Investigation of the sleep electrocorticogram of the common marmoset (Callithrix jacchus) using radiotelemetry

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Abstract

Objective: To evaluate the use of a totally implantable radiotelemetry system for recording the sleep electrocorticogram (ECoG) of a small new world primate, the common marmoset (Callithrix jacchus) without restraint during data collection.

Methods: Under anaesthesia a telemetry transmitter, which allowed the recording of a single ECoG channel, was implanted intraperitoneally. This system allowed ECoG data to be recorded overnight from animals living in pairs within their habitual laboratory environment over a period of 12 months. Data were subsequently scored using modified Rechtschaffen and Kales criteria (A manual of standardized terminology, techniques and scoring system for sleep stages of human subjects. Los Angeles, UCLA Brain Information Service/Brain Research Institute, 1968) into stages of waking, light sleep, deep sleep and probable rapid eye movement sleep (pREM). Concurrent video recording was used to assist in the categorising of pREM.

Results: Results showed that, as in man, the marmoset exhibits sleep cycles with stages alternating between non-REM (deep sleep and light sleep) and pREM sleep throughout the night. In common with other non-human primates the duration of each of the sleep stages was relatively short and punctuated with frequent waking.

Conclusions: These data suggest that sleep in marmosets housed under laboratory conditions (a) can be recorded without restraint and (b) has potential to be used as a model for human sleep. © 2001 Elsevier Science Ireland Ltd. All rights reserved.

Keywords: Sleep; Marmoset; Non-human primate; Electroencephalogram; Telemetry; Electrocorticogram

1. Introduction

Sleep studies have been conducted in a number of species of non-human primates housed under laboratory conditions, including chimpanzees (Bert et al., 1970), macaques (Reite et al., 1965), baboons (Bert et al., 1975) and squirrel monkeys (Adams and Barratt, 1974). The interpretation of the sleep electroencephalogram (EEG)\textsuperscript{1} in these earlier studies is, however, complicated by aspects of the different methodologies used to obtain recordings. These include the use of different scoring regimens and the presence of confounding factors such as degree of restraint and type of nocturnal environment.

Traditionally, techniques used to monitor the EEG of unanaesthetised laboratory species in general, and non-human primates in particular, have involved the use of some form of restraint during recording. In order to record data from non-human primates it is common to either completely restrain the subject in a specially designed chair (e.g. Weitzmann, 1961; Lagarde and Milhaud, 1990), connect the subject via an umbilical to the recording apparatus (e.g. Breton et al., 1986) or fit the animal with an instrumented backpack (e.g. Bert et al., 1975). A consequence of the use of restraint is that it is difficult to record EEG for extended time periods, as repeated restraint poses problems both in terms of scientific quality and animal welfare.

Previous studies have shown considerable within-species variation in the sleep of non-human primates. In the squirrel monkey, for example, two studies reported widely different sleep values with levels of overall sleep ranging from 54.8% (Breton et al., 1986) to 82.4% (Adams and Barratt, 1974) of
the night and levels of paradoxical or REM sleep ranging from 3–7 (Breton et al., 1986) to 22.9% (Adams and Barratt, 1974) of the total time asleep. It is notable that these studies employed markedly different recording methodologies. The study by Breton recorded EEG from an animal tethered individually in a cage within a breeding cage, which provided visual and vocal contact with other animals, whereas Adams and Barratt recorded EEG from individual chair-restrained animals within a sound-attenuated cubicule. Clearly, the latter study imposed a greater degree of restraint within a quiet environment whilst the other allowed more movement and access to a more familiar, but potentially distracting, environment. Under these diverse circumstances, it is difficult to unequivocally describe the sleeping patterns of this species because of the influence of both the recording methodology and environment on the quantity and quality of sleep observed. The importance of the sleeping environment has been clearly illustrated in human subjects where it is well recognised that recordings should be obtained for 2 to 3 nights in a sleep laboratory before sleep measures stabilise. This ‘first night effect’ is not seen in recordings made at home in the subject’s normal sleeping environment (Sharpley et al., 1988).

