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Sleep macrostructure is modulated by positive and negative social experience in adult pet dogs

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The effects of emotionally valenced events on sleep physiology are well studied in humans and laboratory rodents. However, little is known about these effects in other species, despite the fact that several sleep characteristics differ across species and thus limit the generalizability of such findings. Here we studied the effect of positive and negative social experiences on sleep macrostructure in dogs, a species proven to be a good model of human social cognition. A non-invasive polysomnography method was used to collect data from pet dogs ($n = 16$) participating in 3-hour-long sleep occasions. Before sleep, dogs were exposed to emotionally positive or negative social interactions (PSI or NSI) in a within-subject design. PSI consisted of petting and ball play, while NSI was a mixture of separation, threatening approach and still face test. Sleep macrostructure was markedly different between pre-treatment conditions, with a shorter sleep latency after NSI and a redistribution of the time spent in the different sleep stages. Dogs' behaviour during pre-treatments was related to the macrostructural difference between the two occasions, and was further modulated by individual variability in personality. This result provides the first direct evidence that emotional stimuli affect subsequent sleep physiology in dogs.

1. Introduction

Sleep is of vital importance for human emotional well-being, and the occurrence of disturbed sleep has been documented in many psychological and psychiatric disorders. On the other hand, daytime events, especially emotionally stressful events, have an impact on sleep quality and well-being. For example, negative pre-sleep emotions (induced by a failure feedback in response to different cognitive tasks) have been reported to cause decreased sleep efficiency, a decreased percentage of rapid eye movement (REM) sleep and an increased latency to slow-wave sleep [1]. Stress manipulation (telling the participants that they would give a speech in the morning, and that their performance would be evaluated) significantly lowered average rapid eye movement count in the last REM period, and the global slope of increase in rapid eye movement count across successive REM sleep periods was also less steep compared with a control treatment [2]. Furthermore, self-reported pre-sleep depression (measured by the Profile of Mood States questionnaire) has been found to correlate with affect in the dream report of the first REM awakening in healthy young adult participants [3].

Although such effects of pre-sleep emotions have been described in detail in the case of humans (see e.g. [4] for a review), very little is known about other species, with the exception of laboratory rodents [5–7]. Non-human species show both similarities to and differences from human sleep (including quantitative differences

such as sleep cycle length, and qualitative differences such as clear-cut sleep/wake differentiation versus a transitory drowsiness stage in some species) [8]. These are especially important in understanding the general function of sleep [9,10]. The length of a sleep cycle (containing a non-REM and an REM sleep period), for example, can vary from 10 min in rats (*Rattus norvegicus*), through 25 min in rabbits (*Leporidae*) to 85 and 90 min in chimpanzees (*Pan troglodytes*) and humans (*Homo sapiens*), respectively [11], and has been shown to be linked to brain size and body mass of the species [9].

Our study subject is the dog (*Canis familiaris*), a species that has adapted in evolutionary terms to the human social environment and thus shows several human-analogue socio-cognitive skills [12,13]. Dogs are able to discriminate between different human emotional expressions [14,15] and their behaviour is influenced by these in choice situations [16–18]. Furthermore, it has been shown that human emotions are contagious to dogs [19,20]. Humans in turn are able to attribute emotions to dogs' facial expressions [21] and vocalizations [22].

Recent research has proved that dogs can also be used to non-invasively study neuro-cognition [23], including sleep-related cognitive functioning. Data recorded with a non-invasive canine polysomnography technique is directly comparable with that of human subjects [24], and has been successfully used to test the effect of pre-sleep experiences (e.g. learning [25]). In addition, dogs being the most common pet worldwide [26,27] face a variety of social stressors. These include, for example, kennel housing [28], training with aversive stimuli, such as the shock collar [29], being relinquished to an animal shelter and participating in socialization programmes [30], stressful working environment (e.g. military dogs) and environmental changes [31], and sport competitions such as agility [32]. Thus, the question of emotional experience and sleep in dogs is also of vital importance for animal welfare and veterinary science.

