Relationship Between Emotions, Sleep and Well-Being

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8.1 Psychophysiological Functions of Sleep

Sleep is a natural, universal phenomenon present in all living organisms, maintained across all steps of phylogenetic evolution and also observable in species without a centralized nervous system, like jellyfish [1]. Even if sleep is a state defined by the cessation of finalized behaviour and a strong disconnection from the sensory environment, it is not a passive phenomenon [2], but it is a highly active process as vital as respiration or digestion. Sleep is not a unitary phenomenon, but it is composed of a dynamic sequence of stages that show high degrees of inter- and intra-individual variability. In the last few decades, the long-standing question 'why do we sleep?' has received several answers. Since the development of the electroencephalogram (EEG) by Hens Berger in 1929, sleep has been continuously investigated in humans, leading to the definition of rapid eye movement (REM) sleep and non-REM (NREM) sleep, which in turn is divided in three stages, related to the increase of sleep depth (i.e. increase of awakening threshold): N1, N2 and N3. The alternation between sleep stages follows a sequence of cycles during the night, lasting nearly 90 min each (N1-N2-N3 REM; reviewed in [3]). It is now well established that sleep is fundamental for neuronal detoxification, tissue restoration, conservation of energy, enhancement of the immune system and, finally, increasing neuronal plasticity [4]. In order to develop a model of sleep function, the synaptic homeostasis hypothesis has been developed [5, 6]. According to this theory, experience-dependent learning during the day is related to the increase of cortical

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synaptic weight (i.e. wakefulness promotes activity-dependent strengthening of synaptic connections). Conversely, during the night, sleep reverses plasticity rules, thus promoting the activity-dependent weakening of connections, leading to homeostatic down selection of synapses actuated during the day. In this way, sleep basically resets synaptic weight in the central nervous system, allowing the brain to learn again during the following day [5, 6]. Together, these functions are related to slow waves (including sleep slow oscillations (SSO) and K-complexes, very slow, triphasic slow waves with a frequency between 0.5 and 1 Hz, mainly detectable at the frontal level; see [7, 8]), and sleep spindles. Slow waves are low frequency (0.5–4 Hz), high amplitude oscillations generated in the cortex that are critically dependent on the activity of subcortical structures, like the thalamus [9, 10], and the olfactory bulb [11]. Slow waves are abundant in the first part of the night (early sleep) and reduce exponentially during the night, but are increased after sleep deprivation, indicating an important role in homeostatic regenerative functions of sleep [3]. Sleep spindles are brief, fast oscillations, lasting 1–2 s, with a frequency of 11–16 Hz. They are generated through thalamocortical loops and are mainly related to declarative memory consolidation during sleep [12, 13]. Sleep is also fundamental for enhancing learning-related processes, sustained by local slow-wave power (i.e. slow-wave activity) and SSO. Basically, increased daytime, performance-related, synaptic activity in cortical regions (e.g. activity in visuomotor cortices related to the performance of a visuospatial learning task) will be reflected in increased slow-wave activity/SSO in the same regions during the following night [14].

Beyond memory consolidation, one of the main roles of sleep is emotion regulation, although the identity of the specific sleep stages, features and mechanisms involved in this process is currently a hot research topic. Several studies have identified REM sleep as fundamental [15, 16]. In fact, REM sleep is not only associated with the consolidation of conditioned fear memories [17], but also with the unbinding of ('hot') emotional aspects of a memory from the ('cold') memory itself [18], thus facilitating the extinction of conditioned fear. In other words, REM sleep, and particularly the total amount of EEG theta activity, can separate emotionally relevant components of a memory (its 'visceral charge') from emotionally irrelevant ones [19, 20], resulting in a dissipation of subjective emotional intensity and in the consolidation of the information itself, as a sort of 'overnight therapy' [21, 22]. The neurophysiological substrate of this process has been identified as the active inhibition of the amygdala through top-down prefrontal cortex (PFC) connections [23], causing a reduction of the activity of the amygdala, paralleled by an increase of the activity of the hippocampus (the 'sleep to forget and sleep to remember' model [21]).

Even if theoretical connections between homeostatic functions of sleep and emotion regulation have never been directly investigated, they take on particular importance when considering a critical developmental period like adolescence.

8.2 Adolescence, Emotions and Emotion Regulation

Adolescence is a critical developmental age that starts with sexual maturation (puberty) and ends with the achievement of the social roles of young adulthood, usually taking place between 12 and 17 years old. It has been defined as an age characterized by both strengths and vulnerabilities, and is a critical period of development of emotion regulation [24]. During this stormy period, the central nervous system undergoes a slow process of maturation, with several functional and anatomical modifications, most importantly, a massive neuronal pruning [25]. This slow maturing process is most evident within the prefrontal cortices, begins during childhood and continues until early adulthood, resulting in the development of high-order psychological functions [25, 26]. Accordingly, adolescence is characterized by heightened emotional experiences, which are probably caused by the different maturation trajectories of cortical (prefrontal) and subcortical (amygdala) brain structures, leading to a diminished ability to regulate emotions [27].