Radiotelemetry provides an alternative method for recording biological information, such as EEG, from non-human primates (e.g. Pauley et al., 1974; Kaemingk and Reite, 1987) which does not involve restraint at the time of data collection. Such systems involve the implantation of a biotelemetry device, usually subcutaneously (s.c.), which will enable the collection and transmission of biological data for an extended time period (Reite et al., 1974). Totally implantable telemetry systems have no external connectors or cables, which means that in addition to no restriction of movement, there are no exit wounds and所以 the infection risk is greatly reduced. This enables the evaluation of long term sleeping patterns in animals within their home cage environment. In this way, in a series of studies, Reite et al. (1974) and Reite and Short (1986) have remotely evaluated the sleep of infant macaque monkeys living with their mothers in a social group environment. Only recently, however, has it been possible to produce reliable telemetric devices that are small enough in size to enable their use in relatively small animals, such as the rat (Livezey and Sparber, 1990) and marmoset (Schnell and Wood, 1993; Pearce et al., 1998). The ability to miniaturise transmitters for smaller species, however, comes at a cost in terms of the available battery life and number of data channels that can be collected. Unlike methods involving restraint during measurement, where there is scope for multiple channels of biopotential to be monitored, the number of channels available using telemetry is constrained by the size of the implant used.

The present study, following on from previous published work (Pearce et al., 1998), investigated the feasibility of using a single channel telemetry device to evaluate the sleep electrocorticogram (ECOg) of the common marmoset recorded within a home cage environment. It is well known that sleeping patterns in other small laboratory species, such as the rat and guinea pig, are markedly different from man. It was anticipated that by recording sleep in pair-housed unrestrained animals within a familiar environment, a more realistic picture of normal sleeping patterns may be obtained than would be attained using methodologies involving restraint.

2. Methods

2.1. Subjects and husbandry

Four common marmosets (Callithrix jacchus) were used (two males; two females). The daily diet consisted of 20 g pellets (complete primate diet E, Special Dietary Services, Witham, Essex, UK) with supplements of orange segments. A sawdust filled tray, containing small amounts of preferred foods (e.g. rice krispies, sunflower seed), allowed the animals to freely engage in foraging behaviour. Water was available ad libitum.

At the start of the study all marmosets were pair-housed. Two females and one male were housed in mixed sex pairs with males vasectomised, one male was housed in a unisex pair with another male. Animals had access to 4 cage units, each of H72 × W47 × D60 cm, linked by one vertical and two horizontal rigid cage extensions (H18 × W71 × D23 cm and H105 × W17 × D23 cm, respectively). The home room was lit by sodium lights on a light/dark cycle with 1 h dusk, 12 h darkness and 1 h dawn. Light level during the day was 350–400 lux at 1 m above floor level. The room temperature was maintained at 24 ± 2°C with 37 ± 7% relative humidity.

2.2. Surgical procedures

All animals were implanted intraperitoneally with a single channel biopotential telemetry transmitter (19 × 16 × 9 mm) (Data Sciences International, St Paul, MN, USA). Full details of surgery are reported elsewhere (Pearce et al., 1998). All procedures were carried out in accordance with the Animals (Scientific Procedures) Act (1986). Following premedication with 1.0 mg kg⁻¹ diazepam (Valium, Roche) intramuscularly (i.m.), animals were anaesthetised with 0.9 mg kg⁻¹ 0.9% w/v alphaxalone and 0.3% w/v alphadalone acetate (Saffan, Glaxo) i.m. Prophylactic antibiotic cover was provided for 3 days postoperation by daily administration of 0.2 ml of a 7.5% solution of Borgal (s.c.) and postoperative analgesia by a single injection of 0.01 mg kg⁻¹ (i.m.) buprenorphine (Temgesic, Reckitt and Colman).

