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Locomotor Activity Rhythms in Dogs Vary With Age and Cognitive Status

Christina T. Siwak and P. Dwight Tapp
University of Toronto

Steven C. Zicker
Hill's Pet Nutrition

Heather L. Murphey and Bruce A. Muggenburg
Lovelace Respiratory Research Institute

Elizabeth Head and Carl W. Cotman
University of California, Irvine

Norton W. Milgram
University of Toronto

Beagle dogs exhibited diurnal patterns of locomotor activity that varied as a function of age, cognitive status, and housing environment. Aged dogs housed in an indoor facility showed a delayed onset of activity following lights on and displayed shorter bouts of activity, with more rest periods during the day, compared with young dogs. Cognitively impaired aged dogs were more active and showed a delayed peak of activity compared with unimpaired aged dogs. Housing in continuous light did not disrupt activity rhythms. The effect of age was less prominent in dogs housed in an indoor/outdoor facility. This suggests that bright sunlight and natural light–dark transitions are better able to consolidate and synchronize the activity rhythms of the dogs.

Forty to seventy percent of the elderly population suffer from chronic problems associated with sleep (Van Someren, 2000a, 2000b). These include increased nighttime wakefulness and frequent daytime naps, both of which are indicative of disrupted circadian regulation (Hofman, 2000). Elderly people are also less sensitive to entraining cues (i.e., light), and lose synchronization with the environment (Edgar, 1994; Hofman, 2000; Van Someren, 2000a, 2000b; Weinert, 2000). These effects are exaggerated in patients with Alzheimer's disease (AD), who also experience fragmentation of the cycle, with frequent waking at night and daytime napping (Hofman, 2000; Satlin et al., 1991; Satlin, Volicer, Stopa, & Harper, 1995). Patients with AD also show a phase delay, with peak activity occurring later in the afternoon, compared with control subjects (Satlin et al., 1991, 1995). More severe disruption is associated with greater disease severity (Witting, Kwa, Eikelenboom, Mirmiran, & Swaab, 1990).

Variation also exists among AD patients; with a subgroup of individuals exhibiting pacing behavior and higher levels of activity than normal controls, whereas nonpacers are less active than normal aged individuals (Satlin et al., 1991). The alterations associated with dementia vary with the type of dementia (Harper et al., 2001). Circadian disturbances are distinct for AD, frontotemporal dementia, and multi-infarct dementia (Aharon-Peretz et al., 1991; Harper et al., 2001; Mishima et al., 1997; Satlin et al., 1991, 1995).

Age-dependent changes in activity rhythms also occur in animal models. Aged rats, hamsters, and mice show dampened activity rhythms, reduced synchronization with the environment, and greater fragmentation (Weinert, 2000). The free-running period of the circadian activity–rest rhythm shortens or lengthens with age in hamsters and rats as measured under constant lighting conditions (Asai, Ikeda, Akiyama, Oshima, & Shibata, 2000; Turek, Penev, Zhang, van Reeth, & Zee, 1995). Age-dependent disorganization of circadian rhythms in mammals has been linked to degeneration of the suprachiasmatic nucleus of the hypothalamus (SCN; McDuff & Sumi, 1985; Saper & German, 1987; Satlin et al., 1991, 1995; Swaab, Fliers, & Partiman, 1985; Tate et al., 1992; Van Someren, 2000a, 2000b; Weinert, 2000).

Circadian rhythm disturbances may contribute to age-dependent cognitive dysfunction. Impaired cognitive function has been observed in both humans and rodents subjected to intentional sleep disruption during the subjective night period. (Antoniadis, Ko, Ralph, & McDonald, 2000; Bonnet, 1989; Devan et al., 2001; Sandyk, Anninos, & Tsagas, 1991). This suggests that disruptions in circadian rhythms are linked to age-associated cognitive decline (Antoniadis et al., 2000; Sandyk et al., 1991). Disruptions in

Christina T. Siwak, Institute of Medical Science, University of Toronto, Toronto, Ontario, Canada; P. Dwight Tapp and Norton W. Milgram, Department of Psychology, University of Toronto; Steven C. Zicker, Hill's Pet Nutrition, Topeka, Kansas; Heather L. Murphey and Bruce A. Muggenburg, Lovelace Respiratory Research Institute, Albuquerque, New Mexico; Elizabeth Head and Carl W. Cotman, Institute for Brain Aging and Dementia, University of California, Irvine.

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Correspondence concerning this article should be addressed to Norton W. Milgram, Department of Psychology, University of Toronto at Scarborough, 1265 Military Trail, Scarborough, Ontario M1C 1A4, Canada. E-mail: milgram@psych.utoronto.ca

circadian rhythms, specifically activity–rest cycles, could affect cognition in several ways: (a) by producing proactive interference on subsequent learning (Bonnet, 1989; Downey & Bonnet, 1987); (b) by producing retroactive effects by disrupting previous learning (Devan et al., 2001; Sandyk et al., 1991); or (c) by disrupting attentional mechanisms, leading to deficits in cognitive performance (Wimmer, Hoffman, Bonato, & Moffitt, 1992).

The present experiment sought to further explore the relationship between aging, cognitive function, and locomotor activity rhythms in a novel animal model, the beagle dog. Dogs clearly exhibit activity–rest cycles (Tobler & Sigg, 1986), but to our knowledge, age-related alterations have not been examined in this species. Dogs are a viable model system to study activity–rest rhythms because of a prominent daily rhythm of melatonin levels, with higher levels of melatonin during the dark part of the cycle alternating with low levels during the light period; the existence of a retinohypothalamic projection; and the presence of the various sleep stages, slow-wave and REM sleep, like those observed in humans (Lucas, Foutz, Dement, & Mitler, 1979; Schwartz et al., 1986). Studies on activity rhythms in dogs, however, are limited to canine narcolepsy and typically use young dogs (Kaitin, Kilduff, & Dement, 1986; Lucas et al., 1979; Nishino, Tafti, Sampathkumaran, Dement, & Mignot, 1997; Schwartz et al., 1986).

We examined locomotor activity rhythms in young and old dogs housed in two different facilities by using an activity-monitoring device that was worn on a collar. Dogs were acquired from three sources, and to control for possible source effects, we only compared dogs from the same source. To directly compare the effect of the two different housing conditions, dogs from one source were split into two groups and housed at the two different facilities. Dogs showed a clear activity–rest rhythm that varied as a function of both age and test facility. Within the group of old dogs, we also found that the characteristics of the activity rhythms varied with cognitive status.

General Method

Activity patterns were monitored for 5.6 days with the Mini-Mitter Actiwatch-16 activity-monitoring system (Mini-Mitter Co., Bend, OR) adapted for dogs. The Actiwatch was placed inside a specially designed animal case and placed on a collar around the dog's neck. Subjects were allowed to follow their usual patterns of activity, rest, exercise, and feeding, and the time of each event was recorded. For the dogs housed entirely indoors, assessments were collected from Sunday to Saturday. The 5 complete days when the daily routine was similar each day were, therefore, Monday to Friday. Measures were collected between February and October as the weather does not affect the conditions in an indoor facility. Assessments at the indoor/outdoor facility were collected from Thursday through Tuesday. Thus, the 5 complete days were Friday to Tuesday. At this facility, the daily routine during the weekends is the same as during weekdays. Measures were collected between May and June to ensure that the weather conditions at this indoor/outdoor facility were the same for all of the dogs.