Sleep in dogs has been studied for decades with invasive methods, mainly focusing on neurological conditions such as epilepsy [33] and narcolepsy [34]. Data from these invasive studies is mostly in line with the handful of recent non-invasive research. Dogs are known to display polyphasic sleep [35] with short sleep–wake cycles [36]. A clear circadian, diurnal rhythm was also found in dogs [37], and it was reported that dogs are most active after light onset and tend to have a rest during the afternoon [38]. The sleep macrostructure of dogs is composed of the stages of awakeness, drowsiness, non-REM and REM [24,39]. Beta activity (16–30 Hz) is the dominant characteristic of dogs' awake state. The drowsiness stage is a transition between waking and sleep (characteristic of carnivore or insectivore species where the distinction between the awake and sleeping states is not clear [8]), and has been observed in dogs as well, with the highest power in the alpha band. The subdivision of non-REM into different stages is only used in some primates [11], but it is not a widely used practice for dogs, although some studies had distinguished between light and deep non-REM sleep in carnivores (e.g. for the cat [40]; or for the dog [39]). During REM sleep, dominating beta and theta activity can be observed in dogs, along with an inconsistent pattern of rapid eye movements.

In the present study, our aim was to investigate dogs' sleep structure after a socially negative versus positive experience. The REM phase of sleep is involved in emotional memory processing [41] and depotentiation of amygdala activity in response to previous emotional experiences [42], thus we

expected a redistribution of the sleep stages due to the REM phase being differentially affected by positive versus negative emotional experiences. In addition, we expected to find a relation between sleep changes and the behaviours of the dogs, as in humans a connection has been found between sleep quality and, for example, emotion recognition [43].

2. Material and methods

(a) Subjects

Our subjects were 16 adult (mean age $\pm$ s.e.: 4.88 ± 0.71 years, range: 1–10 years) pet dogs (9 males, 7 females) from nine different breeds (2 Hungarian Vizslas, 2 Hovawarts, 1 Golden Retriever, 1 Labrador Retriever, 1 Mudi, 1 Shetland Sheepdog, 1 Belgian Shepherd (Groenendael), 1 Boxer, 1 Jack Russell Terrier) and 5 mongrels. There were no specific requirements for participation except that dogs had to be older than 1 year. Dogs were not trained for the purpose of this experiment.

(b) General procedure

All of our subjects participated in polysomnography recordings of 3 h duration on a total of three occasions. The first occasion was an adaptation session and thus was not analysed subsequently, but merely aimed to familiarize the subjects with the laboratory, the experimenter (E1) and the electrode placement. The second and third polysomnography recordings were preceded by a socially positive or negative pre-treatment of 6 min duration, respectively (within-subject design, counterbalanced treatment order—so that eight randomly chosen dogs participated first in the positive treatment and second in the negative treatment, while other eight dogs participated in the reverse order). The positive and negative behavioural treatments were carried out by three different experimenters (E1 and E2 were both women, E3 was a man). For all dogs in one of the treatments a female experimenter was present and in the other treatment a male was present (E1 or E3 in the positive, E2 or E3 in the negative treatment; counterbalanced between dogs). The time elapsed between the two treatments depended on the owners' availability and ranged from 5 to 29 days (mean $\pm$ s.e.: 13.31 ± 1.72 days).

(c) Behavioural treatments

During the 6 min of the positive social interaction (PSI) dogs had the opportunity to play with the owner and the unfamiliar experimenter (E1/E3) in the behavioural laboratory of the Family Dog Project. E1/E3 and the owner petted the dog every time when the dog approached them, played tug of war and/or throw and fetch depending on the dog's preference, and used dog-directed speech towards the subject. When the 6 min elapsed, E1 accompanied the owner and the dog to another room which was used for the polysomnography recordings.

During the negative social interaction (NSI), owners were asked to leave the dog alone for 2 min in the behavioural laboratory on an approximately 1.5 m leash that was fixed about 1 m away from the door (separation episode, see e.g. [44] for a similar situation). When the 2 min elapsed, the owner entered the room and stood right behind the fixation point of the leash, without greeting the leashed dog and avoiding eye contact with it. Then an unfamiliar experimenter (E2/E3) entered the room and approached the leashed dog from a distance of 5 m (as measured from the fixation point of the leash) moving slowly and haltingly (one step in every 4 s) with slightly bent upper body and looking steadily into the eyes of the dog without any verbal communication (threatening approach test [45]; approximately 1 min). E2/E3 approached the leashed dog to a distance of 2 m, then for the remaining 3 min sat on the ground at the place he/she stopped

at the end of the threatening approach. She was looking at the dog with a neutral facial expression without talking to it and completely unresponsive (still face test, adapted from [46]). When the 3 min elapsed, E2/E3 stood up and left the room. Then E1 entered and accompanied the owner and the dog to another room for the polysomnography recordings.