The body of the transmitter was positioned intraperitoneally. The electrode leads, which were encased in silicone tubing, ran s.c. from the transmitter to the skull. Two 0.9 mm holes were drilled unilaterally through the skull bone over the right side of the frontal cortex approximately
2 mm from the midline and 8 mm anterior from bregma with the second hole lying 5 mm posterior to the first. The stainless steel electrode tips, which protruded from the silicone tubing by 2–3 mm, were placed through the holes such that they were resting on the dura of the frontal cortex and were secured in place on the skull using acrylate cement. In order to prevent any movement of the electrode wires the silicone tubing was secured to the skull using Vetbond (Wellcome). Post mortem revealed the electrodes to be positioned between 5 and 8 mm apart on the surface of the brain. There was some variability between subjects in electrode placement because the electrodes were not stereotaxically located as both lay anterior to level AP 12.5 of the stereotaxic atlas (Stephan et al., 1980)2.

2.3. Transmitter

The transmitter (Data Sciences Int. TA11ETAF40) contained a battery, an amplifier and an epoxy encapsulated electronics module within a thermoplastic case, all coated in a biocompatible silicone coating. Leading from the transmitter were two 15 cm helical stainless steel wires, enclosed in flexible silicone tubing. Manufacturer’s specifications state the bandwidth of the transmitter to be 1–100 Hz, with a maximum input voltage of 2.5 mV. The input impedance was 300 kΩ with an electrode impedance of 15 kΩ. The transmitter sampled the ECoG at a rate of 250 Hz. This sampling frequency was suitable for the sleep ECoG signal as it was more than double the highest frequency of interest. An internal switch enabled the transmitter to be turned on and off using a magnet, which was passed within approximately 1 cm of the transmitter. Activation could be confirmed using a radio set to a frequency of approximately 530 kHz on the amplitude modulation (AM) band. The radio produced a high pitched sound when the transmitter was active. According to manufacturer’s information, the battery had a life of approximately 6 months if used continuously. After implantation, the battery life was maintained for up to 2 years. All transmitters were tested before implantation. Due to the carrier frequency used by these transmitters it was not possible to record sleep from a pair of animals simultaneously.

2.4. Recording of sleep

To enable ECoG recording overnight, a cylindrical receiver (Data Sciences model No.RLA3000, L21 × D4 cm) was attached to the underside of the bucket in which the animals slept (Fig. 1). Each transmitter had a range of approximately 20 cm to any point on the length of the receiver. The receiver cable, which was reinforced by flexible stainless steel tubing, was connected to a consolidation matrix (BCM100) positioned in the animal’s home room. This matrix was connected to a dedicated computer and UA10 Universal Analogue Adapter situated in a separate laboratory where the analogue signal output was connected to a Medilog ambulatory EEG recorder (Oxford Medilog, UK). This system stored raw data as an analogue signal on an AR 90 cassette tape. During sleep recordings ECoG data (amplitude 50–200 µV) was collected throughout the night. Subsequent data analysis was carried out through the Medilog 9200 replay and analysis system (Oxford Medical, UK).

An infra-red camera (Britannia 2000, UK) was placed on top of the cage directly above the sleeping bucket (see Fig. 1). The camera was linked remotely to a time-lapse video recorder with a time display facility, which allowed the animals positions and activity to be recorded throughout the night. Once in the sleeping bucket, the individual being recorded on any one night was clearly identified out of the pair by facial and body characteristics.

2.5. Staging of sleep

The amplitude of the ECoG signal obtained varied slightly between animals, possibly because of small differences in electrode placement. For each marmoset, a calibration value was determined using the amplitude of the delta waves during periods where slow wave sleep (SWS) predominated. The analysis system produced an output of the amount of alpha (8–10.5 Hz) and delta (0.5–3.5 Hz) waves and numbers of sleep spindles and K-complexes for each 30 s segment of ECoG. An initial hypnogram was produced based on algorithms designed for multichannel human sleep analysis. Each 30 s epoch of raw signal was then inspected visually and with support from an auditory signal and video data a sleep stage was manually assigned.

Non-REM sleep was scored according to the rules developed by Rechtschaffen and Kales (1968) for the scoring of sleep in humans. This classification was constrained by the absence of electro-oculogram (EOG) and electromyograph (EMG) information. The ECoG stages identified were wake, probable rapid eye movement (pREM) sleep, light sleep (stages 1 and 2) and SWS (stages 3 and 4). An example of the ECoG signal for each of the sleep stages identified is given in Fig. 2.