A measure of total activity over 24 hr was provided by the Actiware-Rhythm software included in the Mini-Mitter Actiwatch activity monitoring system. The number of minutes between lights on and activity onset were calculated manually. Activity onset was considered to be the first bout of activity lasting for a minimum of 30 min. Activity bouts beginning prior to lights on were assigned a negative value for the number of minutes. The length of the main activity bout was calculated manually as the number of hours that the longest consolidated bout of activity lasted, based on its appearance on an actogram generated by the Actiware-Rhythm software.

A forced-entry regression analysis was conducted to determine whether age accounts for significant variability in the five dependent measures, beyond that accounted for by gender or location. Step 1 entered gender, Step 2 entered location, and Step 3 entered chronological age. The dependent measures were average total activity over 24 hr, length of the main activity bout, minutes between lights on and activity onset, number of daytime activity dips, and number of nighttime activity bouts.

A second regression analysis was performed to determine whether cognitive ability accounts for significant variability in the five dependent measures, beyond that accounted for by gender. Step 1 entered gender, and Step 2 entered cognitive score. This regression was conducted only with the aged dogs from Experiment 1 because cognitive data were not available for the dogs from Experiments 2 and 3.

For Experiment 1 only, a repeated measures analysis of variance (ANOVA) was used to examine the stability of total activity over 24 hr for each of the 5 complete days of recording. Day was the repeated measure, and group was a between-subjects variable.

To examine the qualitative differences between the groups of dogs, a multivariate analysis of variance (MANOVA) was conducted for average total activity over 24 hr, time of onset of activity from lights on (minutes), length of main activity bout (hours), and frequency of daytime activity dips and nighttime bouts of activity as dependent measures for all three experiments. For Experiment 1, group (age and cognitive function) was the between-subjects variable, and Tukey's honestly significant difference test was used for multiple comparisons. Age was the between-subjects variable for Experiment 2, and location was the between-subjects variable for Experiment 3.

Activity for each hour of the 24-hr period was assessed with a two-way repeated measures ANOVA with the repeated measure of hour and the between-subjects variables of group for Experiment 1, age for Experiment 2, and location for Experiment 3. Simple main effects were performed to further examine a significant interaction.

Experiment 1: Changes in Activity Rhythms With Age and Cognitive Function in Beagle Dogs

The first experiment examined activity rhythms in young and aged dogs. We cognitively characterized the aged dogs to determine whether cognitive function is related to activity rhythms.

Method

Subjects. Forty beagle dogs were included in the study: 9 puppies, aged 4–6 months (2 males, 7 females); 15 young dogs, aged 1–4 years (9 males, 6 females); and 16 old dogs (unimpaired: 6 males, 2 females; impaired: 3 males, 5 females), aged 9–14 years. The dogs were housed in an indoor facility with a light intensity, measured on the floor of the rooms, of approximately 300 lux. The dogs were individually housed in 1.07 × 1.22-m pens and maintained on a 12-hr light–dark cycle. The puppies were group housed in one room, which was approximately the size of four individual pens. Water was available ad libitum. Dogs were fed approximately 300 grams of chow daily. The puppies received Hill's Science Diet Puppy Canine Growth Dry Food (Hill's Pet Nutrition, Topeka, KS), and all of the other dogs received Purina Dry Dog Chow (Ralston Purina, St. Louis, MO). Pens were washed daily between 9 and 11 a.m., during which time the dogs were exercised in groups in a separate room. Working hours of the laboratory personnel were from 8 a.m. to 4 p.m. All dogs were in good health at the time of behavioral testing.

Eight dogs (3 young males and 5 old females) from the indoor facility were selected for analysis of activity rhythms under constant light conditions for 5.6 days to determine whether the activity cycles would be more difficult to maintain among older dogs in these conditions.

Cognitive characterization procedures. Cognitive characterization was based on the sum of the dogs' errors on the acquisition of three

neuropsychological tests: a delayed nonmatching-to-position (DNMP) task, an object discrimination learning task, and an object discrimination reversal task (Chan et al., 2002; Milgram, Head, Weiner, & Thomas, 1994). An aged dog was considered impaired if its total score was greater than 2 *SD* from the mean of the young dog group. An aged dog with a score less than 2 *SD* from the mean of the young dogs was placed in the unimpaired group. This resulted in 8 old-unimpaired dogs (6 male, 2 female) and 8 old–impaired dogs (3 males, 5 females).

The test apparatus, as described previously (Milgram et al., 1994), consisted of a wooden box (1.150 m long × 1.080 m high × 0.609 m wide) with vertical aluminum bars at the front, a moveable Plexiglas tray with three food wells, a small overhead incandescent light, and a wooden partition containing a one-way mirror and hinged door. The heights of the vertical bars were individually adjusted for each dog to allow access to the food placed in the tray wells. A dedicated computer program was used for controlling all timing procedures, for specifying the location of the correct choice, and for capturing data. The test sessions occurred once daily.

The object discrimination task used two objects: a blue Lego block and a yellow coffee jar lid. The tray was presented, with the two objects placed over the lateral wells. The dog had to displace the object that was associated with the reward. The dogs were given 10 trials per day with a 30-s interval between trials. Dogs were tested daily until they passed. The learning measure used was errors made until criterion was reached.

The object discrimination reversal task simply changed which object was rewarded, so that the dogs had to learn to go to the previously unrewarded object. For example, if the blue Lego block was positive during the discrimination test, the yellow coffee jar lid was positive for the reversal learning task.

The DNMP task was intended to train dogs to remember the location of a sample stimulus. Each trial of the task involves two components: the sample phase and the test phase. During the sample phase, the dog was presented with an object covering a food reward in one of the three wells. The tray was then removed for a delay of 10 s. After the delay, the tray was presented a second time, with the sample object covering the same well and a new identical object covering a second well, which now contained food. Thus, the dog had to respond to the object in the new location to receive the food reward. The dogs were considered to have made an incorrect choice if they came into contact with the sample object that had previously been presented. The dogs were given 10 trials per day with a 60-s interval between trials. When the dog passed the task at the 10-s delay, it moved on to a 20-s delay and then a 30-s delay. The longer delays make the task more difficult. The learning measure used was errors made to reach criterion for each delay.

Results

The mean (± *SD*) cognitive score and standard deviation for the young dog group was 185 (± 59). Any aged dog with a score greater than 303 was classified as impaired. The distribution of error scores for the combined error score and the age of the dogs are illustrated in Figure 1.

Multiple regression analyses. The results of the overall regression analysis are listed in Table 1. Gender did not significantly account for any variability in the five dependent measures. Location significantly affected the length of the main activity bout, the time between activity onset following lights on, and the number of daytime rest periods. Chronological age was a significant predictor of total activity and accounted for additional variability in the length of the main activity bout, the time between lights on and activity onset, the number of daytime rest periods, and nighttime activity bouts.

