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Sleep in the dog: comparative, behavioral and translational relevance

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The dog *(Canis familiaris)* is a promising non-invasive translational model of human cognitive neuroscience including sleep research. Studies on the relationship between sleep and cognition in dogs and other canines are only just emerging, but still very scarce. Here we provide insight into canine sleep and sleep-related physiological and cognitive/behavioral phenomena. We show that dogs do not only fulfil all behavioral and polygraphic criteria of sleep, but are characterized by sleep homeostasis, diurnal pattern of activity, circadian rhythms, ultradian sleep cycles, socio-ecologically and environmentally shaped wake-sleep structure, sleep-related memory improvement, as well as specific sleep disorders. Developmental patterns of sleep-related physiological indices, as well as parallel trends in age-dependent changes in cognition and sleep were evidenced in dogs.

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Introduction: why is dog sleep relevant for humans?

Behavioral sleep is common in the animal kingdom, whereas polygraphically defined sleep is best characterized in mammals [1], including the dog (Table 1). The dominant (and somewhat implicitly idealized) subject of sleep research is the young, healthy human and the laboratory rodent (most often the rat). Most of our current knowledge on sleep comes from these species (and age group), thus the available knowledge is seriously restricted. The non-human/non-rodent sleep studies are mainly performed on laboratory cats [2].

In accordance with shared evolutionary history (domestication) and social environment of family dogs and humans, the dog has been successfully applied as a model species for comparative investigations of several human socio-cognitive skills [3•]. Considering established parallels in dog and human psychopathology [4], research of brain mechanisms underlying the dog's cognitive, behavioral and social dysfunctions, in the long run, hold promise for an improved understanding of human neuropsychiatric conditions, such as obsessive-compulsive disorder [5], autism [3•], or sleep disorders, like narcolepsy, sleep-disordered breathing and REM behavior disorder (Box 1).

Methodological issues in canine sleep studies

Sleep studies on dogs have been carried out with methods ranging from behavioral observations to surgical procedures, differing in invasiveness, ecological validity and specificity (Table 2). The advantages of the recently established family dog sleep model [13••] include (i) dogs' unique willingness to cooperate during the measurements to an extent comparable to or even exceeding children (thus allowing the use of fully non-invasive methods), (ii) a relatively large sample size (availability of a large number of pet dogs), (iii) subjects that live (and can be measured) in their natural environment, and (iv) significant inter-breed and inter-individual variability in their human analogous social behaviors and cognitive performance, including natural extremes (Figure 1).

Sleep-wake cycle basics in the domestic dog

Overall sleep length in dogs

Comparative databases use the value of 10.1 hours of average daily sleep for the domestic dog [14]. Reported values vary between 7.7 and 16 hours [15]. Whether the 21%/day of drowsiness seen in dogs and several other species but neither humans nor rodents, can be considered 'light sleep' [11] or a transitional state [16] is a matter of debate, and alters the estimations of total sleep time in this species [15]. To put in context, laboratory rats sleep around 13 hours, whereas humans sleep 7–8 hours daily [14].

Table 1

The criteria of sleep and theirs fulfilment in dogs[a]

	Specific criteria	Presence in dogs	Type of evidence (methodology)	$\overline{N}$	Reference(s)
Behavioural criteria	Motor rest	. . . is evidently associated with other signs of sleep	Video recordings, polysomnography (including EMG)	23	[19,24]
	Stereotyped posture(s)	Lying with head on or between the forepaws, or on the side or back, with neck muscles relaxed	Video recordings	24	[24]
	Increased sensory thresholds	Slow wave sleep: 'The dogs do not react behaviorally to external stimuli, but may show a short-lasting desynchronization of the EEG.'	Invasive EEG[b]/ polysomnography	7	[16]
	Reversibility-arousability	. . . was proven by auditory stimulation	Invasive EEG/ polysomnography	5	[56]
	Specific rest sites	. . . are used for sleeping and are frequently provided by the owners	Video recordings	17	[57]
	Homeostatic regulation	. . . was reported in terms of both motor and EEG activity	Actigraphy, invasive EEG/ polysomnography	10	[17,18]
	Circadian organization	Dogs are diurnal in terms of motor activity, core body temperature, plasma melatonin rhythm and EEG/polygraphic criteria	Actigraphy, metabolism kennels, repeated blood sampling, non-invasive polysomnography	15	[17,28••,58,59,25••]
	Eye closure	. . . is present in resting/ sleeping dogs	Video recordings	24	[24]
Polygraphic criteria (mammalian type)	NREM[c]	EEG slow waves and spindles, lack of rapid eye movements; HR[e] <60 beats/min; slow, deep, and less variable breathing; reduced EMG[f]	Invasive and non-invasive EEG/polysomnography	14.2	[16,19,32,33•,60]
	REM[d]	Low amplitude high frequency EEG activity (cortex), hippocampal rhythmic slow activity, rapid eye movements; HR <60 beats/min; rapid, shallow, and irregular breathing; reduced EMG with occasional phasic increase (twitches)	Invasive and non-invasive EEG/polysomnography		