Emotions are highly salient and fundamental qualities of our conscious life, which can modulate attention to stimuli, interrupt cognitive or behavioural processes and trigger actions in the outer world [28, 29]. In order to adapt successfully to the environment, humans have the ability to regulate emotions, applying strategies that modulate, consciously and unconsciously, emotional experience and expression [30], in order to use emotions as resources in decision-making processes within complex social contexts [24, 31]. Emotion regulation begins as the individual acknowledges a new event or situation, and interprets it in the context of his goals [32, 33]. Subsequently, attempts to adaptively regulate the new emotion take place in an iterative way, modulated by environmental feedback, according to the following stages: (1) situation selection, (2) situation modification, (3) attentional deployment, (4) cognitive change (e.g. reappraisal) and (5) response modulation (e.g. behavioural suppression) [32]. At the neurophysiological level, successful emotion regulation in adults is mainly related to increased PFC activity and decreased amygdala activity [34–36], while emotion dysregulation is related to deficit of the top-down inhibition of the amygdala by the PFC [37, 38]. However, emotion regulation has been linked to an expanded prefrontal network, comprising the dorsolateral, dorsomedial, ventrolateral, and the posterior prefrontal cortices, the anterior cingulate cortex and the inferior parietal regions [39] (Fig. 8.1).

Emotion regulation increases with age, from childhood to adulthood [34, 40–42], with a critical period occurring during adolescence [43]. Alterations in this process can lead to the development of severe psychopathological conditions in adulthood. In fact, emotion disturbance and dysregulation are transdiagnostic processes observed in almost all forms of psychopathology, both internalizing and externalizing [44, 45]. As described next, sleep has a fundamental role in the successful development of these abilities.

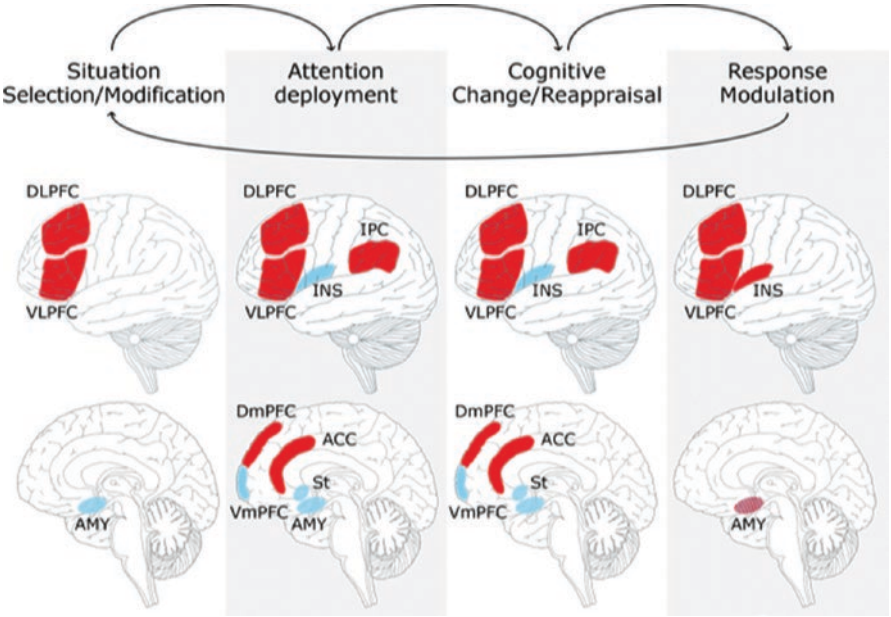

Fig. 8.1 Emotion generation and regulation in the adolescent brain. In blue, functional decrease of activity; in red, functional increase of activity. *DLPFC* dorsolateral prefrontal cortex, *VLPFC* ventrolateral prefrontal cortex, *INS* insula, *IPC* inferior parietal cortex, *DmPFC* dorsomedial prefrontal cortex, *VmPFC* ventromedial prefrontal cortex, *ACC* anterior cingulate cortex, *AMY* amygdala, *St* ventral striatum. Adapted from Ochsner et al. [39] and Gross [32]. (Authors thank Dr. Sergio Frumento for having adapted the figure)

8.3 Sleep and Sleep Deprivation in Adolescence

Across the life span, emotion regulation increases in tandem with continuous change in sleeping patterns, with a reduction in both NREM and REM sleep, and total sleep time. In particular, sleep in adolescence is marked by a progressive reduction of EEG signal amplitude and power (up to 40%) across all EEG frequency bands, which is related to age and puberty stage [46–49]. At the same time, adolescent sleep is related to the progressive increase of sleep spindles in peak frequency and EEG coherence in multiple frequencies, which have been related to the myelination of long-range connections in thalamocortical networks [47, 48, 50–52]. An MRI study has confirmed that this reduction in EEG power during sleep in adolescence is correlated with massive pruning of grey matter [53]. With EEG, Kurth et al. [54] found that progressive reduction of slow-wave activity has a posterior-to-anterior gradient, which follows precisely the local reductions of grey matter, as another study longitudinally assessed with MRI [55].