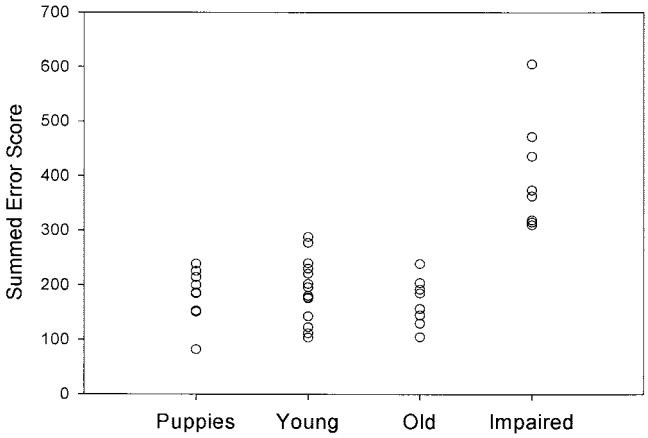


Figure 1. The combined sum of errors required to learn a delayed nonmatching-to-position task and an object discrimination and reversal task are plotted by age group in the indoor-facility dogs. Aged dogs with scores greater than 2 *SD* from the mean of the young dogs were considered impaired.

The results of the second regression analysis examining the influence of gender and cognitive score on the dependent measures are listed in Table 2. Again, gender did not significantly account for any variability in the dependent measures. Cognitive score accounted for variability in total activity averaged over 5 days, the length of the main activity bout, and the number of daytime rest points.

On the basis of the regression analyses results, the data were analyzed separately for each location, and gender was not included as a variable. Our goal was to assess the qualitative nature of the effects of age, cognitive ability, and location.

Interday stability of total activity. The repeated measures ANOVA indicated that the total activity over the 24 hr of each day did not differ between the 5 complete days of recording, $F(4, 144) = 0.43$, $p = .78$. Daily activity was stable over the 5 days. The effect of group was significant, $F(3, 36) = 81.39$, $p < .01$. The puppies were significantly more active than the old, old–impaired, and young dogs ($p < .01$). Old–unimpaired dogs were less active than the old–impaired ($p = .02$) and young dogs ($p < .01$).

Effect of age and cognition on activity level. Dogs exhibited clear activity rhythms, with higher levels of activity during the day in all four groups of dogs (Figure 2). For the total activity measure averaged across the 5 days of recording, the MANOVA revealed a significant effect of age group, $F(3, 36) = 123.66$, $p < .01$. Overall, the puppies ($M = 454.44$, $SEM = 17.33$) were more active than the young dogs ($M = 145.75$, $SEM = 12.47$; $p < .01$), old–unimpaired dogs ($M = 80.07$, $SEM = 5.10$; $p < .01$), and old–impaired dogs ($M = 141.99$, $SEM = 18.17$; $p < .01$). The old–unimpaired dogs were also less active compared with the young ($p = .01$) and old–impaired dogs ($p = .05$). Differences between the groups of dogs were apparent during the daytime hours when activity levels were higher than at night; the groups did not differ during the nighttime.

The ANOVA for the hour-by-hour analysis revealed significant main effects of age group, $F(3, 36) = 81.39$, $p < .01$, and hour, $F(23, 828) = 96.03$, $p < .01$. The interaction between group and

Table 1
Summary of Multiple Regression Analysis for Gender, Location, and Chronological Age

Variable	*F*	*p*	R^2	R^2 change
Total activity over 24 hr				
Model 1: Gender	1.967	.165	.025	.025
Model 2: Gender, location	1.867	.162	.047	.022
Model 3: Gender, location, age	14.887	**.000**	.373	.326
Length of main activity bout				
Model 1: Gender	0.047	.830	.001	.001
Model 2: Gender, location	4.228	**.018**	.100	.100
Model 3: Gender, location, age	21.132	**.000**	.458	.358
Activity onset from lights on				
Model 1: Gender	0.198	.657	.003	.003
Model 2: Gender, location	6.832	**.002**	.152	.150
Model 3: Gender, location, age	19.091	**.000**	.433	.281
Daytime activity dips				
Model 1: Gender	0.597	.442	.008	.008
Model 2: Gender, location	7.284	**.001**	.161	.153
Model 3: Gender, location, age	8.182	**.000**	.247	.086
Nighttime activity bouts				
Model 1: Gender	2.000	.161	.025	.025
Model 2: Gender, location	3.006	.055	.073	.048
Model 3: Gender, location, age	3.312	**.024**	.117	.044

Note. Values in boldface represent statistically significant effects.

hour was also significant, $F(69, 828) = 11.59$, $p < .01$. For the simple main effects, one-way ANOVAs were performed to compare the groups of dogs at each hour to determine when activity levels were significantly different (Figure 3). Hour (H)1 was from 12 a.m. to 1 a.m.

The puppies were significantly more active than the young dogs at H1–2 ($p < .05$), H8–21 ($p < .05$), and H24 ($p < .01$). They were more active than the old dogs at H1 ($p < .01$), H8–22 ($p < .01$), and H24 ($p < .01$). The puppies were also more active than the old–impaired dogs at H1 ($p < .01$), H8–21 ($p < .01$), and H24 ($p < .01$). The puppies did not differ from the other groups from H3 until H7 (approximately 2 a.m. to 7 a.m.).

The young dogs were significantly more active than the old dogs at H10–12 ($p < .05$), which corresponds to 9 a.m. until 12 p.m. Young dogs were more active than the old–impaired dogs at H11 ($p < .01$). The old–impaired dogs exhibited significantly higher levels of activity than the old dogs at H15–17 ($p < .05$), corresponding to 2 p.m. until 5 p.m.

Effect of age and cognition on activity onset, length of main activity bout, daytime rest, and nighttime activity. The time of onset of activity from lights on revealed a main effect of group, $F(3, 36) = 10.22$, $p < .01$. The puppies ($M = 18.18$, $SEM = 7.32$) and young dogs ($M = 35.51$, $SEM = 9.79$) became active sooner after the room lights came on than the old–unimpaired ($M = 120.23$, $SEM = 20.97$; $ps < .01$) and old–impaired ($M = 127.98$, $SEM = 28.53$; $ps < .01$) dogs. Several of the puppies and young dogs exhibited anticipatory activity just prior to when the lights came on in their room.

Table 2
Summary of Multiple Regression Analysis for Gender and Cognitive Score

Variable	*F*	*p*	R^2	R^2 change
Total activity over 24 hr				
Model 1: Gender	3.856	.070	.216	.216
Model 2: Gender, cognitive score	4.927	**.026**	.431	.215
Length of main activity bout				
Model 1: Gender	2.704	.122	.162	.162
Model 2: Gender, cognitive score	4.660	**.030**	.418	.256
Activity onset from lights on				
Model 1: Gender	0.661	.430	.045	.045
Model 2: Gender, cognitive score	0.461	.641	.066	.021
Daytime activity dips				
Model 1: Gender	0.958	.344	.064	.064
Model 2: Gender, cognitive score	4.885	**.026**	.429	.365
Nighttime activity bouts				
Model 1: Gender	0.901	.359	.060	.060
Model 2: Gender, cognitive score	0.727	.502	.101	.040

Note. Values in boldface represent statistically significant effects.