(d) Polysomnography recording

The polysomnography recording followed a protocol validated for pet dogs [24] that had been developed based on the human 10–20 system [47]. Recordings of 3 h duration were conducted during the afternoon (starting time varied between 12.00 h and 18.00 h so that the two recordings of an individual dog were started at the same time ± 1 h). Surface attached scalp electrodes were placed over the anteroposterior midline of the skull (Fz, Cz, Pz; electroencephalography, EEG), and on the zygomatic arch (os zygomaticum), next to the left eye (electrooculography, EOG). The ground electrode was placed on the left musculus temporalis. The Fz derivation was referred to Pz, the EOG derivation was referred to Cz. Electrodes were placed bilaterally on the musculus iliocostalis dorsi for electromyography (EMG), and over the second rib for electrocardiography (ECG). Gold-coated Ag|AgCl electrodes fixed with EC2 Grass Electrode Cream (Grass Technologies, USA) were used for the recordings. Impedances for the EEG electrodes were kept below 20 k Ω . Signals were collected, pre-filtered, amplified and digitized at a sampling rate of 1024 Hz/channel, by using the 25 channel SAM 25R EEG System (Micromed, Mogliano Veneto, Italy), as well as the System Plus Evolution software with second-order filters at 0.016 Hz (high pass) and 70 Hz (low pass). After PSI both the owner and E1 talked to the dog and petted it during the 10–15 min of electrode placement, in order to maintain the positive emotional state induced by the behavioural treatment. After the NSI both the owner and E1 avoided contact with the dog to the extent that it was possible during electrode placement, in order to avoid overwriting the effect of the behavioural treatment (only minimal physical contact accompanied with verbal commands and feedback was needed).

(e) Personality assessment

Owners were asked to fill out a personality questionnaire, the Canine Big Five Inventory [48] (Hungarian translation in [49]) consisting of 43 statements. For each item the owners scored their dog on a five-point scale (from disagree to strongly agree). The questionnaire measures five personality traits: neuroticism (e.g. 'Is emotionally stable, not easily upset'), extraversion (e.g. 'Is full of energy'), openness (e.g. 'Is curious about many different things'), agreeableness (e.g. 'Can be cold and aloof') and conscientiousness ('Tends to be lazy'). All personality factors contain reverse scored items.

(f) Data analysis

During PSI the duration of play with the owner (seconds) and with the experimenter (seconds), as well as the duration of non-social play (seconds), were coded. In addition, the duration of petting by the owner (seconds) and by the experimenter (seconds) were also coded. However, these latter two variables have been found to be highly correlated (Pearson $r = 0.740$, $p = 0.001$), thus in order to avoid multi-collinearity, only the variable 'petting by the owner' was entered in the initial statistical models (the variable 'petting by the experimenter' was added to the models in the forward elimination phase if the final model did not include the 'petting by the owner' variable).

During the separation episode of NSI the duration of looking at the door where the owner left (seconds) as well as the duration of standing next to the door (within 1 m distance; seconds) was

coded. During the threatening approach episode, an average reaction score (0–2) was calculated (following the coding described in [45]) based on the dog moving off when approached (0: does not move away while looking at the experimenter; 1: moves away while looking at the experimenter, but does not move behind the owner; 2: moves behind the owner, while looking at the experimenter), averting gaze (0: continuously looking at the face of the Experimenter; 1: averts its gaze from the experimenter, but looks back; 2: averts its gaze from the experimenter and does not look back), and vocalizing (0: neither barks nor growls; 1: barking and growling last no longer than 4 s; 2: barks repeatedly or growls continuously for more than 4 s). During the still face episode, the duration of looking at the experimenter (seconds), hiding behind the owner (seconds) and vocalizing (seconds) were coded.