These data suggest an important link between slow waves and sleep spindles in brain maturation during adolescence, in particular in the PFC, which develops later than other brain cortices, and is crucial for emotion regulation. In the scientific

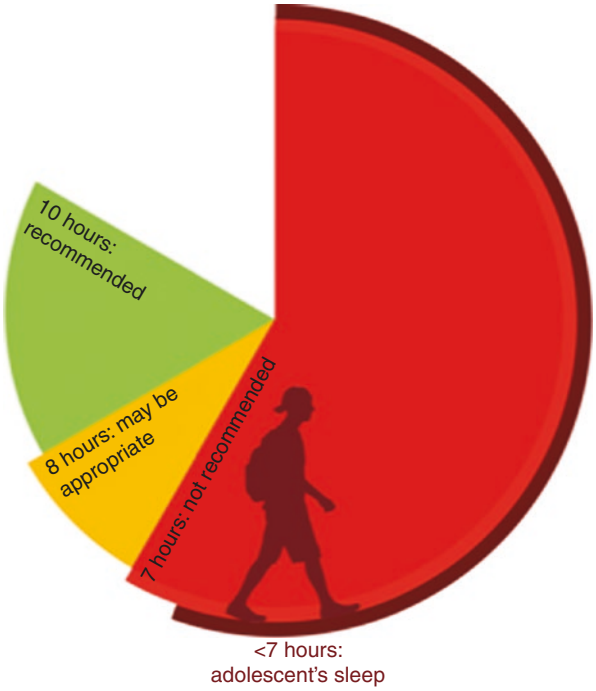

Fig. 8.2 Number of hours the adolescents should sleep per day and how much they actually sleep. Adapted from Hirshkowitz et al. [64]. (Authors thank Dr. Sergio Frumento for having adapted the figure)

literature, links between poor sleep and emotion dysregulation have been intensively investigated in adults (for reviews, see [18, 56–62]), but how poor sleep specifically impacts adults and adolescents is still unknown [63]. Unfortunately, even if the recommended sleep time for adolescents is 9 h per night, the National Sleep Foundation team has stated that adolescents do not get the adequate amount of sleep, sleeping only 6–7 h per night [64] (Fig. 8.2). The reasons for this are complex and biopsychosocial in nature [65]: (1) the physiology of the hormone melatonin in adolescence is completely different from childhood, with its releasing shifted later during the evening [66]; this, together with increased ability to resist sleep pressure, lead adolescents to be 'owls' (i.e. evening type), going to bed later in the night; (2) school start time is often set very early in the morning (7:30 to 8:30), forcing awakening much earlier than the recommended 9 h of sleep (i.e. the so-called 'social jetlag' [67]); and (3) the occurrence of familiar and social major risk factors, as aversive family environment, evening light exposure, computer use and tobacco and caffeine use, lead to significantly reduced sleep time [68]. Collectively, prolonged poor sleep conditions are important risk factors for psychopathology in adolescence and, conversely, psychopathology itself is highly related to co-morbid sleep problems (near 95% [69]). Moreover, poor sleep is related to several cognitive, behavioural and emotional alterations (for reviews, see [70–73]),

which lead to decreased well-being, defined as a reduction of subjective quality of life and life satisfaction, prevalent negative mood and emotions and absence of meaning in life [74].

A large number of cross-sectional studies showed that poor sleep is associated with deficits in emotion regulation, reduction of well-being and health-related quality of life [75–78] as well as increased anxiety [79], depression [80], aggression and hostility [81], academic failure [82, 83], legal and illegal drug use [84, 85] and accidents [82]. Longitudinally, poor sleep in adolescence can cause long-term reductions in well-being and life satisfaction, increased anxiety, depression, substance use and bad educational outcomes [86–93]. To sum up, all the above-mentioned psychological and behavioural outcomes are associated with prolonged conditions of bad sleep (i.e. chronic sleep deprivation or 'sleep debt' [94]), and are united by the lack of emotion regulation [24].