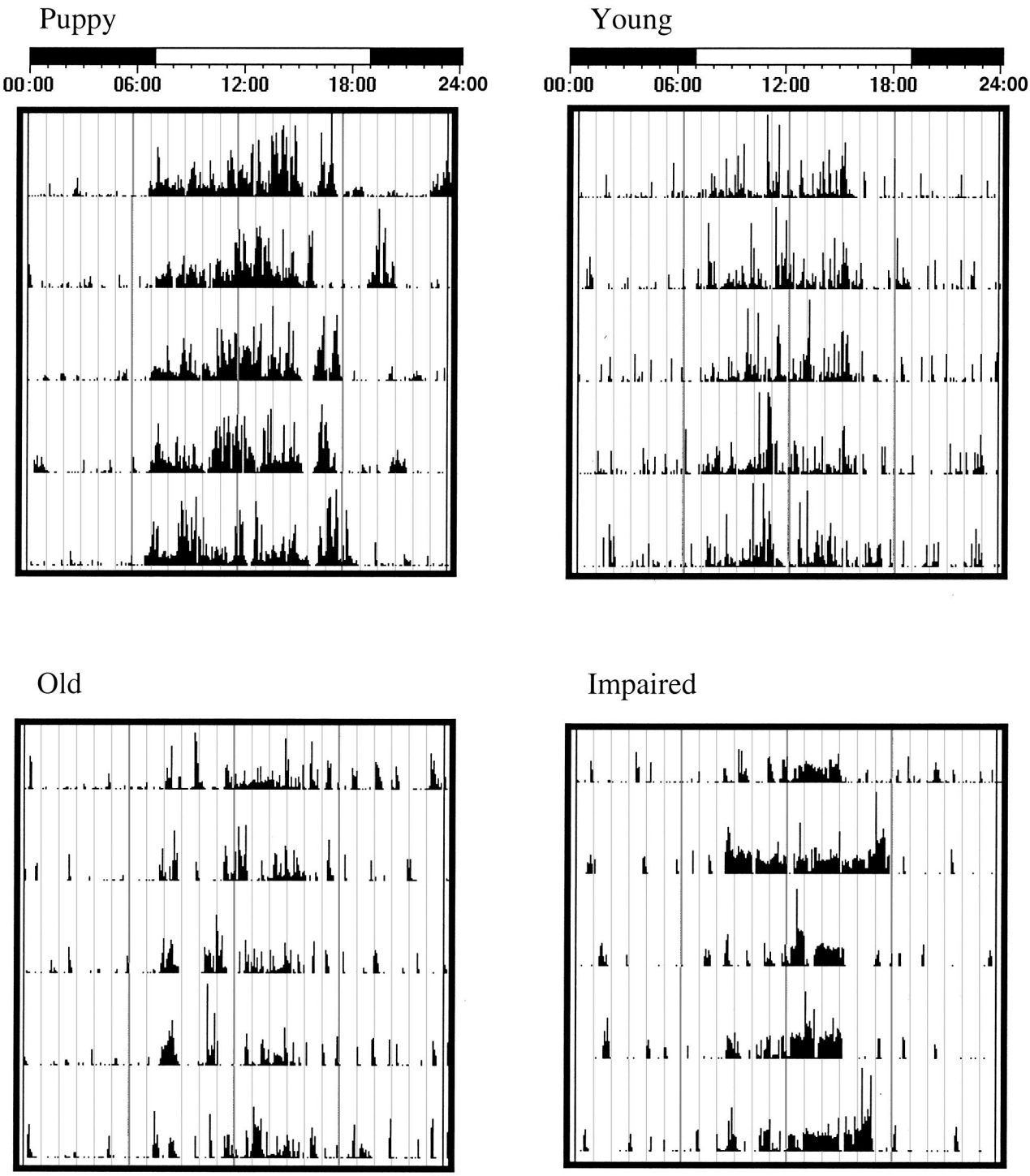


Figure 2. Computer-generated actograms for a representative dog from each group in the indoor-facility dogs. Each actogram plots the activity counts of the dog for each day of recording and the light–dark cycle (Days 1–5, top to bottom in each plot). All dogs exhibit clear activity–rest cycles, with activity being highest during the daytime hours. Differences appear in the time between lights on and onset of activity, the length of the main activity bout, and the number of daytime rest periods.

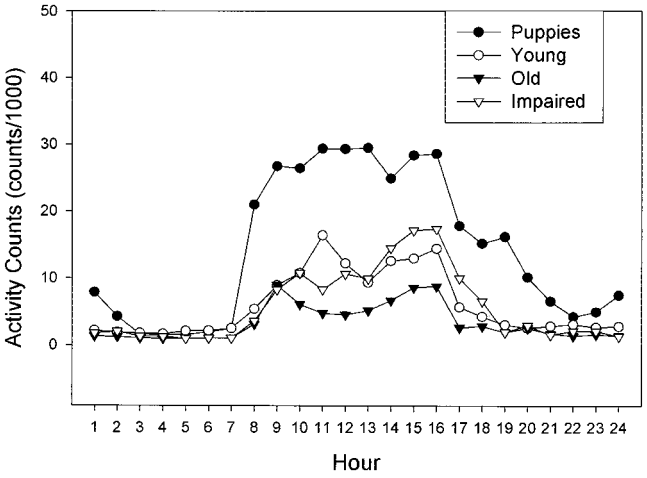


Figure 3. Mean activity count across the 5 days of recording is plotted for each hour of a 24-hr period for the indoor facility dogs: puppies, young, old, and old–impaired. Differences between the groups appear in the pattern of activity. Young dogs are most active in the morning, whereas age-impaired dogs are mainly active in the afternoon. The puppies exhibit high levels of activity during most of the day, whereas the old dogs display low levels of activity throughout the light period.

The length of the main bout of activity was significantly different between the groups, $F(3, 36) = 15.55$, $p < .01$. The puppies ($M = 8.57$, $SEM = 0.47$) and young dogs ($M = 8.71$, $SEM = 0.48$) were active for longer periods of time during the day than both old ($M = 4.51$, $SEM = 0.30$; $ps < .01$) and old–impaired ($M = 5.51$, $SEM = 0.74$; $ps < .01$) dogs.

A significant main effect of group on the number of rest points during the day was obtained, $F(1, 36) = 4.89$, $p < .01$. The old dogs ($M = 2.93$, $SEM = 0.42$) had significantly more rest points during the day than the young dogs ($M = 1.36$, $SEM = 0.25$; $p < .01$) and puppies ($M = 1.42$, $SEM = 0.16$; $p = .02$). The impaired dogs ($M = 1.80$, $SEM = 0.44$) did not differ from any group.