Polysomnography recordings were visually scored (using a custom-made software developed by our laboratory: Fercio's EEG Plus, Ferenc Gombos 2009–2016) according to standard criteria [24] in 20 s epochs by inspecting the EEG, EOG, ECG and EMG channels. This coding identified the following stages: wakefulness, drowsiness, non-REM and REM sleep. Rating was always blind to subject and condition details. The following macrostructural data were exported from the resulting hypnograms: sleep latency (until first epoch of drowsiness, min), relative wake duration (%), relative drowsiness duration (%), relative non-REM duration (%), relative REM duration (%), average REM period duration (min), REM latency (after first epoch of non-drowsiness sleep, min).

The difference between sleep macrostructure following the socially positive/negative behavioural treatment was analysed with generalized linear mixed models (SPSS version 22) with backward elimination. The macrostructural variables were entered as targets, whereas treatment (positive, negative), order of treatment (positive first, negative first), experimenter ID and dog sex were entered as fixed factors.

The individual difference between positive and negative treatment was calculated for each macrostructural variable in the case of all subjects. These individual difference values were used as dependent variables for linear regression analysis (SPSS 22; backward and forward elimination) with the behavioural variables coded during the positive and negative treatments as independent variables.

The Canine Big Five Inventory was scored according to standard instructions (averaging the scores of the variables representing each dimension), and the resulting factor scores (extraversion, agreeableness, conscientiousness, neuroticism, openness) were used as explanatory variables for both dogs' behaviour during PSI and NSI treatments as well as for macrostructural variables (difference between positive and negative treatment). Thus linear regression analyses (SPSS 22; backward elimination) were run with all the behavioural variables and all the sleep macrostructure difference variables.

3. Results

Dogs spent asleep an average $65.81 \pm 3.15\%$ (mean $\pm$ s.e.) of the 3 h recording time after the positive treatment and $72.46 \pm 4.48\%$ after the negative treatment. The average sleep cycle duration was 51.43 ± 4.36 min (positive) and 56.30 ± 5.45 min (negative). Sleep macrostructure was markedly different following positive (PSI) versus negative (NSI) treatments (figure 1a). Sleep latency was higher after PSI compared with NSI pre-treatment ($F_{1,30} = 9.186$, $p = 0.005$), but was not affected by any of the other factors (dogs' sex, experimenter ID, order of pre-treatments; all $p > 0.05$). Relative wake duration was not affected by pre-treatment ($F_{1,30} = 2.281$, $p = 0.151$), but males had a higher percentage of wake duration compared with females ($F_{1,30} = 5.196$, $p = 0.030$) and there