[a] The list of features is based on the criteria summarized by Nicolau *et al.* [1].
[b] EEG – electroencephalography.
[c] NREM – non rapid eye movement sleep.
[d] REM – rapid eye movement sleep.
[e] HR – heart rate.
[f] EMG – electromyography.

Sleep homeostasis in dogs

Several findings indicate the presence of sleep homeostasis in dogs. Lost sleep is recovered in terms of decreased motor activity [17], increased initial slow wave sleep and a later increase in the percentage of REM sleep [18], as well as in increased electroencephalogram (EEG) slow wave/delta activity during NREM sleep [19].

Growth hormone release is strongly associated with early episodes of deep (slow wave) sleep in humans [20], whereas such association is not seen under baseline conditions in dogs [21]. However, canine growth hormone secretion becomes associated with slow wave sleep during rebound sleep after sleep deprivation (i.e. during deeper, more intense sleep containing more slow waves) [21]. That is, the unique neuroendocrine state characterized by increased growth hormone and decreased cortisol during early sleep and its proposed restorative and neurocognitive functions [22] is not emerging during baseline conditions in dogs, but can be induced by increasing sleep pressure.

Box 1 Sleep disorders and behavioral problems in dogs

Canine narcolepsy is characterized by fragmented sleep, REM sleep dysregulation, frequent sleep attacks (excessive sleepiness) and emotion-induced losses in muscular tonus (cataplexy) during play, before feeding, and so on. The condition is caused by the mutation of the canine orexin receptor 2 gene or by the loss of production of the orexin peptides [6,7].

Sleep disordered breathing is associated with episodes of O_2 desaturation and loud snoring during sleep, as well as daytime hypersomnolence, sluggishness, and shortened sleep latency. The English bulldog, the Cavalier King Charles spaniel, as well as other brachycephalic breeds are most commonly affected. The English bulldog has been proposed as a natural model of sleep-disordered breathing [8,9•].

REM sleep behavior disorder is characterized by violent motor activity and/or complex behavioral phenomena emerging during REM sleep. Clinical signs include episodes of violent limb movements, howling, barking, growling, chewing, or biting. Episodes occur both at night and during daytime naps [10]. Behavioral output is clearly unrelated to the actual environment ('hallucinatory'). In some of the dogs, REM sleep behavior disorder was associated with other neurological conditions, whereas congenital forms were also reported [11,12].

Circadian regulation of sleep in dogs

The majority of motor inactivity/polygraphic sleep of dogs occurs between 21.00 and 6.00 with a period of rest during the afternoon [17,23,24]. Night sleep was characterized by higher sleep efficiency and continuity as compared to afternoon naps [25••]. Corroboration of these findings with the reported core body temperature rhythms (increasing temperature during most of the light period and decreasing during the dark) [26,27,28••] clearly indicates a diurnal type of wake-sleep pattern in dogs.

It has to be noted however, that unlike in humans, the circadian variation in cortisol level is not always found in dogs [21,26]. In contrast to human mRNA levels of clock genes period1 and period2 measured in peripheral blood mononuclear cells reflecting evident circadian expression profiles, only period1, but not period2 was characterized by such profile in dogs [26]. Diurnal activity of domestic dogs is hypothesized to reflect an adaptation to humans, as there is evidence for nocturnal, crepuscular or arrhythmic activity pattern in most other canines, like red and arctic foxes, as well as arctic and grey wolves, whereas diurnal activity is a rare observation [15,29]. The weaker circadian regulation (see for example [30]) might result in greater flexibility in the timing of activity in dogs as compared to humans. Thus, patterns of video-recorded sleep-wake cycles in drug detector dogs were not altered when handler-dog teams worked in different day and night shifts. The ability of dogs to cope with changing shifts may be due to their natural brief and frequent sleep-wake cycles which may allow them sufficient and easy adjustment to changing routines, which is usually not the case in humans [31].