The number of nighttime activity bouts also produced a significant main effect of group, $F(1, 36) = 4.59$, $p < .01$. The puppies ($M = 1.62$, $SEM = 0.12$) had significantly fewer bouts of activity during the night than the young ($M = 4.51$, $SEM = 0.49$; $p < .01$) and old ($M = 4.43$, $SEM = 0.98$; $p = .03$) dogs. Impaired aged dogs ($M = 3.80$, $SEM = 0.77$) did not differ from the other groups.

Light–dark cycle versus constant light conditions. Changing the light–dark cycle to constant light conditions for a period of 5.6 days did not produce notable behavioral changes. Two dogs, 1 young male and 1 old female, exhibited higher levels of activity in constant light conditions. The remaining dogs showed no difference in activity levels in the constant light than in the light–dark condition.

All of the dogs exhibited regular patterns of daily activity during the constant light condition. Initially the patterns were synchronized with the previous light–dark cycle but exhibited a phase delay toward the end of the week (see Figure 4). There were no apparent age differences in the response to constant light conditions. There were no significant differences in the period of the cycle between the light–dark (young, 23.65 ± 0.19; old, 24.01 ± 0.14) and constant light (young, 23.85 ± 0.25; old, 24.13 ± 0.05) conditions, $F(1, 6) = 1.33$, $p = .29$.

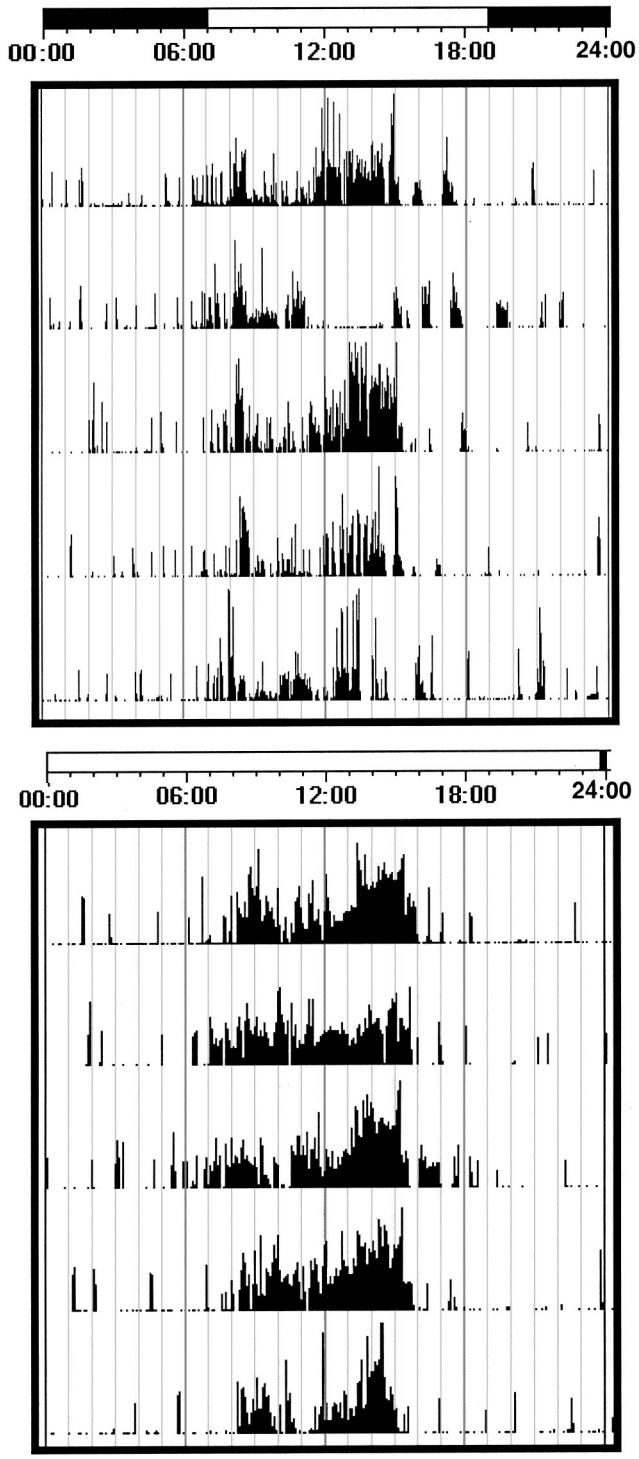


Figure 4. Computer-generated actograms of activity recordings of an indoor-facility dog in the standard light–dark cycle (top) and later in a constant-light situation (bottom). Each actogram plots the activity counts of the dog for each day of recording (Days 1–5, top to bottom in each plot). No differences were evident in the activity rhythm except for the development of a phase delay toward the end of recording in the constant-light situation.

Experiment 2: Activity Rhythms and Age in Beagle Dogs in an Indoor/Outdoor Housing Facility

This study examined differences in activity rhythms in young and aged beagle dogs housed in a facility in which part of the housing cage was indoors and a larger portion was outdoors.

Method

The beagle dogs were born at the facility and consisted of 11 old dogs aged 12–14 years (5 males, 6 females) and 8 young dogs aged 3–4 years (4 male, 4 female). These dogs were housed in natural light in an indoor/outdoor kennels (sunlight intensity is approximately 10,000 lux). The light–dark cycle was determined by the rising and setting of the sun and was approximately 14 hr light:10 hr dark. The dogs were housed either individually or in pairs in kennel buildings with indoor/outdoor runs measuring 6.10 m long × 0.94 m wide. The dog kennels were cleaned between 8 and 10 a.m., and the dogs did not leave the kennel during cleaning. The aged dogs were fed approximately 300 g of Hill's Science Diet Canine Senior Dry Food once a day, with water available ad libitum from a wall spout. The young dogs received Hill's Science Diet Canine Maintenance Dry Food. Working hours of the laboratory personnel were from 8 a.m. to 4 p.m. All dogs underwent clinical examinations for general health prior to the start of any study, and all dogs included in the study were in good health.

Results

Effect of age on levels of activity. The MANOVA revealed that the average total activity was significantly higher in young dogs ($M = 308.43$, $SEM = 25.17$) than old dogs ($M = 159.13$, $SEM = 11.71$), $F(1, 17) = 10.48$, $p < .01$.

For the hour-by-hour analysis, the ANOVA revealed significant main effects of age, $F(1, 17) = 10.06$, $p < .01$; hour, $F(23, 391) = 42.08$, $p < .01$; and a significant Age × Hour interaction, $F(23, 391) = 4.67$, $p < .01$. The one-way ANOVAs for the simple main effects analysis indicated that young dogs were significantly more active than the old dogs at H7–11 ($p < .01$), H15 ($p = .04$), and H21 ($p = .01$; see Figure 5). Actograms are shown in Figure 6.