8.4 Sleep Deprivation and Emotion Dysregulation

Experimental psychophysiological studies of sleep deprivation have detected subjective and objective signs of emotion dysregulation, at the level of both the central and autonomic nervous system. In adults, one night of sleep deprivation increases amygdala activation up to 60%, in reaction to negative pictures (e.g. weapons, snakes, mutilations), indicating an inability to down-regulate negative emotions [95]. Amygdala hyperactivity has been detected also after a more ecological sleep deprivation protocol (five nights of 4-h sleep restriction), using subliminally presented frightened faces [96]. Decreased functional connectivity between the medial PFC and the amygdala, together with the hyperreactivity of the latter, has been related to less than 6 h of habitual sleep per night [97–99]. Moreover, sleep deprivation impairs recognition of emotional facial expressions [100, 101] and increases the distractibility caused by emotional images, paralleled by increased amygdala activation and reduced functional connectivity with the PFC [98]. Taken together, all these studies consider decreased inhibition of the amygdala exerted by the PFC as a marker of emotion dysregulation after sleep deprivation. Recently, in adults who underwent a fear consolidation experimental paradigm, Feng et al. [102] found that sleep deprivation interferes with top-down ventromedial PFC inhibition of the amygdala, increasing also bottom-up arousal signalling by the insular pathway [102]. Notably, insular cortex integrates interoceptive information on the state of the organism arising from subcortical areas, which are fundamental for adaptive emotional behaviour [103–105]. These data reflect an important and still under-investigated link between altered interoception, emotion dysregulation and sleep disorders (see [106]). In addition, suggesting an important involvement of the autonomic nervous system, Franzen and collaborators found, in sleep-deprived adults, that increased sleepiness positively correlated with involuntary pupillary responses to negative emotional pictures [107]. Sleep deprivation also affects heart rate variability (i.e. increased the low-frequency component and decreased the high-frequency component of heart rate variability), indicating an enhancement of

sympathetic activity [108, 109], which has been related to psychopathology and to reductions of flexibility to emotional challenges [110, 111].

Furthermore, sleep deprivation enhances mesolimbic reward system activity, which includes the midbrain ventral tegmental area, the striatum and the PFC (medial PFC and orbitofrontal cortex), and has been related to increased responsiveness to reward-stimuli, possibly leading to impulsivity, risk-taking behaviours and sensation seeking [60] (e.g. licit and illicit drug use; reviewed in [59]). Specifically, sleep deprivation amplifies subjectively reported and objectively detected activity (with functional MRI) throughout the human reward brain network in response to pleasure-evoking stimuli, associated with a reduction of the coupling between the mesolimbic system and the medial prefrontal and orbitofrontal cortices [112].

Unfortunately, unlike adults, sleep deprivation protocols in adolescence are less numerous, because of various methodological and ethical issues [72]. However, experiments on adolescents have found coherent results related to emotion dysregulation: for example, sleep restriction protocols in adolescents decrease emotion regulation, higher level executive functions and positive affect and increase negative affect (e.g. tension, anxiety, hostility, confusion and fatigue) [113–117].

A number of authors have suggested that sleep deprivation can alter emotion generation and emotion regulation via different pathways: (1) sleep deprivation may increase negative emotions by lowering the threshold to aversive stimuli that may be otherwise discarded [18], by decreasing motivation and ability to interpret goal-related events [58] and by increasing the encoding of negative memories, selectively biasing the encoding of positive and neutral ones [118]; (2) sleep deprivation may cause a state of central and peripheral emotional hypersensitivity that impairs the communication between brain and body, fundamental for the 'embodied' perception of emotions and leading to indiscriminate emotional generalization [59, 60]; (3) sleep deprivation may alter emotion regulation through behavioural tendencies and neurophysiological changes, including situation selection (by reducing energy and activity levels), attention (by increasing selective attention to negative stimuli), cognitive appraisal (by promoting overgeneralized conservative responses) and behavioural response (by increasing amplified and maladaptive emotional responses) [58, 61].

Psychophysiological data suggest that adolescence is a particularly vulnerable period for sleep deprivation as compared with adulthood. In this regard, using computerized acoustic analysis, a study found that sleep-deprived adolescents display fewer positive emotions as compared to adults [116]. Unfortunately, there is still a paucity of experimental and longitudinal sleep deprivation studies on adolescents, making it difficult to determine the degree to which psychophysiological consequences of sleep loss overlap (or not) in adolescents and adults [63, 72]. In addition to the well-assessed role of REM sleep in emotions, an under-investigated role, both for the correct maturation of adolescent brain and, consequently, emotion regulation and well-being, may be played by specific features of NREM sleep, like slow waves, SSO and sleep spindles [62]. Again, no study has directly investigated adolescent NREM sleep features in relation to emotion

regulation (but see [119] for sleep spindles in adults). This can be a promising line of research for the future: the study of sleep features in healthy sleep and sleep loss may provide a unique window onto adolescent cortical maturation, emotion regulation and well-being [62, 63].

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