Ultradian regulation of sleep in dogs

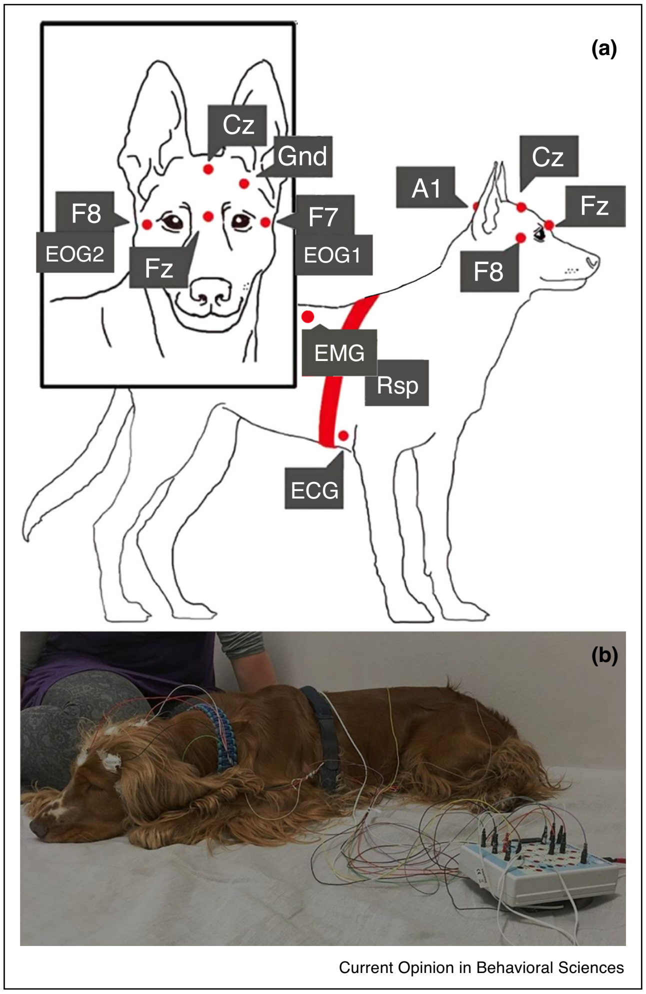
Ultradian sleep cycles of about 20-min length were described in dogs (12 min of drowsiness/NREM and 6 min of REM sleep episodes) with well discernible EEG, EOG (electrooculography), EMG (electromyography), ECG (electrocardiography) and respiration-related features (Figure 2; Table 3) [16,19,23,32,33•]. Rats and humans are characterized by 11 and 90 min cycles, respectively. Dog sleep was found to be mainly polyphasic, with an average of polyphasic wake-sleep cycle length of 83 min

Table 2

Methodological approaches in studying dog sleep

	Method	Ethical consideration	Advantage	Disadvantage	Reference
Invasive	Cisternal puncture/ cerebrospinal fluid extraction (associated with sleep deprivation)	Extremely painful and distressing, potentially lethal	Neurochemical factors can be measured	Low ecological validity, restricted subject pool and sample size	[61]
	Surgically inserted stimulation/recording electrodes	Seriously painful and distressing	High specificity, good signal quality	Low ecological validity, restricted subject pool and sample size	[62,32]
	Needle electrodes introduced into the skin and the cranial muscles, contacting the skull	Moderately painful and distressing (semi-invasive)	Trade-off between signal quality and invasivity	Somewhat restricted subject pool and sample size, pharmacologically altered sleep	[45]
Non-invasive	Video recordings	No distress is caused to subjects	Highest ecological validity	Low construct validity	[24]
	Actigraphy	Not painful, depending on subjects' individual sensitivity might be moderately distressing	High ecological validity	Low specificity in differentiating different sleep states, restricted to motor activity	[17]
	Polysomnography	Not painful, depending on subjects' individual sensitivity might be moderately distressing	High ecological validity combined with electrophysiology, potentially high sample size	Lower signal quality, potential need for adaptation occasion(s) before reaching full ecological validity	[19]