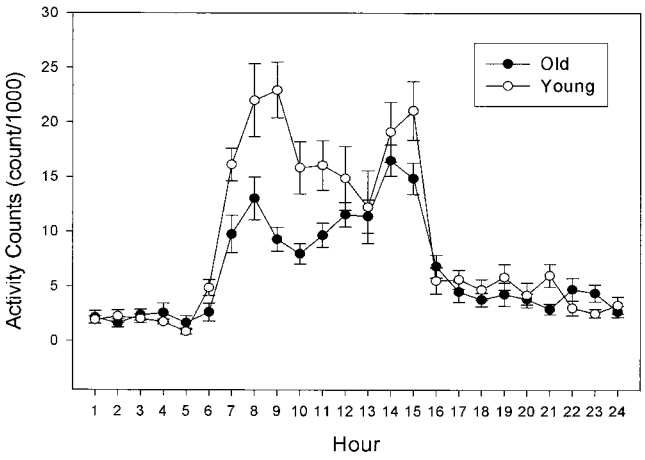


Figure 5. Mean (± *SEM*) activity count across the 5 days of recording is plotted for each hour of a 24-hr period for the indoor/outdoor-facility young and aged dogs. Young dogs were more active than old dogs during most of the daytime hours.

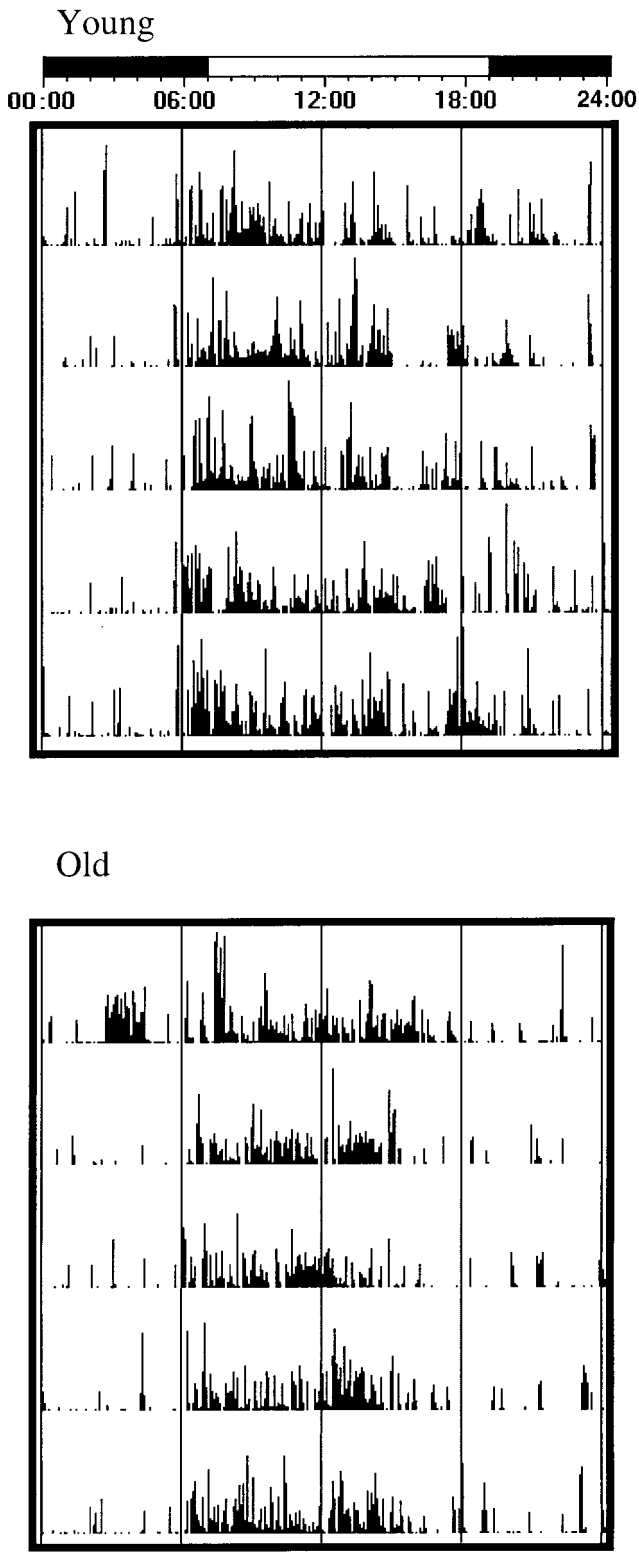


Figure 6. Computer-generated actograms for a representative dog from the young and old age groups in the indoor/outdoor-facility dogs. Each actogram plots the activity counts of the dog for each day of recording and the light–dark cycle (Days 1–5, top to bottom in each plot). All dogs exhibit clear activity–rest cycles, with activity being highest during the daytime hours.

Effect of age on activity onset, length of activity bouts, daytime rest, and nighttime activity. Young (M = 11.08 min, SEM = 5.74) and old (M = 31.75 min, SEM = 9.51) dogs did not significantly differ in the amount of time between lights on (sunrise) and activity onset, $F(1, 17) = 3.22$, $p = .09$, although the average number of minutes was higher in the old-dog group. The length of the main bout of activity did not differ, $F(1, 17) = 0.24$, $p = .63$, between the young (M = 8.86 hr, SEM = 0.61) and old (M = 8.50 hr, SEM = 0.44) dogs.

There were no significant differences, $F(1, 17) = 0.89$, $p = .36$, between the young and old dogs for the number of rest points during the day (young, M = 1.10, SEM = 0.17; old, M = 1.47, SEM = 0.31) or activity bouts during the night, $F(1, 17) = 0.37$, $p = .55$ (young, M = 2.55, SEM = 0.66; old, M = 2.95, SEM = 0.28).

Experiment 3: Comparison of Activity Rhythms in an Indoor Facility and an Indoor/Outdoor Facility in Aged Beagle Dogs

For a more direct comparison of the indoor and indoor/outdoor facilities, we examined the activity cycles of aged dogs originally from a colony where indoor rearing was practiced. One group of dogs was sent to the indoor/outdoor facility and a second group to the entirely indoor facility. This allowed us to compare the effect of facility location and design on activity rhythms in dogs that came from an indoor rearing facility.

Method

Twenty beagle dogs were obtained from a colony that practiced indoor rearing, to directly compare the effects of indoor and outdoor housing so that source effects would be eliminated. Twelve old dogs aged 10–13 years (6 male, 6 female) were transferred to the indoor/outdoor colony, and 8 old dogs aged 9–13 years (2 males, 6 females) were transferred to the entirely indoor facility. At the original facility, the dogs were housed indoors with a 12-hr light–dark. Lights were on from 6 a.m. to 6 p.m. The dogs were transferred to the new facilities at least 1 year prior to the collection of activity-monitoring data.

Results

Effect of location on levels of activity. The results of the MANOVA indicated that the aged dogs housed at the indoor/outdoor facility (M = 240.36, SEM = 29.14) were significantly more active than the aged dogs housed at the indoor facility (M = 136.47, SEM = 11.82), $F(1, 18) = 7.78$, $p = .01$.

The hour-by-hour analysis obtained significant main effects of location, $F(1, 18) = 8.74$, $p < .01$, and hour, $F(23, 414) = 30.97$, $p < .01$. The interaction between location and hour was also significant, $F(23, 414) = 9.91$, $p < .01$. The simple main effects one-way ANOVAs showed that the dogs housed at the indoor/outdoor facility were significantly more active than their counterparts at the indoor facility at H6–8 ($p < .01$), H11–14 ($p < .01$), and H16 ($p < .01$; see Figure 7). Actograms are illustrated in Figure 8.