From the ECoG signal alone it was difficult to distinguish waking and pREM stages. A record was made of all probable pREM and wake periods and the times identified were then checked on the video recording. Awake ECoG was characterised by mixed frequency activity and alpha rhythms and was accompanied by apparent EMG artefacts in the form of bursts of fast activity during waking and movement. This artefact is most probably due to the relatively large temporalis muscle, which is attached to the skull in close proximity to the electrode sites. From the video recording, waking was clearly visible, with animals typically raising their heads and/or moving purposefully within
the bucket. Small twitches, which were frequent during sleep, were recorded separately. In most instances, twitches were not associated with waking. Twitches found to be associated with waking were typically on either side of a prolonged waking period. Light sleep (stages 1 and 2) was characterised by a small amount of delta activity and the presence of both rudimentary sleep spindles and K-complexes. The Rechtschaffen and Kales amplitude rules were not applicable to the definition of SWS (stages 3 and 4) due to differences in both the recording methods and electrode placement between the current study and human studies. These criteria were originally developed for the scoring of EEG recorded through the skull, while recordings here were obtained from electrodes directly in contact with the dura. SWS was therefore scored when the ECoG signal displayed high amplitude delta activity for at least 20% of a 30 s epoch. pREM sleep ECoG was characterised by low amplitude theta and beta waves and a lack of delta waves. In some subjects, jerky eye movement artefacts were also apparent in the ECoG during pREM due to the ECoG electrodes detecting the potential field of the EOG. The absence of a specific EOG channel, however, precluded a full assessment of eye movements during pREM. Video analysis revealed that pREM periods were characterised by irregular breathing movements and were often accompanied by fine shaking of the body fur and on some occasions very slow rolling head movement. In addition, the onset of pREM was often accompanied by a gradual loss of posture, probably as a result of reduced muscle tone. Very short apparent wakenings were frequently seen at both the beginning and end of
each period of pREM. The characteristics seen in pREM varied slightly between animals, although within animals the patterns seen were consistent. Previous studies have likewise reported characteristics of REM sleep including twitching, phasic muscle activity, body and facial movements in non-human primates (Weitzmann, 1961; Reite et al., 1965; Balzamo et al., 1977) as well as small muscle twitches in humans (Rechtschaffen and Kales, 1968).

3. Results

3.1. Sleeping period

Marmosets typically entered the sleeping bucket when the lights changed from dusk to dark, usually falling asleep approximately 15–20 min after final lights out. Some animals, however, were found on some occasions to go to sleep during the period of dusk prior to the lights going out. In the majority of cases, this sleep was brief and light and did not progress to SWS. However, 3 of the animals were seen, on one occasion each, to enter SWS and one of these progressed to pREM during the dusk period. In general, it was observed that animals woke and got up when the lights switched to the dawn levels.

Pair-housed animals typically slept curled up, with one leaning on top of the other. This frequently led to movement in one animal waking the second animal. The uppermost animal of the pair appeared to be more sensitive to the other waking, probably because any movement affected the stability of this animal’s sleeping position. For this reason wakenings in the partner of the animal being recorded were also noted. Wake periods of longer than 2 min in the partner gave a good indication that both animals were actually awake. This type of disturbance might be expected to lead to a fragmentation of sleep patterns, however, this was only noted on one occasion in which an animal was woken from pREM sleep by its partner. Typically throughout the night, one animal of a pair woke more frequently than the other.

3.2. Distribution of sleep stages

It can be seen from Table 1 that the majority of marmoset sleep was classified as light (61.34 ± 2.24%), with smaller amounts of both SWS (21.80 ± 1.07%) and pREM (16.90 ± 1.46%) sleep. All animals spent between 9 and 10 h of the dark period in sleep. There was, however, a relatively high proportion of wakefulness scattered throughout the night totalling approximately 1.5–2 h. SWS occurred predominantly during the first half of the night, becoming almost absent during the second, while, in contrast, pREM sleep was seen to occur mainly during the second half of the night. On all occasions the first episode of pREM sleep was found to occur later in the night than the first episode of SWS.