Figure 1



Non-invasive polysomnography in the pet dog. **(a)** Placement of the recording electrodes and devices as follows: (i) Electroencephalography (EEG) is performed by frontal midline (Fz), central midline (Cz), left orbitofrontal (F7) and right orbitofrontal (F8) contacts, with the A1 used as common reference and Gnd as ground (because of lower artifact contamination the offline re-referencing of Fz-Cz is most frequently used), (ii) Electro-oculography (EOG) is performed by the bipolar reference between F7 and F8 (which are the same as EOG1 and EOG2), (iii) Electromyography (EMG) electrodes assessing muscular tonus were bilaterally placed on the musculus iliocostalis dorsi, (iv) Electrocardiography (ECG) is assessed over the second rib, (v) Respiration (Rsp) is assessed by respiratory inductance plethysmography using a respiratory belt. The owner is present and the dog is positively reinforced during the electrode attachment procedure (technical details of the attachment are equivalent to the ones used in human studies). **(b)** A photo of a dog with electrodes attached. Note the close proximity of the owner. (Modified from Refs. [33•] and [25••]).

[16,23]. In dogs, 2.9 hours is the estimated daily amount of REM sleep, whereas humans and rats are characterized by 1.9 and 2.4 hours, respectively [14]. Similar to some other species like the rat, the hedgehog and the rabbit, awakening after active sleep (assumed REM sleep, based on video-recordings) was found to be more common in dogs, than in humans, providing perhaps an opportunity to be more alert towards their surroundings after a period of reduced responsiveness [24].

Is there an intraspecies allometric scaling of sleep physiology in dogs?

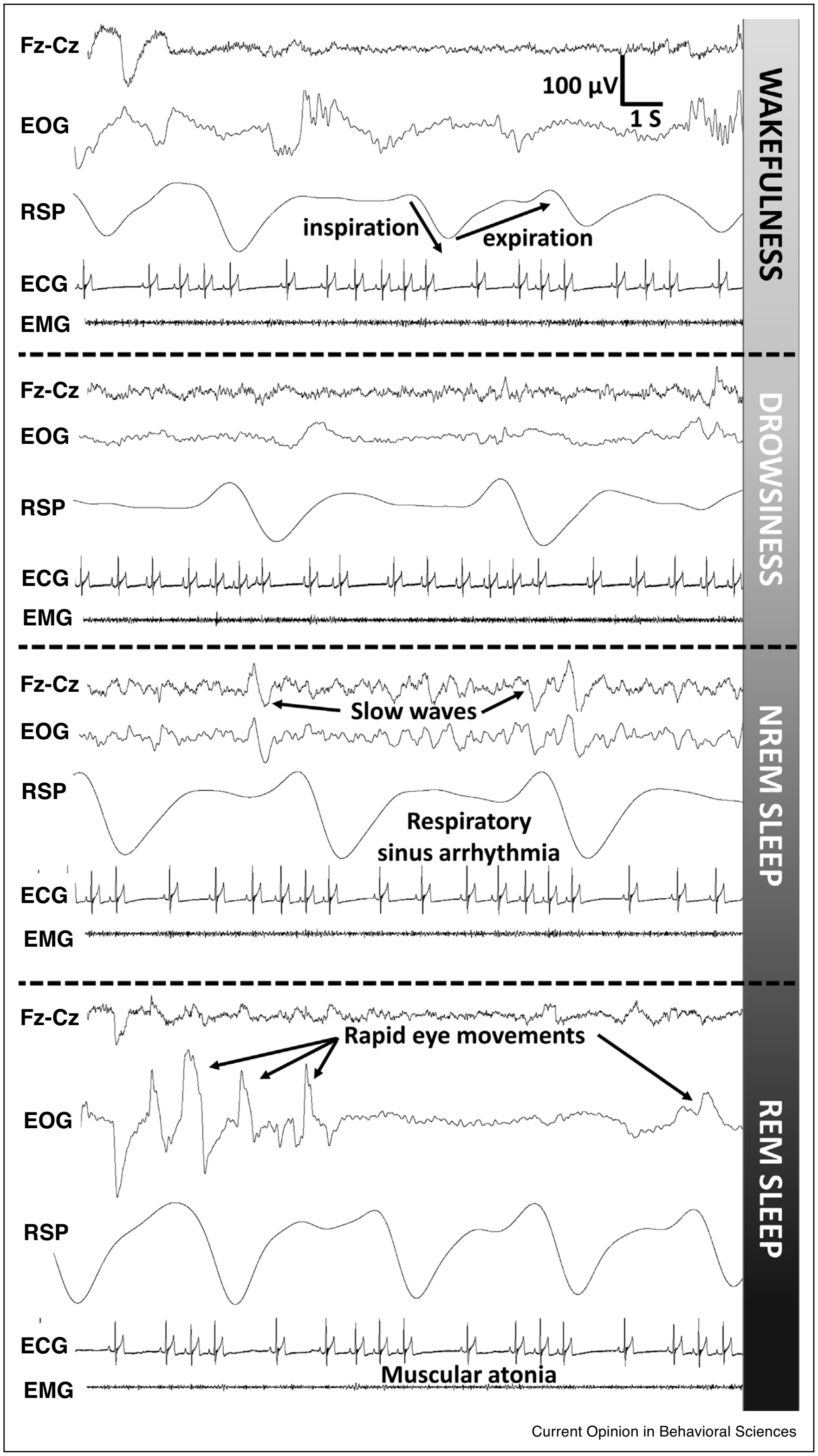
An additional factor to be considered is the huge individual (between-breed) variation that characterizes dog morphology [34]. Although the effect of body size on dogs' longevity is well-documented [35], the hypothesis of the intraspecies allometric scaling of physiological measures, like heart rate is controversial, as both confirmatory findings [36] and recent null-results on datasets containing rest/sleep measurements [33•,37] were reported. Although intriguing, the intraspecies allometric modulation of sleep in dogs was not yet systematically investigated, thus we do not know whether measures like total sleep time or sleep cycle length are different among breeds with different body weights.

