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Individual Variation in Sleep and Motor Activity in Rats

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Abstract

We examined individual differences in sleep and motor activity across two consecutive days in rats. EEG and motor activity were recorded via telemetry in Wistar rats ($n=29$) for 48 h under well-habituated conditions. Rats were grouped based on sleep amounts and stability across days (short [SS, $n=7$], intermediate [IS, $n=15$] and long [LS, $n=7$] sleep) and comparisons were conducted to determine group differences for measures of sleep and motor activity. We found that correlations across recording days were significant for all selected sleep measures and motor activity counts. Rankings for 24 h total sleep time and non-rapid eye movement sleep (NREM) were $SS < IS < LS$ rats whereas amounts of rapid eye movement sleep did not differ among groups. Further analyses of NREM episode parameters found significant differences in mean episode length ($SS < IS < LS$) but not in the number of episodes. Total and average motor activity counts (per waking min) were greater (32–38%) in SS compared to LS rats on both recording days. The results indicate that individual differences in sleep and motor activity in Wistar rats are stable across days. Differences between SS and LS rats have parallels to those reported for short and long sleep humans.

Keywords

individual differences; rat; sleep; motor activity; short sleeper

Introduction

Studies of sleep in inbred animal strains under baseline conditions have provided evidence that many sleep parameters are genetically determined. Reported differences in sleep parameters between strains include variations in the time spent in total sleep, in rapid eye movement sleep (REM) and in non-REM sleep (NREM) evaluated for 24-h recording periods and for the light and dark periods considered separately. There have also been reported differences among strains in the average length and number of NREM and REM episodes and in the diurnal ratio (Light/Dark) of total sleep, NREM and REM [6,10,15,18,20].

In humans, studies in monozygotic twins [9,16,27] also provide evidence suggesting that sleep parameters are genetically determined [6,15,18,20]. Repeated measurements across days within human subjects suggest that differences in habitual sleeping time are stable traits within individuals [23], and there is increasing interest in determining the significance of individual differences in sleeping time [23]. Early studies in humans suggested that, as a group, people with short sleep tend to be energetic and efficient in their general social roles [7,8]. However, more recent work has linked habitual short sleeping time to higher rates of obesity, heart

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disease, mortality and psychiatric problems [12,23,24], suggesting that understanding the biological basis of individual differences in sleep amounts and architecture may be important for elucidating the relationship between sleep and disease processes. This may be difficult to accomplish in humans due to the influence of society and different lifestyles. Experimental rodents can be easily bred and maintained in standardized environments, and thus have the potential to provide models for examining the biological basis of individual variation in sleep.

Basic requirements for rodent models would include stability in sleep amounts across time within individuals as well as significant differences in sleep amounts between individuals. An early study found stability in the sleep measures of individual rats as indicated by significant correlations for total sleep time and REM time across two 6-h recording sessions on separate days [11]. However, within and between day variation in total sleep, NREM, REM, the length and number of NREM and REM episodes, and in the light-dark distribution of sleep have not been extensively studied in individual rats under standard baseline conditions.

In this study, we examined sleep parameters in genetically heterogeneous outbred Wistar strain rats. We recorded sleep in twenty-nine animals over two uninterrupted days under well-habituated conditions and we examined correlations between days for sleep and motor activity to determine the stability of measures within individuals. We then sorted the rats into short (SS), intermediate (IS) and long (LS) sleep groups based on rankings of sleep amounts and consistency of sleep across recording days and we used these groupings to determine whether nominal SS and LS rats differed significantly in amounts of sleep and motor activity. Our purpose was to determine whether this strain of rats show stable sleep and motor activity phenotypes that could be used to model the biological variability of sleep exhibited in humans.

Methods

Subjects

Twenty-nine male Wistar rats (Harlan, Indianapolis, IN) served as subjects. The rats were approximately 90 days of age at the start of the experiment. They were singly housed [cage size 45 (length) × 24 (width) × 20 (height) cm] and given ad libitum access to food and water upon arrival until the completion of the experiment. The same room was used for housing the rats and recording sleep. The room was kept on a 12:12 h light - dark cycle with lights on from 0700 to 1900 h, and ambient temperature was maintained at 24.5±0.5 C. Light intensity was 90-110 lux in the room, about 60 lux in the cage during the light period, and less than 1 lux during the dark period.