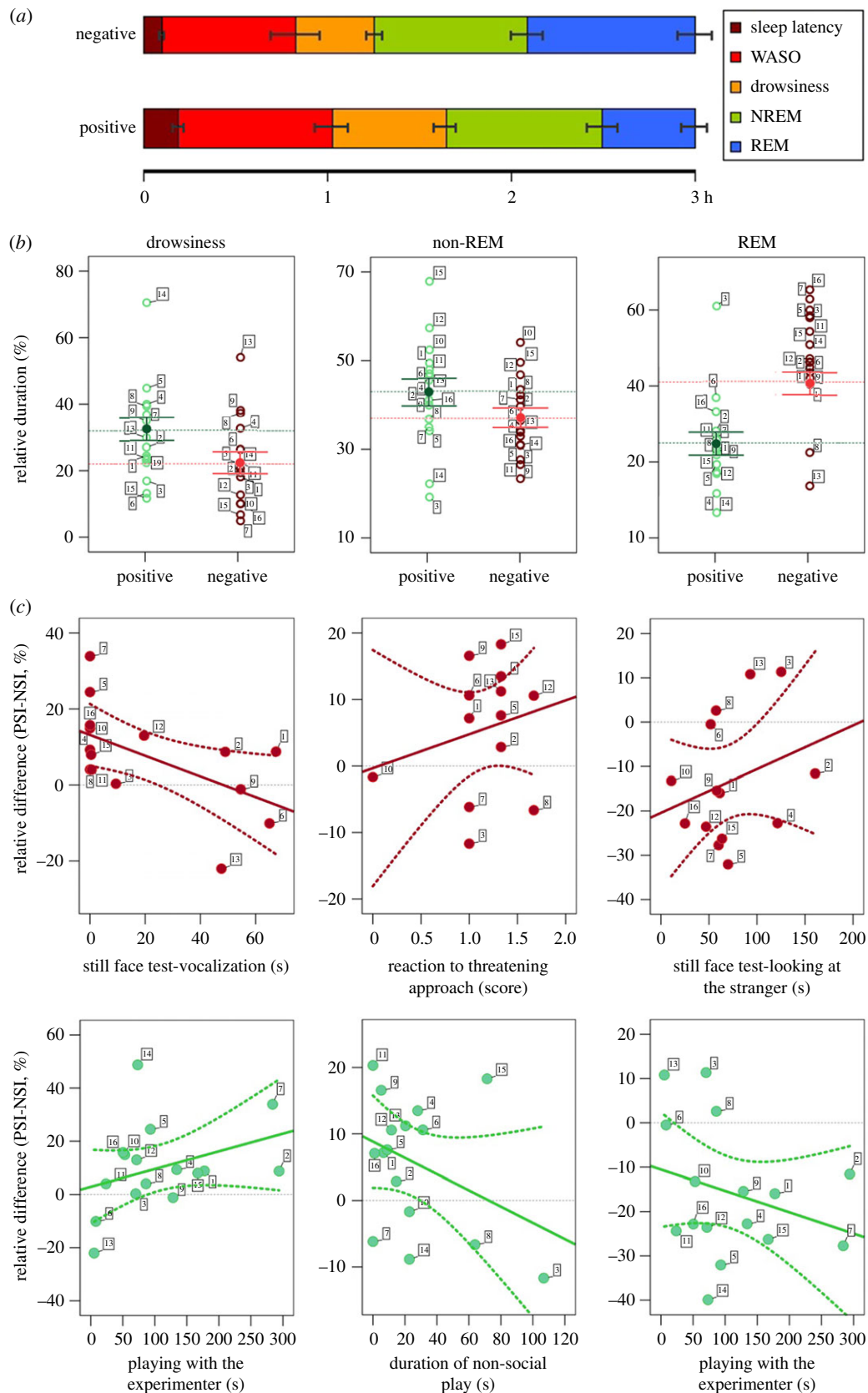


Figure 1. Redistribution of the sleep stages due to the behavioural pre-treatments as reflected in (a) time spent in the different sleep/wake stages (mean $\pm$ s.e.) following the negative versus the positive social interaction, (b) the relative duration of the different sleep stages (drowsiness, non-REM, REM) following the positive versus the negative social interaction, and (c) the relationship between certain behaviours during both positive and negative social interactions and change in the relative duration of the given sleep stage. The y-axis depicts (b) the relative duration (%) of the given sleep stage or (c) the difference of the relative duration between the two pre-treatment conditions, with positive values indicating an increase after the positive social interaction, negative values indicating an increase after the negative social interaction and zero indicating no difference between the treatments. Individual case number labels are consistent across all sub-figures. (Online version in colour.)

was no effect of the other factors (all $p > 0.05$). The different types of social pre-treatment resulted in a redistribution of sleep stages; relative drowsiness duration was higher after

PSI compared with NSI ($F_{1,30} = 5.937$, $p = 0.021$), while it was unaffected by the other factors (all $p > 0.05$). Relative non-REM duration was also higher after PSI compared with

NSI ($F_{1,30} = 5.126, p = 0.031$; unaffected by the other factors: all $p > 0.05$). On the other hand, relative REM duration was lower after PSI compared with NSI ($F_{1,30} = 17.577, p < 0.001$; unaffected by the other factors: all $p > 0.05$; figure 1b). In addition, the average REM period duration was shorter after PSI compared with NSI ($F_{1,30} = 11.592, p = 0.002$; unaffected by the other factors: all $p > 0.05$). REM latency was not affected by positive/negative pre-treatments nor by any other factors (all $p > 0.05$).