Behavioral and learning-related aspects of sleep in dogs

Effects of sleep location and pre-sleep experiences on sleep

Dogs sleeping indoors were reported to spend 80% of the night in behaviorally defined sleep, whereas this ratio was 70% for dogs sleeping outdoors in a yard, and 60% for dogs sleeping outdoors in a non-fenced area [24]. A polysomnography study demonstrated a later emergence of the first REM episode in laboratory conditions as compared to home sleep [25••]. These findings cohere with the view that active sleep (a behavioral definition of a REM sleep-like state) is emerging in safe sleeping conditions mainly [24]. Following a behaviorally active day, dogs, like other mammals, including humans slept more, were more likely to have an earlier drowsiness and NREM, and spent less time in drowsiness and more time in NREM and REM sleep [19,25••]. In addition to physical settings and circumstances, the social context plays a decisive role in the sleep of dogs and other canines as well (Supplementary text). Pre-sleep socio-emotional experiences with negative valence (separation from the owner, threatening approach by a stranger) were followed by shorter REM sleep latency and increased REM sleep time compared to sleep following positive social interactions (petting and ball play). Within-subject changes in sleep structure were associated with behavioral reactions to pre-sleep social interactions (e.g. time spent playing or looking at the door [38••]). Pre-sleep social interaction-dependent changes in cardiac activity were not seen during sleep in dogs, whereas increased heart rate (HR) and decreased heart rate variability (HRV) after positive as compared to negative interaction could be observed during post-interventional wakefulness. This direction of change is in contrast with the expected findings and previous research on humans, perhaps

Figure 2



Exemplary segments of a non-invasive polysomnography records of night time sleep in an adult dog. Horizontal broken lines delimit the states of wakefulness, drowsiness, non-rapid eye movement (NREM) sleep and Rapid eye movement (REM) sleep (see notation on the left). Wakefulness is characterized by low amplitude, high frequency electroencephalogram (EEG) (frontocentral midline, bipolar derivation Fz-Cz) with occasional (eye movement) artifacts, clear eye movements and blinking as indicated by large deflections of the electro-ocuologram (EOG), a respiratory (RSP)