Surgery

Each rat was implanted with a transmitter (DataSciences ETA10F20) for recording EEG and motor activity via telemetry as described previously [17]. The body of the transmitter was implanted subcutaneously off midline and posterior to the scapula and it was attached to the skin with three sutures for stabilization. Leads from the transmitter were led subcutaneously to the skull and the bare ends placed in contact with the dura through holes in the skull [A: 2.0 (Bregma), L: 1.5; P: 7.0 (Bregma), L: 1.5 contralateral]. The electrodes were anchored to the skull with screws and dental cement. All surgical procedures were performed stereotactically under aseptic conditions. Surgical anesthesia was achieved with isoflurane (5% induction; 2% maintenance). Buprenorphine (0.05 mg/kg, SC) were administered for potential post-operative pain. The rats were allowed a minimum of 14 days to recover prior to beginning the recording. All procedures were conducted in accordance with the National Institutes of Health *Guide for the Care and Use of Experimental Animals* and were approved by Eastern Virginia Medical School's Animal Care and Use Committee (Protocol # 02-029).

Data collection

Telemetric recording of EEG and motor activity was conducted using procedures similar to those we have used in mice [20] and rats [17]. For EEG, the signals were processed by a DataSciences analog converter. The AD converter digitized the EEG signals at 128 Hz and motor activity signals at 2 Hz, and then the digitized data were transferred to the computer and displayed graphically by the program on the computer monitor. Movement of the animal in relation to the telemetry receiver generated transistor-transistor logic (TTL) pulses that were collected and counted as a measure of motor activity. EEG and motor activity data were collected for 48 h after recovery from surgery. The study was conducted over a period of four months using four groups ($n = 7, 7, 8$ and 7) of rats. For each group of rats, the data were recorded concurrently.

Data analysis

Trained observers visually scored the EEG and motor activity records in 10 s epochs to determine wakefulness, NREM, and REM. Episode durations were the sum of continuous epochs scored as wakefulness, NREM or REM and an episode would be terminated by the occurrence of a single epoch scored as a different sleep or wake state. Wakefulness was scored based on the presence of low-voltage, fast EEG and irregularly spaced and clustered TTL pulses on the motor activity channel. NREM was scored based on the presence of spindles interspersed with slow waves or desynchronized EEG. During REM, the EEG was characterized by a regular, low-amplitude theta rhythm. Compared to quiet wakefulness, during REM EEG power is significantly reduced in the lower frequency band (0.5- 4 Hz) and increased in the range of theta activity (6.5-9 Hz, peak at 7.5 Hz). A concurrent display of EEG power spectra for each epoch thus was used to aid in discrimination of REM from wakefulness. Inactivity during sleep was confirmed by the lack of TTL pulses though a few sporadic single TTL pulses may be seen during NREM and REM periods.

The time spent (min) in NREM, REM and total sleep time (NREM+REM) as well as motor activity counts were processed and plotted to reveal hourly patterns of sleep and motor activity during the two day recording period. Afterwards, the data were processed to obtain total 24 h, 12 h light and 12 h dark period totals for each day. The numbers of NREM and REM episodes, average duration of NREM and REM episodes (total time/number of episodes, min), NREM and REM percentage (NREM or REM time/total sleep time*100%), and the diurnal ratio of sleep, NREM and REM time (Light/Dark) were also analyzed for the total 24 h and the 12 h light and dark periods.

All statistical analyses were conducted using SigmaStat software (SPSS, Inc.). Comparisons between groups were conducted using between subjects analysis of variance (ANOVA) procedures. Significant ANOVAs were followed by Tukey Tests when all pairwise comparisons among means were considered. Pearson's product moment correlation was used to examine the relationships of measures obtained within individuals across recording days.

Results

Stability of sleep and motor activity across recording days

Descriptive statistics of 24 h total sleep time (min) that included all rats suggested similar amounts of sleep across days. The means $\pm$ SEM for day 1 and day 2 (in brackets) were 634 ± 10.1 (648 ± 8.3). Median values for total sleep were 628 (645) with minimum, maximum and range were 550 (557), 744 (722) and 194 (165), respectively. Lower and upper quartiles were 593 (611) and 676 (685). Statistically, total sleep time did not differ across days (paired t-test; $t = 1.1$, $p = 0.28$).

