Rechtschaffen and Foulkes (1965) showed that even a minimum awakening after external stimuli showed signs of incorporation of stimuli in dreams. Only somatosensory stimuli, such as sprays of water on the head or pressure on the arm, caused a moderate rate of dream incorporation (Sauvageau et al, 1998). A caveat has to be made here concerning the relatively small amount of stimulus incorporations into dreams. Only those dreams followed by an awakening are noticed, while stimuli which are integrated into a dream but do not lead to an awakening, are not noticed and not counted in the number of dream incorporations.

A mysterious feature of the incorporation of external stimuli into dreams during REM sleep is that it is unlike incorporation into wakefulness. The mind during REM sleep has its own, mysterious type of consciousness (Hobson and McCarley, 1977; Coenen, 1998; Hobson, 2009), and this might be related to the reconstruction of external stimuli, in emotional tone, stimulus modality or story plot, so that the reconstructed stimuli better fit into the ongoing dream scenario (Solomonova and Carr, 2019). Examples of the widely diverged manners of the reconstruction of identical external stimuli in different dream scenarios by the REM-sleeping mind are reported by Nielsen (1993). Despite the enigmatic reconstruction of the sensory stimuli in the dream, the basic message, for example 'danger', remains to be understood by the dreaming mind, implying that a wake-up call can take place. All in all, sensory gating during REM sleep is mostly similar to sensory gating during non-REM sleep. An additional difficulty during REM sleep is that the presence of rapid eye movements selectively prevents the processing of stimuli in dreams (Koroma et al, 2020).

It is interesting to note that the incorporation of external stimuli often happens in a brain-wandering situation at sleep onset. External stimuli are reconstructed at sleep onset into hypnagogic hallucinations, which are presently regarded as genuine dreams, while the immediate sleep after sleep onset is related to REM sleep (Waters et al, 2016). Hence, it is almost impossible to conduct a study on the reconstruction of external stimuli into dreams during REM sleep, it can be done much easier using the study of the reconstruction of external stimuli into a hypnagogic hallucination at sleep onset.

The most well-known hypnagogic hallucination is from the chemist Friedrich Kekulé (1890) who studied the molecular structure of benzene. In the report, he noted: 'I was deeply thinking about the structure of benzene, I turned my chair to the fire and dozed. The atoms were gamboling before my eyes. Smaller groups kept modestly in the background, and my mental eye, could distinguish larger structures of conformation; long rows sometimes fitted together all twining and twisting in a snake-like motion. But look! A snake had seized hold of its own tail, and the ring form whirled mockingly before my eyes. As if by a flash of lightning I woke up; and I spent the rest of the night working out the consequences of the hypothesis: the ring structure of benzene!' In this hypnagogic hallucination, all features appear from a transition of the realistic series of stimuli in the mind to a hallucination in a dream, complete with a wake-up call. A creative change of thinking in this hallucination is observed too.

Hypnagogic hallucinations are often linked with creativity, in the sense that these dreams can aid creativity and problem-solving behavior (Barrett, 2017). Recently, Lacaux et al (2019) found in narcoleptic patients, who had many hypnagogic hallucinations, high scores in tests for creativity with enhanced original thinking. In a follow-up experiment, Lacaux et al (2021) exposed participants to mathematical problems without knowing that a hidden rule could solve these problems easily and instantaneously. They found that spending a short time in the twilight zone tri-

Figure 7. After the presentation of the mathematical problem (with a hidden rule that allowed for solving the problem quickly), subjects had a rest in a chair in a dark room with their eyes closed, while holding a bottle in their hand (circled). They were told to report any mental content if the bottle fell. Subjects were at the stage of sleep onset when the bottle fell, waking them up, and they could report a hypnagogic hallucination. Subjects were then given the problem again and they were able to present the solution directly by cracking the hidden rule, in contrast to the control subjects. Adapted from Lacaux et al, 2021

pled the chance to discover the hidden rule (Figure 7). This finding suggests that there is a creative sweet spot in the sleep onset period, where a realistic event may change into a hallucinatory story, perhaps associated with creative insights. The incorporation of an external narrative into a dream story may be associated with creative solution-solving behavior. When this remarkable phenomenon can be replicated, it implies that sensory gating during REM sleep is not only a complicated and dynamic process great for sleep and life but also great for conscious and subconscious creativity!