From the hypnograms in Fig. 3 it can be seen that in the marmoset, as in humans, sleep occurs in cycles alternating between non-REM and REM sleep. The duration of these cycles for the marmoset was, on average, 50 min with a range of between 10 and 17 cycles occurring during the night. This cycle is considerably shorter than is typically seen in humans, where inter-REM intervals are on average approximately 90 min, with 4–6 cycles occurring throughout an 8 h night (Kryger et al., 1994).

The duration of marmoset pREM periods was short and typically lasted between 1 and 12 min, although periods of up to 21 min were observed in one subject. When pREM periods were long they were usually broken by short wakes of 0.5–
In addition, the marmosets were often observed to ‘skip’ one pREM period during the early part of the night. When this occurred the expected pREM was usually replaced by a period of waking. Overall, in the marmoset, it is apparent that the sleep stages are of short duration, with frequent transitions between the various stages. This is contrasted by the relatively longer duration of the stages illustrated in the typical human sleep hypnogram (Fig. 3b).

In order to examine the stability of sleep within subjects over time, the proportion of time spent in each sleep stage was plotted (Fig. 4). It can be seen that although between subjects there is some variation in the percentage of time spent in each stage, the proportions of light sleep, SWS and pREM sleep appear to be relatively stable at the different time points analysed.

In human studies, measures of sleep latency are typically calculated as an indicator of sleep efficiency. Data for sleep latency measures for the marmoset were assessed for the second sleep recording made for each of the 4 subjects and are presented in Table 2. Sleep latency measures were found, however, to be variable between animals and not as reliable as the actual amount of each sleep spent in each stage (Table 1).

Latency measures calculated for the onset of different

Table 1
Mean sleep data for each of the 4 marmosets M1, M2, M3 and M4 (f, female; m, male; n = 6 recordings per animal)

<table>
<thead>
<tr>
<th></th>
<th>M1 (f)</th>
<th>M2 (f)</th>
<th>M3 (m)</th>
<th>M4 (m)</th>
<th>Mean (± SEM)</th>
</tr>
</thead>
<tbody>
<tr>
<td>TST</td>
<td>564 (7.5)</td>
<td>573 (16.3)</td>
<td>579 (7.4)</td>
<td>561 (14.0)</td>
<td>569 (4.3)</td>
</tr>
<tr>
<td>WAKE</td>
<td>135 (5.7)</td>
<td>99 (6.6)</td>
<td>136 (4.3)</td>
<td>132 (16.9)</td>
<td>125 (9.0)</td>
</tr>
<tr>
<td>LS</td>
<td>334 (8.0)</td>
<td>335 (7.8)</td>
<td>345 (9.0)</td>
<td>382 (15.5)</td>
<td>349 (11.4)</td>
</tr>
<tr>
<td>SWS</td>
<td>136 (5.7)</td>
<td>123 (9.4)</td>
<td>132 (7.6)</td>
<td>106 (3.6)</td>
<td>124 (6.6)</td>
</tr>
<tr>
<td>first half</td>
<td>111 (7.2)</td>
<td>98 (10.2)</td>
<td>113 (9.4)</td>
<td>85 (2.6)</td>
<td>102 (6.5)</td>
</tr>
<tr>
<td>second half</td>
<td>28 (3.1)</td>
<td>26 (2.8)</td>
<td>18 (2.7)</td>
<td>21 (2.3)</td>
<td>23 (2.3)</td>
</tr>
<tr>
<td>pREM</td>
<td>94 (3.3)</td>
<td>114 (2.2)</td>
<td>104 (2.9)</td>
<td>73 (1.9)</td>
<td>96 (8.8)</td>
</tr>
<tr>
<td>first half</td>
<td>36 (3.6)</td>
<td>36 (1.4)</td>
<td>37 (4.2)</td>
<td>25 (2.0)</td>
<td>33 (2.8)</td>
</tr>
<tr>
<td>second half</td>
<td>58 (3.2)</td>
<td>78 (1.7)</td>
<td>67 (3.0)</td>
<td>48 (0.8)</td>
<td>63 (6.4)</td>
</tr>
<tr>
<td>Mean IRI</td>
<td>51 (1.2)</td>
<td>43 (1.2)</td>
<td>49 (2.2)</td>
<td>57 (2.4)</td>
<td>50 (2.8)</td>
</tr>
<tr>
<td>No. sleep cycles</td>
<td>13 (0.5)</td>
<td>15 (0.5)</td>
<td>14 (0.7)</td>
<td>12 (0.5)</td>
<td>13 (0.7)</td>
</tr>
<tr>
<td>% LS</td>
<td>59.24 (1.1)</td>
<td>58.61 (0.5)</td>
<td>59.48 (1.4)</td>
<td>68.05 (1.1)</td>
<td>61.34 (2.2)</td>
</tr>
<tr>
<td>% SWS</td>
<td>24.13 (1.0)</td>
<td>21.40 (1.2)</td>
<td>22.63 (1.2)</td>
<td>19.06 (1.0)</td>
<td>21.80 (1.1)</td>
</tr>
<tr>
<td>% pREM</td>
<td>16.72 (0.5)</td>
<td>19.99 (0.7)</td>
<td>17.89 (0.5)</td>
<td>13.01 (0.4)</td>
<td>16.90 (1.5)</td>
</tr>
<tr>
<td>% WAKE during 12 h darkness</td>
<td>21.71 (1.0)</td>
<td>20.46 (2.3)</td>
<td>19.54 (1.0)</td>
<td>22.12 (1.9)</td>
<td>20.96 (0.6)</td>
</tr>
</tbody>
</table>

