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In this study we recorded locomotor activity of two inbred of mice (B6 and C) in two photoperiod conditions (LD 12:12 and DD) to characterize behavioural parameters of the endogenous rhythms of locomotor activity with particular attention to the ultradian rhythms. Literature reveals discordant data for these parameters, both for animals belonging to the same strain and to those in the same laboratory or monitored in the same conditions. Our results show that C strain has a shorter and unstable endogenous circadian period, while B6 strain has a longer and stable endogenous rhythm. In our study, B6 showed a longer and stable period than C, so we can confirm the presence of a genetic component underlying this trait. Ultradian rhythms are expressed independently of either the photoperiod or the circadian rhythm. There are no strain-dependent differences in the periods of 12, 8 and 4 h. The situation was different for the length of the ultradian period in the range 1–8 h and for the weighted power in the ranges 480–300 and 300–100 min, for which there were differences between photoperiods and strains.

Keywords: circadian rhythms; ultradian rhythms; locomotory activity; inbred strains; radar doppler

Introduction

All living organisms have "biological clocks" that regulate physiological and behavioural functions by means of rhythms similar to the geophysical rhythms of the earth; these rhythms have an evident adaptive value (Sharma 2003). In mammals, the pacemaker neurons that generate the endogenous circadian rhythm are located in the suprachiasmatic nucleus (SCN), which receives information from the retina. Underlying these oscillations are molecular clocks able to maintain a rhythm even in the absence of external signals (Aschoff and Wever 1965; Daan and Pittendrigh 1976; Aschoff 1981). Various genes have been implicated in the control of the molecular clock and of the parameters expressed by the biological clock, e.g. the period (Mayeda and Hofstetter 1999; Toth and Williams 1999).

Inbred strains of mice, like knock-out mice, are a powerful tool in behavioural research, since they give insights into the role of specific genes in behaviour

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(Sprott and Staats 1979; Goldowitz et al. 1992). Inbred strains differ in the expression of the endogenous circadian rhythm and amplitude of daily locomotor activity, as well as the daily level of activity; hence these parameters are strain-dependent (Possidente and Stephan 1988; Schwartz and Zimmerman 1990; Hofstetter et al. 1995; Mayeda et al. 1996). Nevertheless, a careful reading of the literature reveals discordant data for these parameters, both for animals belonging to the same strain for to those in the same laboratory or monitored under the same conditions (Table 1).

Most studies, however, have concentrated on circadian rhythms, giving little attention to ultradian rhythms. Short rhythms differ from circadian rhythms in that they do not correspond to any environmental periodicity, even though they frequently show very precise oscillations with very large amplitude. Therefore, they should be considered an important factor in the temporal organization of behaviour (Daan and Aschoff 1981).

Several authors have reported ultradian rhythms in mammal locomotor activity (Honma and Hiroshige 1978a, b, c; Beau 1991, 1992; Gerkema et al. 1993; Poon et al. 1997; van Oort et al. 2005; van der Veen et al. 2006). Some very detailed studies on different rat strains have reported ultradian rhythms with periods of 12, 6, 4 and 4.8 hours, especially when the circadian rhythm was less preponderant, as in conditions of continuous illumination (Büttner and Wollnik 1984; Wollnik and Dohler 1986; Wollnik et al. 1987). Other observations on rats and mice monitored in different photoperiod conditions have confirmed the presence of ultradian rhythms with particularly significant periods of eight and six hours (Ticher and Ashkenazi 1995). More recently, Ashkenazi's group replicated those results, reporting 12- and 8-hour ultradian rhythms in the C57 and Balb strains, as well as a 4-hour period in the latter strain (Peleg et al. 2001).

The study of ultradian rhythms is particularly difficult, since it is necessary to identify short rhythms that have wide variability by means of mathematical algorithms and the monitoring system must not create masking effects or influence the normal behaviour of the animal. For example, a commonly used instrument, rotating drums, tends to affect the activity patterns of rodents and must be considered an active recording system that masks the endogenous structure of the rhythms expressed by the animal, especially the ultradian rhythm (Ticher and Ashkenazi 1995).

The aim of the present study was to characterize behavioural parameters of the endogenous rhythms of locomotor activity in two inbred strains of mice, with particular attention being paid to the ultradian rhythms.