A correlation analysis also was conducted to examine the stability of sleep parameters and motor activity levels across days. Scatter plots and regression lines for selected measures are presented in Figure 1. Almost all sleep measures that were examined and the motor activity counts were significantly correlated across days whether the data were considered as 24 h totals or as separate 12 h light and dark periods (Table 1). The single sleep parameter that was not significantly correlated across days was dark period REM episode length. Stability was also suggested by significant correlations across days for the diurnal ratios (light/dark) of time spent in total sleep ($r = 0.74$, $p < 0.001$), NREM ($r = 0.74$, $p < 0.001$) and REM ($r = 0.76$, $p < 0.001$).

The means $\pm$ SEM of total sleep time for each of the four groups of rats during day 1 were 638 ± 17.9 (n=7), 609 ± 21.7 (n=7), 644 ± 21 (n=8) and 643 ± 20.8 (n=7). These groups were compared using a one-way between subjects ANOVA to determine if sleep amounts varied with cohort. There were no significant differences in total sleep time amongst the groups [$F(3, 28) = 0.63$, $p = 0.61$].

Sleep and motor activity in short, intermediate and long sleep rats

Total sleep times for individual rats on days 1 and 2 are shown in Figure 2. The upper panels of Figure 2 are plotted to show individual rankings of total sleep time on day 1, and the lower panels show individual rankings for day 2. The rats were initially divided into three groups (SS, IS and LS) based on tertile rankings for day 1. Three SS rats and three LS rats showed intermediate amounts of sleep on day 2, and six IS rats made corresponding changes to either the SS or LS groups. Changes in groups from day 1 to day 2 are indicated by bar fill effects in Figure 2. Based on amounts of sleep and stability across days, we grouped the rats into final sets of SS (n=7), LS (n=7) and IS (n=15) for further analysis. Sleep parameters for the groups on both recording days are presented in Table 2. Mean differences in amounts of total sleep for days 1 and 2, respectively, were 53 and 54 min for SS and IS rats, 81 and 51 min for IS and LS rats, and 134 and 105 min for SS and LS rats.

Figure 3 presents the hourly sleep amounts and motor activity counts in SS and LS rats. As shown in the figure, the main effects of groups in two-way ANOVA were significant in the measures of total sleep, NREM and motor activity counts in two days, with no significant differences obtained in the measure of REM in two days. Overall, SS rats exhibited less time spent in total sleep and NREM, and greater motor activity counts than did LS rats. Post-hoc Tukey test revealed that those differences did reach significant levels during some hourly time bins. Differences in motor activity counts were greater during the dark period on both days. For clarity, plots for IS rats are not shown.

Table 2 shows selected sleep measures and motor activity counts for SS, IS and LS rats over the total 24 h recording period and for the 12 h light and dark periods for both recording days. Total sleep time and total NREM time were significantly reduced in SS rats compared to LS rats in all analysis periods. Further analyses of NREM episode parameters found significant group differences in mean episode length but not in the number of episodes. Significantly shorter episode length in SS compared to LS rats was found in all measurement periods on days 1 and 2.

One-way ANOVA did not reveal significant differences between groups in REM time, number of REM episodes or REM episode length. However, compared to IS and LS rats, on both days SS rats exhibited non-significant trends toward decreased 24 h totals of REM amount and number of REM episodes. SS and LS rats did not significantly differ in NREM and REM percentage (relative to total sleep); however, SS rats showed trends toward lower NREM percentage and higher REM percentage compared to LS rats on both days.

SS rats consistently exhibited greater motor activity than did LS rats during the total 24-h recording period and during separate light and dark periods on days 1 and 2. Similar significant differences were found in average motor activity counts per each waking min (obtained by total motor activity count/total wakefulness time in min), except during the light period on days 1 and 2.

The values for sleep and motor activity parameters in the IS rats fell between those of SS and LS rats in almost all analysis periods. Exceptions were that IS rats showed similar amounts of NREM time and total sleep to SS rats during the dark period on days 1 and 2, and that IS rats displayed similar amounts of 24-h REM time to LS rats on days 1 and 2.