In line with these results we found that variation in dogs' behaviour during both PSI and NSI explain many aspects of the observed PSI–NSI difference in dogs' sleep macrostructure (figure 1c). The difference in sleep latency was related to the duration of play with the owner during PSI ($\beta = -0.697, p = 0.005$), to dogs' reaction to threatening approach ($\beta = 0.568, p = 0.014$) and to duration of standing behind the owner during the still face task ($\beta = -0.541, p = 0.018$). Difference in relative drowsiness duration was related to duration of looking at the stranger during the still face task ($\beta = -0.426, p = 0.028$), duration of vocalization during the still face task ($\beta = -0.510, p = 0.007$) and duration of play with the experimenter during the positive treatment ($\beta = 0.714, p = 0.001$). Difference in relative non-REM duration was related to duration of play both with the owner ($\beta = -0.539, p = 0.031$) and the experimenter ($\beta = -0.827, p = 0.009$), and to the duration of non-social play ($\beta = -0.555, p = 0.022$) during PSI, as well as to the duration of standing next to the door during the separation episode ($\beta = 0.777, p = 0.017$) and to dogs' reaction to threatening approach ($\beta = 0.889, p = 0.008$) during NSI. The difference in relative REM duration was related to the duration of looking at the experimenter during the still face task ($\beta = 0.553, p = 0.046$) and the duration of play with the experimenter during PSI ($\beta = -0.667, p = 0.020$). The difference in average REM period duration was related to the duration of petting by the owner ($\beta = 0.553, p = 0.001$) and the duration of non-social play ($\beta = 0.690, p < 0.001$) during PSI, as well as to the duration of vocalization during the still face task ($\beta = 0.936, p < 0.001$) during NSI. Difference in REM latency was not associated with the observed variations in any of the behavioural variables (all $p > 0.05$).

Dogs' personality (measured via questionnaire) was related to several aspects of their behaviour during both NSI and PSI treatment. More 'agreeable' ($\beta = -0.515, p = 0.008$) and less 'open' ($\beta = 0.639, p = 0.002$) dogs spent more time behind their owner, while less 'conscientious' dogs vocalized more ($\beta = -0.526, p = 0.044$) during the still face episode of NSI. Less 'extroverted' ($\beta = -0.567, p = 0.013$) and less conscientious ($\beta = -0.526, p = 0.019$) dogs received less petting from their owner, while more 'conscientious' dogs showed more non-social play ($\beta = 0.672, p = 0.004$) and more 'extroverted' dogs played more with the experimenter ($\beta = 0.525, p = 0.037$) during PSI. The other behavioural variables (play with the owner, looking at the door and standing next to the door during separation, reaction to threatening stranger, looking at stranger during still face task) were not affected by dogs' personality (all $p > 0.05$).

Based on these relations we expected sleep latency to be influenced by agreeableness and openness factors of the big five personality inventory (through influencing standing behind the owner during the still face task); however, these factors had no effect (both $p > 0.05$). Yet the effects of extraversion ($\beta = -0.707, p = 0.008$), conscientiousness ($\beta = -0.915, p = 0.001$) and neuroticism ($\beta = -0.703, p =$

0.013) were significant. Drowsiness was not affected by any of the personality factors (all $p > 0.05$), although conscientiousness (through vocalization during the still face task) and extraversion (through play with the experimenter during PSI) could be expected to do so. Dogs that attained higher scores for conscientiousness showed a greater increase in relative non-REM sleep after positive treatment ($\beta = 0.636, p = 0.008$) as it could be expected through its relation to non-social play. No other personality factor had an influence on non-REM sleep (all $p > 0.05$), although higher scores for extraversion could be expected based on its relation to play with the experimenter. REM sleep was not affected by any of the personality factors (all $p > 0.05$), although a relationship with extraversion could be expected (through play with the experimenter). Average REM period duration was influenced by conscientiousness ($\beta = 0.542, p = 0.030$), as predicted by its relationship to petting by the owner, non-social play and vocalization during the still face task. But this measure was not related to extraversion ($\beta = -0.047, p = 0.863$), as predicted by relation to petting by the owner or the other three personality factors (all $p > 0.05$). REM latency was not affected by any of the personality factors (all $p > 0.05$), which is in agreement with the finding that no behavioural variables had an influence either.

4. Discussion

We found that sleep macrostructure in dogs differs after socially positive versus negative experience. The affected macrostructural variables include relative REM sleep duration and sleep latency, which have been implicated in human studies as well [1]. However, the direction of the change is opposite to that found in humans: after negative treatment, dogs' relative REM duration increased and their sleep latency decreased. This conforms with previous warnings [9,10] advising to study sleep and its function in a diverse set of species, as its relation to awake behaviours and experiences might not be uniform across the whole animal kingdom. We should also note that there are several inherent procedural differences between the pre-sleep emotional exposure of dogs and humans, thus one cannot be sure that the emotional valence and intensity of social interactions on dogs and humans are functionally equivalent. Another possibility is that dogs did not experience our treatments as we expected (e.g. the negative social interaction might not be perceived as negative). However, this is not likely to be the case, as there is physiological evidence (heart rate and heart rate variability) that separation from the owner and threatening approach by a stranger are perceived as stressful by dogs [50,51].