Materials and methods

Subjects

We used 8-week-old male mice belonging to the BALB/c strain (C) $n = 12$ and the C57BL/6 strain (B6) $n = 12$ (Charles Rivers Laboratory; Calco, Como, Italy). The mice were housed individually with food and water *ad libitum*, L:D 12:12 (lights on 8 – 20), temperature of 21 $\pm$ 1°C and humidity of 55 $\pm$ 5%.

Experimental procedure

The mice were housed individually in 369 $\times$ 156 $\times$ 132 (h) mm cages. After three days, we began the 28-day period of radar-recording: the first week in LD 12:12, the

Table 1. Studies on rodent activity patterns show different results.

(tau in hours)	Photoperiod	Device	Lab.	Ref.
CIRCADIAN PERIOD				
C (23.40)	free run, m.i.	m.i.	m.i.	Haus et al. 1967
C (22.70)	DD (red light)	Running-wheel	m.i.	Possidente and Hegmann 1982
B6 (C57BL/6J – 23.59)	DD (0 lux)	Running-wheel	m.i.	Ebihara et al. 1978
B6 (C57BL/10Sn – 23.90)	DD (red light)	Running-wheel	m.i.	Possidente and Hegmann 1982
B6 (C57BL/10Sn – 23.47)	DD (0 lux)	Running-wheel	m.i.	Ebihara et al. 1978
B6 (23.28)	free-run, m.i.	Running-wheel	S.L.A.C	Ebihara et al. 1988
B6 (C57BL/6J – 23.52)	DD (red light 0.2 lux)	Running-wheel	m.i.	Abe et al. 1989
B6 (23.92)	DD	Infrared-beam*	JAX	Mayeda and Hofstetter 1999
B6 > C (23.73–22.90)	DD	Running-wheel	m.i.	Possidente and Stephan 1988
B6 > C (24.05–23.98)	**LD 12:12**	**Radar**	**C.R.L.**	**This study**
B6 > C (23.77–22.94)	DD	Running-wheel	JAX	Schwartz and Zimmerman 1990
B6 > C (23.64–22.80)	DD	Running-wheel	JAX	Shimomura et al. 2001
B6 > C (23.88–22.98)	**DD**	**Radar**	**C.R.L.**	**This study**
AMPLITUDE				
C > B6	**LD 12:12**	**Radar**	**C.R.L.**	**This study**
C > B6	DD	Ir actograph	C.R.L.	Beau 1991, 1992
B6 > C	DD	Running-wheel	JAX	Shimomura et al. 2001
C > B6	**DD**	**Radar**	**C.R.L.**	**This study**
ACTIVITY				
C > B6	LD 12:12	Ir actograph	C.R.L.	Beau 1991, 1992
C > B6	LD 12:12	Infrared-beam†	I.C.	Kopp et al. 1998
B6 > C	LD 12:12	Infrared-beam*	H.O.	Rogers et al. 1999
B6 > C	LD 12:12	Telemetry	JAX	Toth and Williams 1999
C > B6	LD 12:12	Infrared-beam*	JAX	Tang et al. 2002
C > B6	**LD 12:12**	**Radar**	**C.R.L.**	**This study**
B6 > C	DD	Running-wheel	JAX	Shimomura et al. 2001
C > B6	**DD**	**Radar**	**C.R.L.**	**This study**

†Transitions (an infrared photocell detect transition between two boxes – not continuous detection of the movement); *Line (a bank of horizontal infrared photocells sensor – continuous detection of the movement); m.i. – missed information in original journal paper; C.R.L. – Charles River Laboratory; JAX – Jackson Laboratory; I.C. – IFFE CREDO (France); H.O. – Harlan-Olac (United Kingdom); S.L.A.C. – Shizuoka Laboratory Animal Center.

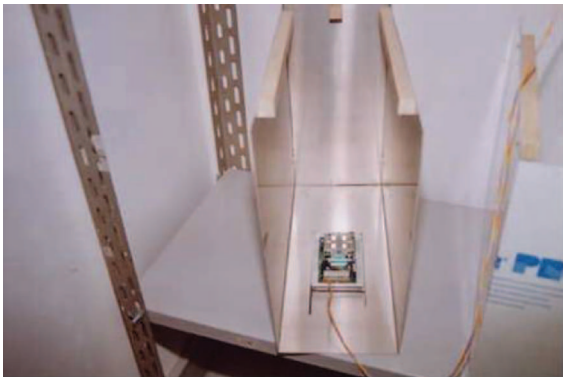

Figure 1. One of the 12 elements of the monitoring system.

next three weeks in DD. For the behavioural analyses, we only considered the 7 days in LD 12:12 and the last 7 days in DD (the 2 central weeks were considered as habituation and thus excluded). The recordings were carried out in a sound-proof and air-conditioned room with controlled incandescent lighting (light = $\sim$150 lux). In DD we used red dim (light $<$0.5 lux) only during the cleaning.