Discussion

The rats were maintained in constant housing conditions from their time of arrival from the supplier until the completion of the experiment. This allowed sleep and motor activity data to be collected under well-habituated conditions that should have mitigated possible environmental influences on baseline sleep and motor activity [18]. External disruptions in sleep also might produce negative correlations across days as reduced sleep would be subject to homeostatic compensation. Therefore, as suggested by earlier work [11], the positive correlations obtained across days should reflect stability of these measures within individuals. The correlations that we obtained for sleep measures in rats generally appear to be greater than those obtained in similar types of analyses of human sleep [5,9,14,22,27]. However, some rats showed significant variation across days. This is apparent in Figure 2 where three rats initially categorized as SS (mean day 1 vs. day 2: 594 vs. 640 min [46 min increase]) and three rats initially categorized as LS (mean day 1 vs. day 2: 663 vs. 647 min [16 min decrease]) showed intermediate amounts of sleep on day 2. Figure 2 also shows that the two longest sleeping rats (rats 28 and 29) on day 1 had less sleep on day 2.

In humans, polysomnographic studies of short and long sleepers have typically been conducted on subjects pre-screened via self-report measures from a much larger population [1,8,25,26]. Subjects with intermediate sleep durations served as controls, whereas those who exhibited much shorter or longer duration of sleep were used as study subjects [1,8,25,26]. By comparison, the present analysis was conducted on rats that were not selected in any systematic way. The subjects were simply Wistar rats purchased over a four month period that were then implanted and studied. It is worth mentioning that the average amounts of NREM and REM we observed in these twenty-nine rats recorded with telemetry were very similar to the average amounts of these states we obtained in this strain using cable recordings [18]. The fact that a small number of outbred rats could show significant and consistent differences in sleep suggests that inter-individual variability could be a significant factor in statistical analysis of studies investigating sleep. For example, differences in total sleep between SS and LS rats was 134 min on day 1 (a 19% difference) and 105 min on day 2 (a 15% difference). Interestingly, attempts to develop animal models that better represent individual differences in clinical populations have included selecting animals that respond differently, for example, low and high responders to stressors in genetically heterogeneous outbred strain rats [3,4]. This suggests that differentiating SS and LS rats may lead to insight regarding the potential significance of sleep duration in these animals.

Significant differences among SS, IS and LS rats for NREM amounts but not REM amounts are consistent with differences observed in short and long sleep humans [1,8,25,26]. Both correlation analyses and comparisons between groups indicated that increased NREM time was closely linked to increases in the average length of NREM episodes. Interestingly, our previous work in mice illustrated that increased NREM time and reduced motor activity induced by heavier recording cables was associated with decreases in the average length of

NREM episodes [19]. By comparison, increases in NREM time accompanying putatively reduced internal arousal levels, such as that accompanying certain brain lesions, are associated with increases in the average length of NREM episodes [17,21]. The finding that rats that have greater NREM time exhibit longer average lengths for NREM episodes suggests that the increases in NREM time is a function of the natural demand for NREM.

REM amounts in SS, IS and LS rats did not significantly vary across days or with differences in total sleep time. This finding parallels other studies in rats and mice that have found relative stability of REM compared to NREM. For example, rats that showed greater locomotion in the open field and reduced total sleep and NREM did not show decreased REM [2]. In mice, significant strain differences in 24 h total sleep and NREM can occur without significant differences in REM amounts [20]. However, some strains do show less REM. For example, Fischer 344 rats show over 3.5 h less total sleep time, and 22 min less total REM time compared to longer sleep Lewis rats [18]. In contrast, Lewis rats did not differ in amounts of REM compared to non-selected Wistar rats even though they exhibited significantly more total sleep [18]. Webb and Agnew [26] suggested that absolute amounts of REM would be a function of total sleep time, and that there was a point at which reductions in total sleep time would result in reductions in REM. Indeed, they found that long sleep humans had more REM (155 min) than did short sleep humans (96 min) who, in turn, did not differ from non-selected controls (101 min) [26]. Individuals that showed markedly less sleep (around 3 h per night) showed only about 40 minutes of REM [13]. In the present study, SS rats showed non-significant trends toward decreased 24 h totals of REM and number of REM episodes on both recording days compared to IS and LS rats (approximately 10% less compared to both). These findings suggest that significant alterations in REM may occur only with large increases or decreases in habitual sleep.