A further important finding is that sleep pattern differences between positive and negative treatments were related to several aspects of dogs' behaviour. This suggests that specific characteristics of the treatment (e.g. the duration of play a dog experienced) caused a change in sleep macrostructure. However, our study also provides evidence that at least part of the sleep characteristic changes are influenced by the dog's personality (e.g. playful dogs react to social stressors in a different way). This is in line with the findings that individual differences at the behavioural level (e.g. selecting food or owner in a Y-maze) are related to brain activity differences (e.g. caudate activation to food- and praise-predicting stimuli) in dogs [52]. The investigation of further individual differences,

such as age or emotional reactivity, will be an important further step. Breed and morphology in general might be of particular interest as dogs show considerable variability in their skull shape that is known to co-vary with both brain morphology and behaviour [53–55].

The effects of behavioural treatments similar to those used in the present study have already been described in terms of endocrine response, although these studies compared positive or negative treatments with a no-treatment control, while the present study directly compared positive and negative treatments in order to avoid noise from unknown experiences prior to the test in a no-treatment group. Positive dog–human social interactions (including softly talking to the dog, gently stroking the dog with long smooth strokes, low-key playing and scratching the body and ears of the dog) have been found to increase both dogs' and humans' blood level of oxytocin (an antagonist of cortisol) as well as to increase levels of beta-endorphin, prolactin, phenylacetic acid and dopamine [56–58]. Cortisol is typically implicated in dogs' stress reaction to situations like separation from the owner and threatening approach by the stranger [59], although individual differences (e.g. in dog–owner attachment bond) might modulate cortisol reactivity [60]. Such endocrine markers have already been shown to relate to sleep parameters both in humans and laboratory rodents (e.g. oxytocin [61], prolactin [62], cortisol [63]) and might thus be potential mediators to some of the sleep pattern changes observed in dogs. This suggestion is consistent with the polyvagal theory [64,65] that describes an evolutionarily adaptive neural physiological mechanism to foster engagement and disengagement with the environment. The theory predicts a shift in the proportion of sleep phases and thus explains the increased REM duration after negative treatment, as REM is the active sleep stage characterized by increased heart rate and decreased heart rate variability (in human newborns [66]), while oxytocin is known to have the opposite effect (in dogs [67]). Changes in sleep latency (e.g. dogs fell asleep more quickly after negative

treatment), on the other hand, might be related to stress-induced quiescence (protective sleep in response to stress), a phenomenon that can be induced by several stressors (e.g. in *Caenorhabditis elegans* [68]) and that can also be observed as part of the human immune response during sickness [68].

In sum, evidence was found for the first time that socially positive and negative emotional experience influences subsequent sleep macrostructure in dogs. Sleep *per se* has been suggested as a good welfare indicator in dogs [69], and our finding that short emotional treatments influence sleep macrostructure also suggest that sleep research could be usefully implemented in the field of canine well-being. Furthermore, the present findings show that individual variability, both in terms of behaviour during positive versus negative social interactions and general personality traits, modulate sleep pattern differences.

Ethics. Research was carried out in accordance with the Hungarian regulations on animal experimentation and the Guidelines for the Use of Animals in Research described by the Association for the Study of Animal Behaviour (ASAB). The Hungarian 'Animal Experiments Scientific and Ethical Committee' issued a statement (under the number PE/EA/853-2/2016) approving the non-invasive study experimental protocol. All owners volunteered to participate in the study.

Data accessibility. All data used in these analyses are available as electronic supplementary material.

Authors' contributions. Substantial contributions to conception and design by A.K., A.G., R.B. and J.T. A.G., Á.G. and J.A. contributed to acquisition of data. A.K., A.G., J.A. and F.G. contributed to analysis and interpretation of data. A.K. drafted the article. All authors revised the article critically for important intellectual content and final approval of the version to be published. Agreement to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved by all authors.

Competing interests. We declare we have no competing interests.

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