Radar apparatus for the recording of locomotor activity

The apparatus used to monitor the mice was a custom-built system named VIVARD-12 (Pasquali et al. 2006), consisting of 12 microwave radar devices based on the Doppler effect, operating at the frequency of 9.9 GHz (Mw-12, Lince Italia Srl). All the radar devices were connected to a computer via a digital I/O board. A program written in C language (written by Micaloni, Pasquali, and Renzi) continually read the channels of the I/O board, so that the computer acted as a data logger. Various parameters could be set via the program, e.g. duration of the experiment (minutes or days) and collection interval of the given datum (seconds or minutes). The following controls were carried out before the recordings were begun: (a) interference between adjacent radars, (b) the same measurements by all the radar devices, (c) temporal stability of the settings. All the radar devices were set up with the aid of a mechanical object with standardized movement.

Data analysis

All time series were smoothed (three-point moving average) and the linear trend was removed before analyses. The treated series were then analysed with Discrete Fourier Transform (DFT) to obtain information in the domain of frequencies. The output of the DFT analysis was initially analysed with the Kolmogorov–Smirnov test for comparison with a random distribution of the peaks. For series significantly different from a random distribution (all of them), only the peaks with power greater than 2.88 standard deviations from the mean were subsequently considered significant ($p < 0.01$). To estimate the circadian period, we analysed the data with the periodogram of Sokolove and Bushnell (1978) (Wintau program written by Refinetti), testing the period 20–26 hours.

The amplitudes of the circadian and ultradian periods were defined in terms of the spectral power of the peaks resulting from the spectral analysis (Low-Zeddies and Takahashi 2001). We considered different measures of spectral power: maximum value for a single peak and weighted mean for a range. The maximum values were considered for the periods of 24, 12, 8 and 4 h, while the total weighted mean power was considered for the time bands of 480–300 min and 300–100 min.

The data for photoperiod (LD 12:12 and DD) and strain (B6 and C) were analysed by repeated measures ANOVA. When appropriate, we used the post-hoc Fisher test. The level of statistical significance was $p < 0.05$.

Results

The mean spectra of the two strains showed strong circadian rhythms of activity and different ultradian peaks (Figure 1). We further analysed the data to characterize the locomotor activity of the C and B6 strains, focusing on four general parameters: number of movements (activity), circadian period (period), amplitude of the circadian rhythm (amplitude) and amplitude of different ultradian bands (in the range 12–1 h).

Locomotor activity

The activity level of each animal was determined as the number of signals counted by the software. Figure 2a shows the distribution of this parameter in each strain. In general, C was more active than B6 (Table 2). ANOVA revealed an effect only for Strain [$F(1, 22) = 25.67$, $p < 0.001$], C mice were more active than B6 either in LD that in DD.

Circadian period and amplitude

The mean period in the two strains was: 24.05 h in LD and 23.88 h in DD for B6; 23.98 h in LD and 22.98 h in DD for C. There were significant differences between the two strains [$F(1, 22) = 21.97$, $p < 0.001$] and between the photoperiods [$F(1, 22) = 25.28$, $p < 0.001$]; the interaction was also significant [$F(1, 22) = 12.89$, $p < 0.001$] (Figure 3b). The post-hoc analysis did not show significant differences between LD and DD for B6, whereas the differences were significant in C ($p < 0.0001$). Moreover, the mean period in free-running (DD) was significantly different between the two strains ($p < 0.0001$) (Figure 3b).

The amplitude of the circadian rhythm reflected the results observed for the activity levels (Figure 3c). The C strain had a larger amplitude than B6 in both LD and DD [$F(1, 22) = 102.62$, $p < 0.001$], and a significant difference was also observed for photoperiod of LD and DD in each of the strains [$F(1, 22) = 29.33$, $p < 0.001$] (Fig. 3c).