Early studies in humans reported that short sleepers were active, tended to work hard and to keep busy and engendered the hypothesis that short sleepers are relatively more active in nature [7,8] whereas more recent work has linked short sleep to obesity, heart disease, mortality and psychiatric problems [12,23,24]. In this study, we found that SS rats displayed greater motor activity (counts per waking min) on day 1 (32%) and day 2 (38%) compared to LS rats suggesting that SS rats are indeed more active during wakefulness. IS rats showed an intermediate level of motor activity counts. However, the correlation (-0.43 , data was not presented) between motor activity counts and total sleep time was relatively modest. Other work has demonstrated that individual rats that initially exhibit greater locomotion in the open field also have decreased total sleep [2].

Interestingly, in a recent survey of over 1000 Chinese university students ($n=1070$, age 19.7 ± 0.99), we found that those students reporting longer sleep also reported less difficulty in falling asleep at night and fewer instances of nighttime awakenings than did students reporting short sleep [28]. However, those reporting short sleep could be separated into “poor” short sleepers who reported worse nighttime sleep and perceived worse daytime cognitive functioning and “good” short sleepers who reported fewer problems in nighttime sleep and daytime activities [28]. These findings require confirmation, but they suggest that the relationship between sleep duration and sleep quality may be quite complex.

In summary, we found that the outbred Wistar strain contained individual rats that showed stable SS and LS phenotypes. SS rats were also behaviorally more active than LS during wakefulness. These findings suggest that this strain has the potential to serve as a model for examining the biological basis of individual variation in sleep.

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Figure 1.

Correlations in time spent in total sleep, NREM and REM and motor activity counts (No: total number of TTL pulses over 24 h) between days 1 and 2 in individual rats during total 24 h recording periods (*, $p < 0.001$).

Figure 2.

Total sleep time (min) in individual rats during day 1 (Upper Panels) and 2 (Lower Panels), plotted from lowest (Left) to greatest (Right) amount of sleep, and sorted into SS, IS and LS groups. Fill effects for each group are maintained in the plots of day 2 and illustrate that three SS and three LS rats increased or decreased total sleep across days.

Figure 3.

Time spent in total sleep, NREM and REM as well as motor activity counts (No: total number of TTL pulses per hour) plotted hourly for short (SS, $n=7$) and long (LS, $n=7$) sleep rats for each of two recording days. Values are means $\pm$ SEM. F and p values for main effect of group in two-way ANOVA that reached significant levels are indicated in the figures. Significant differences between groups within block are indicated by dark circles in SS rats (Tukey test, $p < 0.05$).

Table 1

Correlations in sleep measures and motor activity counts between day 1 and 2 in individual rats during total 24 h and separate 12 h of light and dark periods.

	<u>Total 24 h</u>	<u>Light 12 h</u>	<u>Dark 12 h</u>
Total Sleep	0.81 ***	0.71 ***	0.71 ***
NREM			
Time	0.87 ***	0.78 ***	0.76 ***
Episode Number	0.58 **	0.54 *	0.79 ***
Episode Length	0.68 ***	0.66 ***	0.71 ***
REM			
Time	0.71 ***	0.81 ***	0.59 **
Episode Number	0.57 *	0.69 ***	0.58 *
Episode Length	0.63 **	0.52 *	0.34 ***
Percentage	0.85 ***	0.86 ***	0.72 ***
Motor activity	0.96 ***	0.86 ***	0.96 ***

Significance level of correlations:

*
p < 0.01

**
p < 0.001

p < 0.0001

Table 2

Selected sleep measures and motor activity counts in short (SS, n=7), intermediate (IS, n=15) and long (LS, n=7) sleep rats during total 24 h and separate 12 h light and dark periods in two consecutive recording days. Values are means $\pm$ SEM. Different letters indicate significant differences from the other groups (Tukey test, $p < 0.05$).