Effect of location on activity onset, length of activity bouts, daytime rest, and nighttime activity. The amount of time between lights on and activity onset was significantly shorter, $F(1, 18) = 10.41$, $p < .01$, in the dogs housed at the indoor/outdoor facility (M = 19.00, SEM = 4.64) than those at the indoor facility (M = 121.90, SEM = 38.96). The length of the main activity bout was significantly longer, $F(1, 18) = 24.45$, $p < .01$, for the dogs housed at the indoor/outdoor facility (M = 7.46, SEM = 0.47) than for the dogs at the indoor facility (M = 3.99, SEM = 0.49).

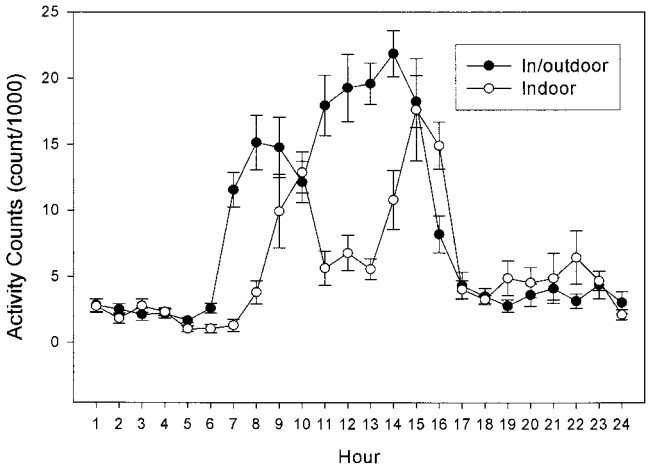


Figure 7. Mean (± *SEM*) activity count across the 5 days of recording is plotted for each hour of a 24-hr period for the dogs at the indoor/outdoor facility and at the indoor facility. The dogs housed partially outdoors exhibited higher levels of activity during most of the daytime hours.

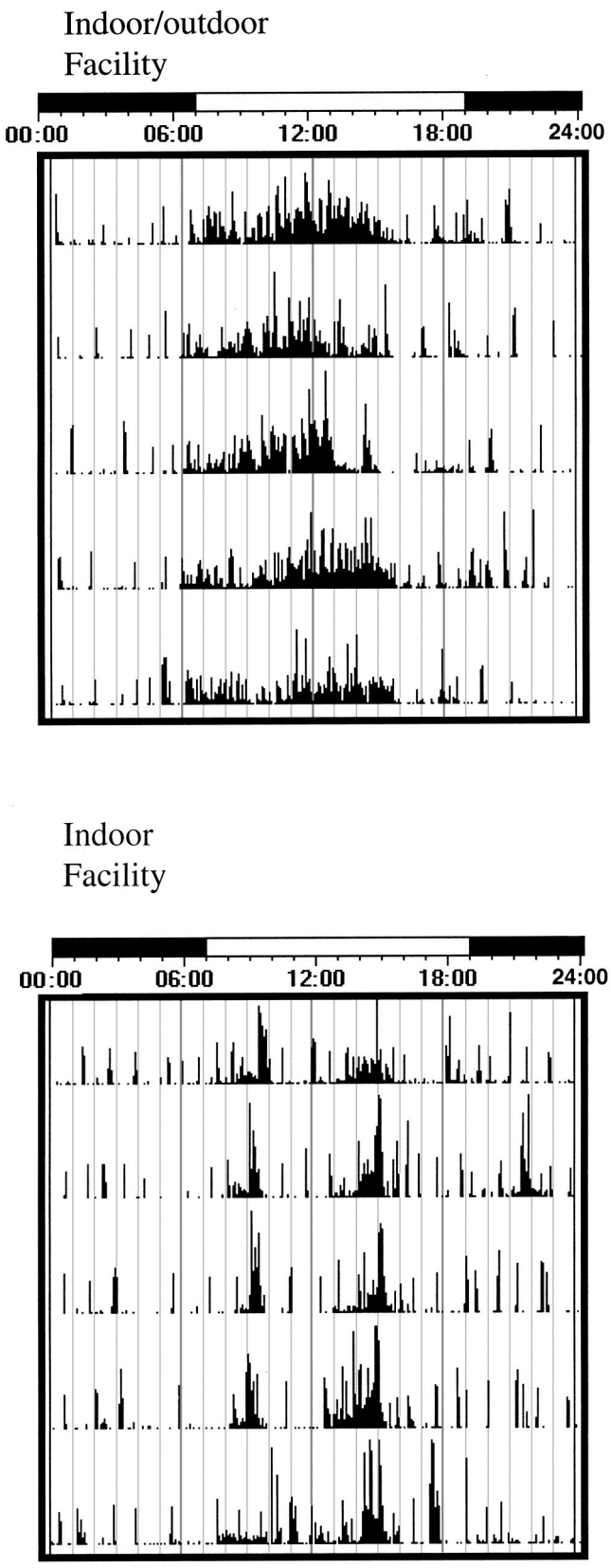
Location had a significant effect on the number of daytime rest periods, $F(1, 18) = 23.12$, $p < .01$, but not on nighttime activity bouts, $F(1, 18) = 2.90$, $p = .11$. The dogs at the indoor facility (M = 2.35, SEM = 0.46) exhibited more rest periods during the day than the dogs at the indoor/outdoor facility (M = 0.43, SEM = 0.12). The dogs at the indoor/outdoor facility (M = 3.20, SEM = 0.28) and at the indoor facility (M = 4.00, SEM = 0.39) did not differ for nighttime activity bouts.

General Discussion

This study demonstrates that beagle dogs exhibit clear activity–rest rhythms, which vary as a function of age, cognitive status, and housing environment. Activity levels were high during the day and low at night. The activity rhythms of the dogs did not merely reflect the presence of exogenous triggers; in some instances dogs became active before the lights came on and before the laboratory staff started work.

Activity Rhythms and Aging

Age-related differences are present in activity rhythms, but their manifestation depends on the housing environment. Experiment 1 demonstrated age differences in the activity–rest cycles in dogs housed in an indoor facility. At the indoor facility, the younger dogs became active earlier in the day and displayed longer, more consolidated bouts of activity than the aged dogs. The results were not replicated in Experiment 2, in which the dogs were housed in an indoor/outdoor environment. In a natural-light situation (i.e., outdoors), the onset of activity and length of time active was not different between young and aged dogs. The differences are probably linked to levels of brightness, with the outdoor environment



providing more intense light. The bright light of the sun seems to be more effective in synchronizing and consolidating the activity cycle than standard indoor lightbulbs. The results of Experiment 3 support this supposition. The dogs transferred to the outdoor facility were active earlier and exhibited more consolidated bouts of activity than their indoor counterparts. The differences between the indoor and outdoor housing situation were consistent with the other two colonies of dogs.