Ultradian rhythms

The spectra obtained by DFT analysis showed that all the animals had different ultradian rhythms of locomotor activity in a range 100–720 minutes. We concentrated on the periods 12, 8 and 4 h (for these periodicities, we considered the maximum spectral power of the peaks at 720, 480 and 240 min – P12, P8, P4). For periodicities

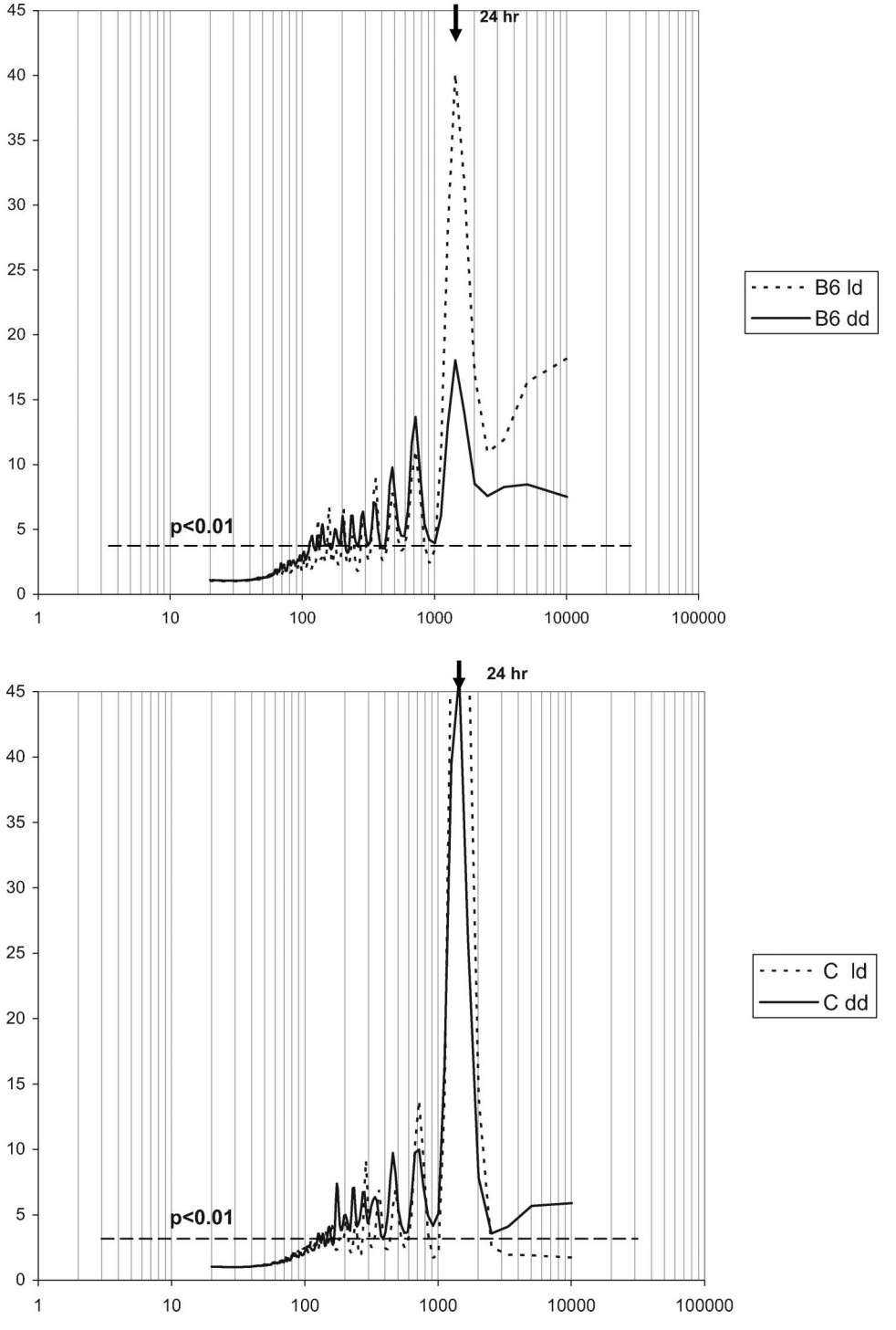

Figure 2. Power spectra of C57 (above) and BALB (below). Power values on the *y*-axis; *x*-axis is periods (in minutes) in logarithmic scale.

Table 2. Principal strain-dependent parameters (mean ± SD).