	Total	Day 1		Day 2	
		Light	Dark	Light	Dark
Total Sleep					
SS	574 (7.9) c	426 (13.8) c	147 (8.4) b	595 (6.9) c	151 (3.1) b
IS	627 (6.8) b	478 (3.7) b	149 (6.5) b	649 (7.7) b	168 (6.2) b
LS	708 (11.3) a	512 (6.6) a	196 (9.1) a	700 (7.4) a	198 (6.9) a
NREM Time					
SS	483 (9.7) c	361 (14.5) c	122 (6.8) b	504 (9.2) c	127 (3.6) b
IS	528 (7.0) b	405 (3.5) b	123 (5.9) b	548 (7.7) b	140 (5.4) b
LS	608 (11.4) a	444 (8.3) a	164 (7.6) a	602 (9.9) a	166 (4.8) a
NREM %					
SS	84.1 (0.7)	84.6 (1.0)	82.7 (1.3)	84.7 (0.7)	84.0 (1.1)
IS	84.2 (0.5)	84.8 (0.6)	82.3 (1.0)	85.1 (0.7)	83.2 (1.1)
LS	85.9 (0.5)	86.7 (0.9)	83.9 (0.7)	85.9 (0.6)	83.8 (1.2)
Number of NREM Episode					
SS	179 (5.6)	120 (6.1)	59 (2.3)	172 (5.0)	58 (3.5)
IS	168 (4.2)	108 (2.8)	60 (2.8)	176 (5.4)	66 (3.2)
LS	168 (2.2)	107 (2.1)	61 (3.0)	173 (5.3)	65 (4.3)
Average NREM Episode Length					
SS	2.7 (0.10) c	3.0 (0.19) c	2.1 (0.14) b	2.9 (0.09) b	2.2 (0.09) b
IS	3.2 (0.06) b	3.8 (0.10) b	2.1 (0.07) b	3.2 (0.10) ab	2.2 (0.09) ab
LS	3.6 (0.10) a	4.2 (0.11) a	2.7 (0.16) a	3.5 (0.14) a	2.6 (0.13) a
REM Time					
SS	91 (3.4)	65 (3.2)	26 (2.5)	91 (3.7)	24 (1.5)
IS	99 (3.4)	73 (3.2)	26 (1.6)	100 (4.5)	28 (2.1)
LS	100 (3.4)	68 (4.5)	32 (2.2)	98 (3.5)	32 (3.2)
REM %					
SS	15.9 (0.7)	15.4 (1.0)	17.3 (1.3)	15.3 (0.1)	16.0 (0.0)
IS	15.8 (0.5)	15.2 (0.6)	17.7 (1.0)	15.5 (0.1)	16.8 (0.0)
LS	14.1 (0.5)	13.3 (0.9)	16.1 (0.7)	14.1 (0.0)	16.2 (0.1)
Number of REM Episode					
SS	57 (2.2)	38 (1.7)	19 (1.3)	56 (1.3)	19 (1.2)
IS	59 (2.2)	41 (1.7)	18 (1.1)	64 (2.6)	22 (1.7)
LS	62 (1.6)	41 (1.7)	22 (1.4)	64 (1.9)	24 (1.1)
Average REM Episode Length					
SS	1.6 (0.04)	1.7 (0.07)	1.3 (0.06)	1.6 (0.05)	1.3 (0.02)
IS	1.7 (0.04)	1.8 (0.05)	1.4 (0.04)	1.6 (0.05)	1.3 (0.04)
LS	1.6 (0.05)	1.7 (0.08)	1.5 (0.08)	1.5 (0.05)	1.3 (0.08)
Total Motor activity Count					
SS	36469 (5053) a	7712 (1391) a	28757 (3738) a	36303 (4416) a	27926 (2979) a
IS	28082 (2783) ab	5305 (617) ab	22777 (2275) ab	28385 (2617) ab	22205 (2138) ab
LS	22087 (2579) b	4081 (731) b	18006 (1999) b	20067 (1919) b	16172 (1293) b
Average Motor activity Count in Each Waking Min					
SS	44 (4.4) a	29 (4.6)	55 (5.9) a	44 (5.8) a	50 (5.6) a
IS	34 (3.3) ab	22 (2.5)	40 (3.8) ab	36 (3.4) ab	40 (3.7) ab
LS	30 (3.3) b	20 (3.6)	34 (3.5) b	27 (2.8) b	31 (2.6) b
Total Sleep					
SS	3.0 (0.25)	3.1 (0.27)	2.8 (0.42)	2.9 (0.08)	2.9 (0.34)
IS	3.3 (0.17)	3.4 (0.18)	3.0 (0.26)	2.9 (0.15)	2.9 (0.41)
LS	2.7 (0.13)	2.7 (0.13)	2.3 (0.29)	2.6 (0.11)	2.2 (0.37)