These results therefore suggest that age differences in activity rhythms vary as a function of light intensity. Dogs housed outdoors in natural light conditions showed fewer age differences in features of the activity rhythms than dogs housed indoors. An effect of light intensity is also reported in AD patients. Satlin, Volicer, Ross, Herz, and Campbell (1992) found that higher intensity light is able to ameliorate the alterations in the activity–rest pattern that occur in AD patients. Furthermore, Yamadera et al. (2000) found that bright-light therapy improved the cognitive state of mildly demented AD patients, and Kelly et al. (1997) found that bright light had beneficial effects in normal young men. The most likely explanation for these effects is that higher intensity light is better able to synchronize the activity–rest cycle through the retinohypothalamic tract, which connects the eye to the SCN. Light transmission through the eye and sensitivity of the visual system to light decline with age (Van Someren et al., 1996). In AD patients, degeneration of the optic nerve and retinal ganglion cells has been reported. Thus, entrainment is likely to be hampered by a reduction in perceived environmental light (Van Someren et al., 1996).

Another factor is the type of transition from light to dark between day and night. The natural light–dark cycle of the outdoors has gradual transitions between light and darkness at dawn and dusk. The indoor environment has abrupt transitions between light and dark. Kavanau (Moore-Ede, Sulzman, & Fuller, 1982) found that adding the gradual light–dark transitions to laboratory light–dark cycles increased the strength of entrainment. It is not clear why, but this supports the argument that gradual transitions contributed to the stronger entrainment to the light–dark cycle of the dogs that were housed in the outdoor facility.

At the indoor facility, the aged dogs exhibited significantly more periods of daytime inactivity than the puppies, young dogs, and impaired dogs. This probably reflects an increase in the number of naps during the day. No differences were observed at night, except that the puppies experienced fewer bouts of activity than the other groups. If one dog wakes up and barks during the night, the other dogs will be disturbed because of the housing arrangement, in which all the dogs were in the same area and could hear the other dogs. During the day, a dog taking a nap is not going to affect the other dogs. Thus, the activity cycle seems to be fragmented in the aged dogs, but not the impaired dogs. Reduced fragmentation of the cycle in the impaired dogs could be due to the higher levels of

Figure 8. Computer-generated actograms for a representative dog from each location. Each actogram plots the activity counts of the dog for each day of recording and the light–dark cycle (Days 1–5, top to bottom in each plot). All dogs exhibit clear activity–rest cycles, with activity being highest during the daytime hours. Differences between the locations appear in the time between lights on and onset of activity, the length of the main activity bout, and the number of daytime rest periods.

activity of this group, as activity itself can induce organization of the activity cycle (Hastings, Duffield, Smith, Maywood, & Efling, 1998).

Activity Rhythms and Cognition

Experiment 1 revealed that cognitive status also correlated with the activity–rest rhythm. Cognitively impaired aged dogs were more active than the normal aged dogs, primarily during the afternoon. The impaired aged dogs showed a delay in peak activity compared with the other dogs, similar to the phase delay observed in AD patients (Satlin et al., 1991, 1995). The impaired dogs were also significantly more active than unimpaired dogs as measured by the Actiwatch system in the home cage. We previously reported that cognitively impaired dogs were more active than unimpaired aged dogs in the open-field test (Siwak, Tapp, & Milgram, 2001). Satlin et al. (1991) also found that a subgroup of AD patients, called *pacers*, exhibit higher levels of activity than normal aged individuals and AD nonpacers. The present results parallel those observed in dementia, in which the timing mechanism of demented individuals appears to be compromised.

Cycle disruption in AD patients could be linked to senile plaques and neurofibrillary tangles, which develop in the SCN, the endogenous clock (Swaab et al., 1985; Van Someren, 2000a, 2000b). Age-related neuropathology in the SCN of dogs has not been examined to our knowledge, except for reports of increased reactivity to stress (Reul, Rothuizen, & de Kloet, 1991; Rothuizen, Reul, Rijnberk, Mol, & de Kloet, 1991; Rothuizen et al., 1993). Dogs show neuropathology similar to that of AD patients in other areas of the brain (Head, McCleary, Hahn, Milgram, & Cotman, 2000), suggesting that the SCN in impaired dogs may undergo changes similar to those observed in AD.

Activity Levels

An age-associated decline in motor activity has been reported in several species, including humans (Bassey, 1998; Hillerås, Jorm, Herlitz, & Winbald, 1999; LeWitt, 1988), mice (Dean et al., 1981; Elias, Elias, & Eleftheriou, 1975; Elias & Redgate, 1975; Goodrick, 1975; Ingram, London, Waller, & Reynolds, 1983; Lamberty & Gower, 1990, 1991; Rosenthal & Morley, 1989; Sprott & Eleftheriou, 1974), rats (Dorce & Palmero-Neto, 1994; Goodrick, 1971; Kametani, Osada, & Inoue, 1984), and monkeys (Emborg et al., 1998; Gerhardt et al., 1995). Siwak, Murphey, Muggenburg, and Milgram (2002) demonstrated an age-related decrement in locomotor activity in dogs using an observational test of the home cage. The present data, based on the Actiwatch, support this finding, indicating that young dogs are more active than old dogs. The differences in activity were only observed during the daytime hours, not at night.

The size of the housing area and type of facility (indoor vs. partially outdoor) influenced the level of activity of the dogs. The housing cages were 1.31 m^2 at the indoor facility and 5.73 m^2 at the indoor/outdoor. The smaller housing area limits the movement of the dogs compared with the larger kennel runs. Dogs housed in the larger runs, which were partially outdoors, displayed higher levels of activity compared with the dogs in the smaller, indoor areas. Tobler and Sigg (1986) reported that motor activity of dogs is influenced by the type of housing enclosure, with larger housing areas leading to reduced activity. The larger housing enclosures in that study, however, were indoors and isolated from laboratory activities. In the present study, the larger housing areas were partially outdoors, exposing the dogs to a variety of stimuli not present in an indoor facility. The dogs housed outdoors were also exposed to a longer light period, perhaps allowing them to be active for a longer period of time. This indicates that both the size of the housing area and exposure to the outdoors affect the motor activity of dogs.

The puppies at the indoor facility were housed in larger enclosures and displayed higher levels of activity than all of the other groups of dogs. During the morning hours of 9–11 a.m., however, all of the dogs were placed into these conditions during cleaning. The dogs were placed in a large room in groups while their housing areas were washed. This equates the conditions of all of the groups, and the younger dogs, both puppies and the young dog group, were more active than the aged groups. Thus, although the activity levels of the puppies may have been elevated because of their differential housing condition, the age difference was still apparent when all dogs were placed in the same conditions.

Activity Rhythms in Dogs

Dogs are capable of adapting their activity rhythms to their living environment. Feral dogs show higher levels of activity at night than during the day (Scott & Causey, 1973). Pet owners frequently report sleep disturbances in their dogs, but these data are based on the perception of the owner and have not been assessed experimentally in controlled environmental settings. The activity–rest cycle of dogs is probably adaptable to their living conditions, and differences are likely among feral dogs, laboratory dogs, and pet dogs. Feral dogs are active when it is safe, laboratory dogs are influenced by the constant routine and daily activity of the facility, and the activity of pet dogs will largely depend on their owners' schedules.

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