	Activity (total × week)		Tau circadian (hours)		Amplitude circadian (power)	
C (LD)	**136056**	42425	**23.98**	0.06	**75.73**	13.94
C (DD)	**116343**	61987	**22.98**	0.28	**46.17**	18.21
B6 (LD)	**50540**	28110	**24.05**	0.31	**40.14**	12.91
B6 (DD)	**70429**	33465	**23.88**	0.64	**18.04**	9.53

Table 3. Comparisons of photoperiods and strains.

LD		DD
PHOTOPERIOD		
C > B6	activity	C > B6
C = B6	tau 24	C > B6
C > B6	P 24	C > B6
C = B6	P 12	C = B6
C = B6	P 8	C = B6
C = B6	P 4	C = B6
C = B6	tau 1–8	C = B6
C = B6	PP 480–300	C > B6
C = B6	PP 300–100	C < B6
C		B6
STRAIN		
LD = DD	activity	LD = DD
LD > DD	tau 24	LD = DD
LD > DD	P 24	LD > DD
LD = DD	P 12	LD = DD
LD = DD	P 8	LD = DD
LD = DD	P 4	LD = DD
LD < DD	tau 1–8	LD = DD
LD < DD	PP 480–300	LD = DD
LD = DD	PP 300–100	LD < DD

less than 4 h, we had difficulty identifying a precise reference period; therefore, we considered two temporal bands in which the ultradian rhythms were concentrated, 480–300 min and 300–100 min (PP 480–300, PP 300–100), for which we considered the mean amplitude (i.e. the weighted mean spectral power of the two bands).

In the spectral analyses, all the mice showed a highly significant peak at 12, 8 and 4 h in both LD and DD (Figure 2). The statistical analysis did not show any effect on the amplitude values; therefore, the powers were equal between strains and between photoperiods.

Although not adequate for the purpose, we used Wintau to calculate the most significant length of the period in the range 1–8 h (tau 1–8). The period in DD was generally longer than in LD, but the difference was significant only for C. ANOVA revealed significance for photoperiod [$F(1, 22) = 9.44$, $p < 0.01$], but there were no differences between strains (Figure 4).

A similar pattern was found for the weighted power in the range 480–300 min. ANOVA revealed a significant Strain*Photoperiod interaction [$F(1, 22) = 5.63$,