Table 3

Reported polygraphic signs of different sleep-waking states in dogs

Ref.	Wakefulness	Drowsiness	NREM	REM
[32]	low amplitude and fast frequency pattern cortical activity (desynchronization), mixture of low voltage slow and fast waves in the hippocampal traces	slow waves and spindles in the cortex, irregular slow activity in the hippocampus		neocortical desynchronization, 3-5 Hz rhythmic hippocampal activity
[23]	low-voltage (5-10 µV) fast frequency (> 15 Hz) EEG from one or both cortical areas, frequent eye movements and a tonic but irregular neck EMG	high voltage slow waves (up to 40 µV) EEG	12-14 Hz spindle bursts (40-50 µV) against a background of slower 4-8 Hz activity (10-20 µV) recorded from the sensorimotor cortex (light sleep); high amplitude (up to 50 µV) stow waves (2-8 Hz) recorded from the visual cortex (slow wave sleep)	relatively low-voltage (5-10 µV) fast frequency (>15 Hz) tracing recorded from the cortical leads, frequent and characteristic binocular, conjugate, rapid eye movements and a suppression of the neck EMG
[16]	beta activity of <50 µV in cortical derivations (ratio alpha/beta power ≤1), no spindles; short-lasting theta activity (2-10 s) in the hippocampus with higher frequencies superimposed; EMG is relatively great	mixed and unstable frequency pattern: 9.5-13.5 Hz waves vary with synchronous waves at 4–7 Hz, 50-100 µV on a background of low voltage fast activity (ratio alpha/beta power >1); spindles are lacking; slow eye movements may be present	waves of 3-4 Hz become predominant; spindles of >100 µV, lasting 0.2-0.5 s, mainly in the frontal cortex; the EMG is small and there are no eye movements (light sleep); slow waves (1–4 Hz) of 100-250 µV, superimposed on waves of 6-7.5 Hz of 50-100 µV; spindling at 10–14 Hz, 200 µV or more; EMG is small and there are no eye movements (deep slow wave sleep)	beta activity of 50-100 µV (ratio alpha/beta power <1); hippocampal theta activity (5 Hz); rapid eye movements; the EMG is small, but amplitude increases appear simultaneously with facial or leg twitches or myoclonic jerks
[19]	fast activity in the EEG, high amplitude and frequency eye movements in the EOG, elevated muscle tone and frequent movements (EMG channel)	fast EEG activity in the EEG channel, decreased amplitude and frequency eye movements, lowered but observable muscle tone, fairly regular respiration	≥15 µV delta (1–4 Hz) activity, no or low amplitude eye movements, regular respiration, decreased muscle tone	rapid eye movements, fast EEG activity, muscular atonia, irregular respiration and heart beat

indicating that increased activation/emotion intensity is a key factor, irrespective of emotional valence [39•].

Sleep and memory in the domestic dog

Sleep-related improvement in memory consolidation of humans and rats [40] may apply to dogs' inter-specific communication skills (learning new commands). A 3-hour-long post-learning non-invasive polysomnography study [41••] indicated increased NREM delta and REM theta, as well as decreased NREM alpha activity in post-learning as compared to baseline sleep in dogs. Behavioral performance significantly increased after the 3-hour-long rest/sleep compared to the pre-sleep baseline, whereas the within-subject increase in performance correlated with certain aspects of the sleep EEG spectrum (REM beta and delta power). Besides sleep, post learning walk and play were also associated with increasing performances approximately one week later, whereas learning of unrelated tasks had detrimental effects on memory consolidation [41••]. A behavioral study [42] somewhat contrastingly found that playful activity during retention enhanced memory

(Figure 2 Legend Continued) frequency (frequency range) of 15/min as indicated by respiratory inductance plethysmography and clear respiratory sinus arrhythmia (the heart rate as indicated by electrocardiography [ECG] increases during inspiration and decreases during expiration as in all further panels and corresponding states). Muscular tonus is indicated by the amplitude of the electromyogram (EMG). Drowsiness: slower theta-alpha frequency EEG components, slower eye movements, slow regular breathing and maintained muscular tonus. NREM sleep: slow EEG waves of 1−2 Hz frequency, around 12/min respiratory frequency, lowered heart rate and decreased muscular tonus are seen. REM sleep: low amplitude, high frequency EEG, rapid eye movements (EOG), relatively accelerated respiration (15/min) and a further decrease in muscular tonus. Note that the vertical scale refers to the EEG traces only. The rest of the derivations are adapted for illustrative purposes and visibility, but their scaling is consistent across the panels. Filter settings: EEG: 0.5–50 Hz; EOG: 0.2–10 Hz; RSP: 0–1 Hz; ECG: 0,5–50 Hz; EMG: 10–50 Hz.

performance in the short run to a greater extent compared to a resting period.