* Data are presented for the time spent in min ± s.e.m. during the night in the various sleep stages, the percentage of time asleep spent in each of the sleep stages and the number of sleep cycles during the night. (TST, total sleep time; WAKE, awake; LS, light sleep; SWS, slow wave sleep; pREM, probable rapid eye movement sleep; IRI, inter-REM interval.)

Fig. 3. A typical sleep hypnogram from (a) the common marmoset and (b) a human.
stages of sleep were variable, probably as a result of the occurrence of sleep in some subjects during the dusk phase prior to the final lights out. pREM sleep appeared to be influenced by the occurrence of previous sleep, with animals that slept during the dusk period showing considerably shorter pREM latencies than other subjects when this early sleep was excluded. Therefore, measures from first sleep provide the most reasonable values for this parameter.

4. Discussion

In the present study, the use of totally implantable biotelemetry enabled a continuous ECoG signal to be obtained overnight from freely moving marmosets within their home cage environment. Using a single channel of ECoG data and a concurrent video recording it was possible to stage the sleep of marmosets from recordings made over a 12 month period. This study extends recent work by Suchi and Rothe (1999) on the diurnal activity of this species.

Typically marmosets slept for a single period of approximately 10 h within the 12 h of total darkness. Analysis indicates that the majority of the marmosets sleep was light (61.34%), with smaller amounts of SWS (21.8%) and pREM sleep (16.9%). The duration of the various sleep stages was generally short, with frequent transitions between stages. Brief wakenings were often seen during light sleep and pREM sleep, but rarely during SWS. The proportion of wakeness found in the present study is considerably higher than that typically reported for humans where less that 5% of the night is spent awake (Carskadon and Dement, 1994). Higher quantities of waking may be expected in these small primates whose natural arboreal habitat affords dangers of predation, and in whom a degree of nocturnal vigilance is therefore required. Previous studies with other non-human primate species (see Table 3) have shown a similar predominance of light sleep as well as a high proportion of wakeness (Reite et al., 1965; Breton et al., 1986). A relatively high proportion of light sleep (2–5% of stage 1 and 45–55% of stage 2) and lesser amounts of SWS (3–8% of stage 3 and 10–15% of stage 4) are also observed in humans (Carskadon and Dement, 1994). The percentage of total pREM sleep reported here for the marmoset can be seen to be consistent with the majority of previous studies carried out in other non-human primates (e.g. Weitzmann, 1961; Reite et al., 1965; Bert et al., 1970). REM sleep values for humans, however, are substantially higher than those reported for all of the non-human primate species studied.