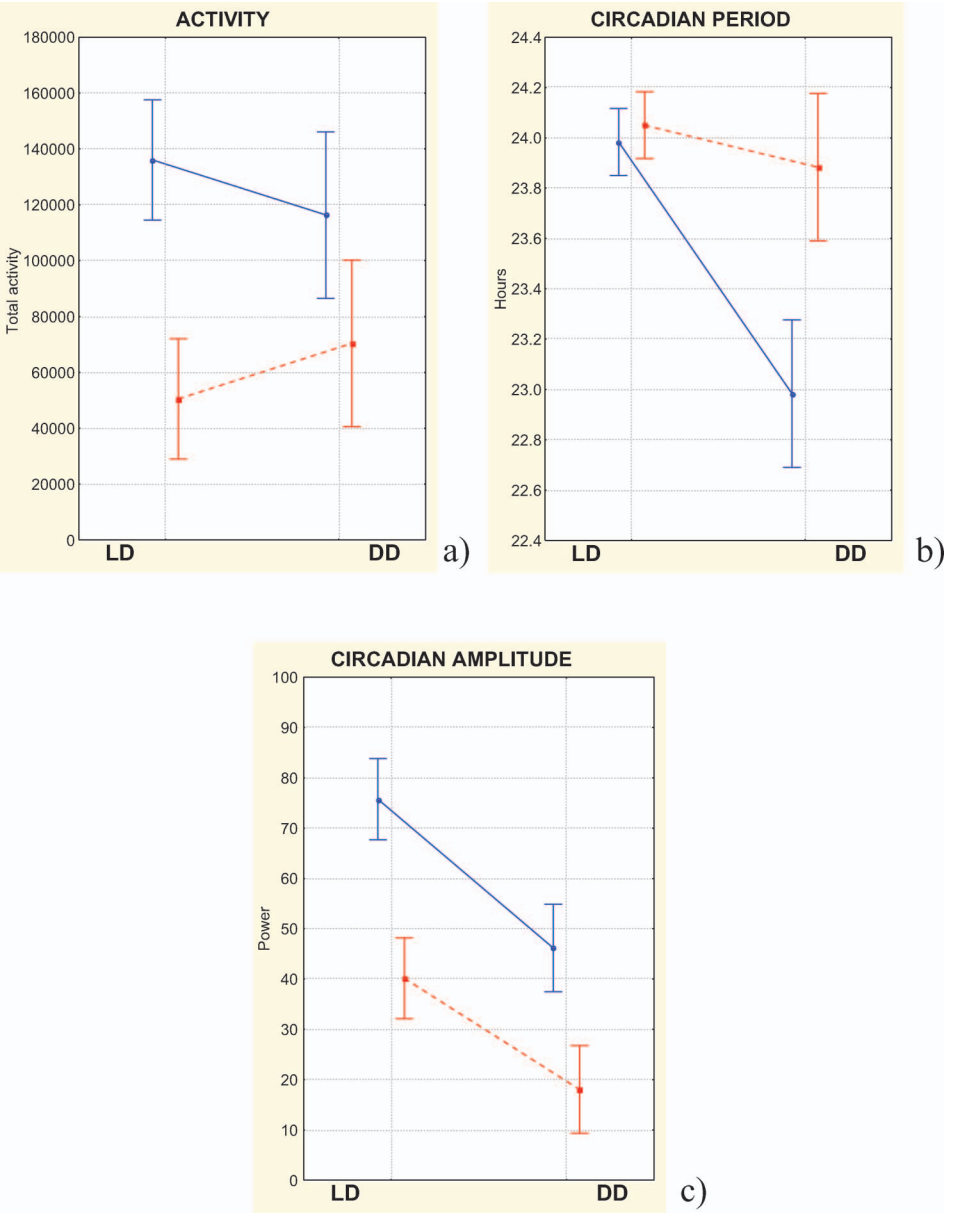

Figure 3. Distribution of three strain-dependent parameters; continuous line C, dashed line B6.

$p < 0.05$], with a significantly higher power for C than for B6 in DD ($p < 0.01$) and a difference between LD and DD for C ($p < 0.05$) (Figure 4).

For the range 300–100 min (which always presented significant peaks), we observed an effect of strain [F (1, 22) = 4.37, $p < 0.05$] and photoperiod [F (1, 22) = 11.25, $p < 0.01$]. In this case, B6 showed a significant difference between LD and DD ($p < 0.01$), as well as a higher power than C in DD ($p < 0.05$) (Figure 4).