The effect of learning on sleep was apparent when analyzing the same dataset [41••] for sleep spindles [43••]. Sleep spindles are major hallmarks of NREM sleep in humans playing a definitive role in offline neuroplasticity [44]. Spindle waves are not easy to assess in dogs, as they are both shorter in duration (0.2–0.5 s) as compared to humans (>0.5 s) and of a very low amplitude (at least in surface/non-invasive traces). Sleep spindles have, however, been described in dogs using both invasive [16] and semi-invasive [45] sleep/propofol restraint EEG recordings, whereas quantitative EEG analyses seem to be effective in detecting spindle-like activity in dogs even from non-invasive scalp recordings [43••]. The occurrence rate of such automatically measured sleep spindles in the surface (non-invasive) EEG records was higher after learning compared to control dogs and the same measure correlated with performance increase.

Development and aging: changes in sleep and cognition

Developmental steps in the sleep EEG of dogs are characterized by gradual emergence of sleep slow-wave activity transiently peaking around 6–8 weeks of age and thereafter decreasing till at least 16 weeks of age [46]. Such transient peaking in the amplitude of NREM sleep slow wave activity is well known in prepubertal human subjects and laboratory rats paralleling the age-dependent trends in synaptic density and brain energy consumption [47]. In addition, adult-like sleep spindles emerge around 5 weeks in dogs [46] and around 12 weeks in humans [48].

Dogs have been shown to manifest a cognitive decline with increasing age (called the Canine Cognitive Dysfunction Syndrome; [49]), which parallels human ageing in many aspects. Cognitive decline in dogs has been associated with several behavioral signs, including owner-reported sleep-wake cycle alterations [50]. Furthermore, lower amplitude of circadian core body temperature rhythm was reported in aged dogs with lowest spatial memory ability [28••]. Aging was also characterized by reduced overall REM sleep amount, as well as increased NREM sleep during daytime and wakefulness during nighttime [51]. This type of wake and sleep fragmentation during day time and night time, respectively, together with reduced REM sleep are well known features of sleep in the aged human subjects and were shown to relate with cognitive aspects of aging [52,53]. Older dogs (within an age range of 2–8 years-old) were characterized by decreased delta activity and increased alpha and beta activity both during NREM and REM, but not during drowsiness [19]. In addition, sleep spindle analysis in over 150 dogs indicated that centrally measured (Cz) slow (9–13 Hz) spindle density declined and fast (13–16 Hz) spindle frequency increased with age, while on the frontal electrode (Fz), an age-related amplitude decline in slow sleep spindles was observed [54••]. There is also some indication that contrary to the age-dependent decline of rapid eye movement density (REMD) reported in humans, dogs' age is positively associated with REMD. It has to be noted however, that the above mentioned effect seems to characterize male dogs with short REM sleep duration, but not the whole population, indicating the need for further studies clarifying its generalizability [55•].

Conclusion

Like most terrestrial mammals, the domestic dog is characterized by unequivocal sleep in terms of behavioral and physiological criteria. The relationship between socio-ecological and physical environmental, as well as cognitive-behavioral factors with sleep improves our insight into the functional significance of sleep, as well as into the still unraveled mysteries of dog behavior. This new emerging evidence strongly suggests that dogs are valid and useful models of sleep-related cognition. However, the achievement of these goals needs further research investment, some of which could deepen our knowledge on both dog and human behavior and physiology.

Research agenda:

- Selective breeding for deeper (more intense, thus cognitively more efficient) sleep
- Investigating the parallelism between cognitive development and sleep EEG maturation in dogs by means of non-invasive methods
- Unravelling the functions of NREM and REM sleep by selective manipulations (e.g. deprivation) of these sleep stages
- Integrating cognitive and affective aspects of sleep-related memory consolidation
- Depicting sleep electrophysiological profiles of natural dog models of human psychiatric conditions
- Understanding the effects of domestication on sleep by further comparisons of dogs and wolves in terms of sleep phenotypes and physiology
- Understanding the effects of different lifetime experiences (free-ranging dogs, pet dogs, and shelter dogs) on sleep and sleep-related cognitive processes

Conflict of interest statement

Nothing declared.

CRediT authorship contribution statement

Róbert Bódizs: Conceptualization, Funding acquisition, Visualization, Data curation, Writing - original draft, Writing - review & editing. **Anna Kis:** Conceptualization, Funding acquisition, Visualization, Writing - original draft, Writing - review & editing. **Márta Gácsi:** Conceptualization, Funding acquisition, Data curation, Writing - original draft, Writing - review & editing. **József Topál:** Conceptualization, Funding acquisition, Writing - original draft, Writing - review & editing, Supervision.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.cobeha.2019.12.006.

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