Epilogue

A main function of the thalamus is the control of the flow of sensory information to the cerebral cortex, in particular during sleep-wake states. During sleep, the reticular thalamic nucleus inhibits the thalamocortical relay neurons, reducing the stream of activity to the cortex. The inhibition of signals at the level of the thalamus is established by single-unit recordings and by average evoked potentials. Particularly, the mid-latency complex in the evoked potentials shows a clear increase in inhibition, while the earliest wave does not show significant differences between wakefulness and sleep. This suggests that the early wave contains main sensorial information, in contrast to the mid-latency waves. The transfer of the visual, auditory and somatosensory activity to the cerebral cortex is about half of the original activity and the reduction in the number of external stimuli facilitates sleep onset and sleep maintenance. Although the sensory activity passing the thalamus is considerably reduced, the preserved sensorial activity arriving at the cerebral cortex can be analyzed to some extent by the cognitive cortex. Simple discrimination tasks between stimuli can be done, as well as easy learning tasks; however, deep processing and learning of complex tasks, such as a foreign language, are unlikely.

Sensory information ascends to the primary sensory cortex and in interaction with adjacent cortical layers of the corticofugal system, sensory information becomes more acute through egocentric selection and coloring of the information according to the state of the brain. The corticofugal system, with cell axons of layers 5 and 6, bounces the modulated information back to several subdivisions of the thalamus, after which the information ascends to the appropriate primary and non-primary cortical areas. The external information arriving at the primary cortex is in modulated form and widely distributed to all relevant parts of the cerebral cortex. In these parts of the sensory cortex, the relevant sensory information of the visual, auditory and somatosensory, as well as other senses, assemble in these areas, creating sensory imagery. The sleeper becomes subconsciously aware of what is going on in the environment and can make decisions and draw conclusions. The integration of all senses is necessary for adequate processing and behavior.

A sleeper is particularly sensitive to two types of stimuli: those indicating a risk or danger and those which carry information for the sleeper. The amygdala plays a role in the interpretation of attentional, emotional and threatening stimuli and this information may create a wake-up call. This implies that the analysis of the environment is crucial for the protection and well-being of the sleeper. The complicated system between the thalamus and cortex also plays a role in such phenomena as the first-night effect, local sleep and wakefulness states, as well as in unihemispheric sleep.

REM sleep, a type of sleep which is highly associated with dreaming, has been compared to non-REM sleep, based on features of higher consciousness and a higher vigilance. External stimuli can pass the thalamic gate and reach the cerebral cortex. However, the incorporation of an external stimulus into REM sleep is fairly different from the incorporation into non-REM sleep. The sensory stimulus is reconstructed during the integration into a dream to better fit into the dream scenario. Nevertheless, despite the enigmatic change of the stimulus, the basic message of the signal, e.g., danger, implies that a wake-up call remains possible. This means that, despite the discrepancy in perception of incoming stimuli in dreams, sensory gating during REM sleep is rather similar to that of non-REM sleep.

The study of the incorporation of stimuli in dreams is done by the study of external stimuli in hypnagogic hallucinations. Hallucinatory dreams are often linked with creativity and problem-solving behavior. Recently, in an experimental study, Lacaux et al (2021) found a creative period in a hypnagogic hallucination during the sleep onset period. When this remarkable phenomenon can be replicated, it implies that sensory gating during sleep is a process, which is not only great for sleep and well-being but also for (sub)conscious creativity during REM sleep!

The process of sensory gating, with a partial decoupling between brain and environment, facilitates sleep by reducing the flow of activity to the cerebral cortex and protects the sleeper by analyzing the environment and noticing deviant signals. By these two features of sensory gating in sleep, relaxation of the brain and monitoring the environment, the vigilant sleeper is born.

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