SWS and pREM sleep occurred in cycles which were of short duration, typically lasting 40–50 min, approximately half the length observed in humans, where a typical cycle lasts on average 90 min (Carskadon and Dement, 1994). Previous sleep studies in large non-human primates have reported sleep cycles intermediate in length between those reported in humans and those obtained here in the marmoset. Examples of values for other non-human primate species include 75–85 min for the adult pigtail macaque (Reite et al., 1965) and a mean of 72.5 min (range 35–130 min) for the squirrel monkey (Breton et al., 1986). However, the majority of these previous studies in adult monkeys used restraint type recording methods and therefore comparisons are limited.

A typical marmoset hypnogram shows approximately 14 sleep cycles (range 10–17) occurring during a 12 h night, considerably more than the 4–6 cycles usually observed during an 8 h night in adult humans (Carskadon and Dement,

<table>
<thead>
<tr>
<th>Table 2</th>
<th>Sleep latency measures for the second sleep recording made for each of the 4 marmosets M1, M2, M3 and M4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sleep before lights out</td>
<td>Latency to SWS from first sleep</td>
</tr>
<tr>
<td>M1 (f)</td>
<td>Yes</td>
</tr>
<tr>
<td>M2 (f)</td>
<td>No</td>
</tr>
<tr>
<td>M3 (m)</td>
<td>Yes</td>
</tr>
<tr>
<td>M4 (m)</td>
<td>Yes</td>
</tr>
<tr>
<td>Median</td>
<td>45</td>
</tr>
<tr>
<td>Lower quartile</td>
<td>25.25</td>
</tr>
<tr>
<td>Upper quartile</td>
<td>68.25</td>
</tr>
</tbody>
</table>
### Table 3

Summary of data reported in a selection of previous studies of sleep in primates

<table>
<thead>
<tr>
<th>Authors</th>
<th>Human</th>
<th>Chimpanzee</th>
<th>Baboon</th>
<th>Rhesus macaque</th>
<th>Infant pigtail macaque</th>
<th>Squirrel monkey</th>
<th>Marmoset</th>
</tr>
</thead>
<tbody>
<tr>
<td>% LS (stages 1–2)</td>
<td>47–60</td>
<td>46</td>
<td>92</td>
<td>78</td>
<td>48.7 (+14.6 drowsy)</td>
<td>58.7(+2.2 drowsy)</td>
<td></td>
</tr>
<tr>
<td>% Intermediate</td>
<td>n/a</td>
<td>n/a</td>
<td>n/a</td>
<td>n/a</td>
<td>12</td>
<td>n/a</td>
<td>14.3</td>
</tr>
<tr>
<td>% SWS (stages 3–4)</td>
<td>13–23</td>
<td>39</td>
<td>3</td>
<td>11</td>
<td>13.6</td>
<td>28.7*</td>
<td>27</td>
</tr>
<tr>
<td>% REM/REM</td>
<td>20–25</td>
<td>15</td>
<td>6</td>
<td>11</td>
<td>11.1</td>
<td>11*</td>
<td>22.9</td>
</tr>
<tr>
<td>Recording period</td>
<td>8 h</td>
<td>14 h</td>
<td>12 h</td>
<td>12 h</td>
<td>14.5 h</td>
<td>11 h</td>
<td>12 h</td>
</tr>
<tr>
<td>% WAKE</td>
<td>5</td>
<td>31*</td>
<td>23</td>
<td>20</td>
<td>36*</td>
<td>18.4*</td>
<td>17.6</td>
</tr>
<tr>
<td>Level of restraint</td>
<td>n/a</td>
<td>Externally mounted radiotelemetry</td>
<td>Externally mounted radiotelemetry</td>
<td>Restraint chair</td>
<td>Biotelemetry</td>
<td>Restraint chair</td>
<td>Tethered</td>
</tr>
</tbody>
</table>

*a* Data calculated based on figures provided in the paper.
References

Adams PM, Barratt ES. Nocturnal sleep in squirrel monkeys. Electroenceph clin Neurophysiol 1974;36:201–204.