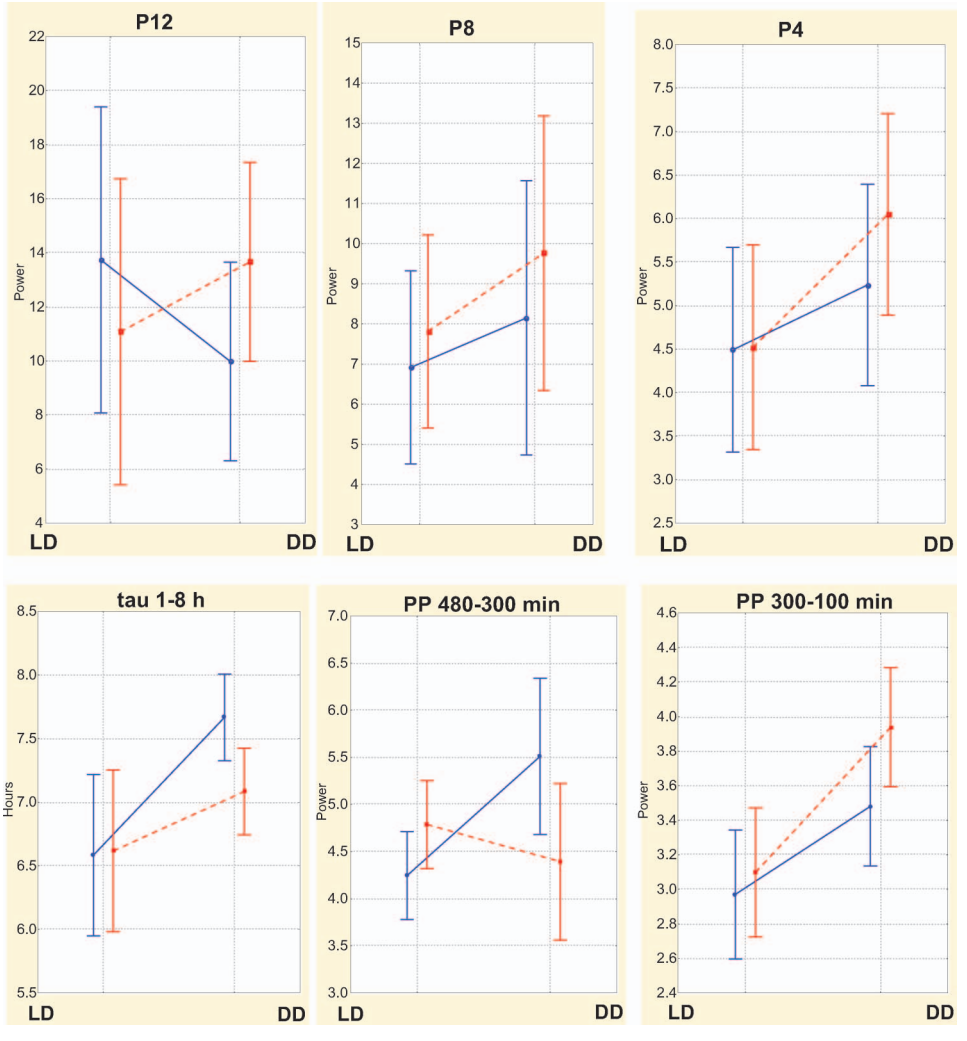

Figure 4. Distribution of the ultradian parameters; continuous line C, dashed line B6.

Discussion

In this study, we recorded the locomotor activity of two inbred strains of mice (B6 and C) in two photoperiod conditions (LD 12:12 and DD). Our aim was to precisely characterize the ultradian parameters of activity in C and B6. The results showed, in both strains, a compound structure of the locomotor activity, with the presence of different ultradian rhythms (but not all significant).

These two inbred strains present well documented, genetically based differences in several behavioural parameters, including very different lengths of the circadian period of locomotor activity. Previous studies have described the C strain as having a shorter and more unstable endogenous circadian period. In other words, it is strongly influenced by variations of the environmental conditions; in fact, the period varied significantly from 24 hours in DD. The B6 strain has a longer and more stable

endogenous rhythm, not particularly influenced by external environmental conditions; in fact, the period in DD was very similar to that in LD. Also in our study, B6 showed a longer and more stable period than C. Since our data agree perfectly with the preceding literature, we can confirm the presence of a genetic component underlying this trait (Mayeda and Hofstetter 1999).

However, the situation is different regarding the level of activity and the amplitude of the circadian rhythm, since the literature contains conflicting data for animals belonging to the same strain, to the same laboratory and monitored with the same instrumentation (Table 1). Indeed, our data disagree with some studies and agree with others (Table 1). In general, they are in line with data deriving from passive monitoring systems (Beau 1991, 1992; Kopp et al. 1998; Tang et al. 2002), i.e. the ones we believe should be considered most appropriate (for the reasons set out in the Introduction). A final note concerning the amplitude: in both strains, the power in DD was much less than in LD.

We consider the correspondence of our data with those in the literature a further validation of our monitoring system, over and above our specific study in this regard (Pasquali and Renzi 2005; Pasquali et al. 2006). The concordance of our results with the literature on circadian rhythms assures us about the ''goodness'' of the data.

As reported in the Results, the spectral analysis revealed a clear ultradian rhythmicity with various peaks between 1 and 12 h in both LD and DD, periodicities that were highly significant. Although some differences were observed, we can conclude (at least until further replications are carried out) that there are no strain-dependent differences in the various parameters of ultradian rhythmicity considered in this study. In particular, the periods of 12, 8 and 4 h showed the same power in both strains and in both photoperiod conditions. The situation was different for the length of the ultradian period in the range 1–8 h and for the weighted power in the ranges 480–300 and 300–100 min, for which there were differences between photoperiods and strains. In contrast to the results of Ticher and Ashkenazi (1995), we observed a 4-h period in all the mice, without a strain-dependent difference.

As demonstrated by this study, the ultradian rhythms are expressed independently of either the photoperiod or the circadian rhythm. Although more visible in DD, they are still expressed in LD and with a similar amplitude. In the literature, they are often reported in DD conditions or with light–dark cycles that are different from LD 12:12. This is probably because the statistical-mathematical algorithms manage to reveal them more easily when there is a reduction of the amplitude of the circadian period. Therefore, it would be interesting to study this rhythmicity using different photoperiods.

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