

Evidence for Two Asynchronous Circadian Systems of Emotionality: Theoretical Aspects in Comparative Psychology

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ABSTRACT. This theoretical article is devoted to the chronobiological and chronopsychological foundations of emotion. Circadian fluctuations of experimentally induced emotionality have been reported from murine models (Poirel, 1982). Further research into rhythmometric investigations revealed that the temporal organization of emotional life expressed two oscillatory circadian systems. The circadian fluctuations that were rhythmometrically detected and compared expressed a noticeable phase concordance between the temporal periodicities related to vigilance and to indicators of basic emotionality. In contrast, the rhythmometric data for behavioral responses of emotionality displayed a marked phase displacement of the psychological circadian patterns and tended to manifest a functional dissociation between behavioral and visceral modalities of reactional events.

Such experiments provide a quantitative approach for a better functional understanding of cerebral mechanisms regulating the time of the occurrence of stress-related events and make it possible to take into consideration the development of new heuristic concepts in psychology and comparative chronobiology.

More specifically, the chronopsychological organization of emotional life with its two asynchronous components, as well as the multimodal oscillations that we have proposed, opens the discussion to new concepts of order by fluctuation and the consideration of chaotic systems governing psychological events of emotionality.

THE CURRENT THEORETICAL RESEARCH, devoted to a conceivable circadian organization of emotional life, relates to particular problems regarding the biological and psychological foundations of emotion and to innovative concepts of comparative chronopsychology.

The murine ethological studies that are reported and their theoretical implications for general psychology provide some heuristic approaches for research on circadian rhythms of emotionality and may provide one set of reference standards for similar work in the field of comparative psychophysiology. In this respect, “the fact that the expression of emotion seems to be a special ability of

mammals" (Shepherd, 1988) leads us to consider that we should give preference to approaching such circadian regulations in superior vertebrates whose development of nervous tissue (cerebrospinal system and autonomic nervous system) makes it possible to discern certain explicit behavioral reactions such as bodily processes and certain implicit physiological reactions such as visceral processes, since the first studies made by Charles Darwin (1872).

Taking for granted that emotional activity represents a very complex psychosomatic function involving widespread visceral and bodily changes, we have compared, over a 24-hr span, different physiological and behavioral variables serving as emotional or stress-related indicators that are functionally dependent on subcortical and cortical integration.

Experimental Studies in Behavioral Chronobiology

The specific procedures involving the exploration of circadian rhythms of experimentally induced emotionality in mice were described in previous studies (Poirel, 1975, 1988). For the behavioral chronobiology investigations, the subjects were female Swiss/Albino (Rb) mice, approximately 4 weeks old at the beginning of the experiments and in the same anestrus stage, as determined by cytologic examination of vaginal tissue. They were kept one pair per cage to control for apparent group effects upon organization of behavioral rhythms (Poirel, cited in Brown & Graeber, 1982). After weaning, the mice were separated and reared in controlled environmental chambers with photoperiodicity regimens corresponding to a light/darkness: LD 12:12 cycle.

During the observation circadian times, the animals were studied individually in an openfield situation for 30 min under standardized conditions (Walsh & Cummins, 1976). Frequencies of defecations and micturitions were recorded and used as neurovisceral indicators of basic emotionality (Broadhurst, 1958; Poirel, 1974; Willingham, 1956); using the syntactical rules of description defined by Golani and Fentress (1985), the number of uninterrupted bouts of face grooming was recorded, and those behavioral responses, having been observed in stressful situations (Fentress & Stilwell, 1973), were used as psychological indicators of more corticalized integration of stress-related events (Colbern & Gipsen, 1988; Gellhorn, 1968; Poirel, 1988). At the same time that the experimental ethological observations were being made, the level of vigilance was analyzed on the basis

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of polygraphic recordings that have been classically related to states of slow-wave sleep or cortical arousal (Poirel, 1975, 1991). Data were gathered across the experimental group every 4 hr, over a 24-hr span at 1600 (t_1), 2000 (t_2), 2400 (t_3), 0400 (t_4), 0800 (t_5), and 1200 hr (t_6).

The observation sequences for each animal constituted a "fixed random" program (Fisher & Yates, 1963). That random rotation design allowed us to avoid any aftereffects from successive direct observations or from the introduction of an artificial 4-hr period (for specific details, see Naitoh, 1982; Sechter & Poirel, 1985). We thus had six reference times per 24 hr for determining individual "macroscopic temporal patterns" of specific reactional events.

On the basis of biometric comparisons, such experimental studies involving several psychophysiological variables indicate that mice tend to exhibit temporal variations of basic emotional activity, which tend to fluctuate in close correspondence with vigilance level. Such psychophysiological rhythms manifest circadian fluctuations of central activation (Poirel, 1974, 1982), the peak of which occurs in the second part of the dark span (scotofraction). In contrast, such data suggest that experimental subjects do not exhibit similar circadian fluctuations of behavioral emotional reactivity, the highest of which occurs toward the end of the light span (photofraction).

Taken together, such statistically demonstrated 24-hr fluctuations allow (a) the hypothesis that such psychophysiological variations could respond to circadian processes, (b) detection of the temporal structure of this type of cerebral integration, and (c) a possible predictive model for chronopsychological studies of emotionality.

Table 1 includes a summary of one chronobiological study (Poirel, 1974, 1991) regarding the circadian fluctuations of (a) neurovisceral responses, (i.e., defecation and micturition reactional activities), (b) behavioral responses (i.e., derived activities such as stress-related grooming events), and (c) states of vigilance.

Single Cosinor Model and Behavioral Chronobiology

Reflecting the macroscopic approach to possible circadian* fluctuations of emotionality (see Table 1), conventional statistic methods (Halberg, 1953) were applied to the data to compare possible differences between the reference times (i.e., the clock hour; see Poirel, 1975, after Siegel, 1956).

However, biometric studies do not yield parameter values for any periodicities. Consequently, rhythmometric analyses with inferential statistical methods must be used for estimating and comparing circadian parameters and for determining the temporal structure of physiological and psychological functions. In

*Franz Halberg coined the universally recognized term *circadian* (*circa*, about, approximately, and *dies*, day or 24 hr) in scientific research to characterize rhythms whose period corresponds to 24 ± 04 hr.

TABLE 1
Distribution of Reactional Events and Variation of
Vigilance Levels Over a 24-hr Period

Variable	Observation time (clock hr)							<i>p</i> ^a
	<i>N</i>	<i>t</i> ₁	<i>t</i> ₂	<i>t</i> ₃	<i>t</i> ₄	<i>t</i> ₅	<i>t</i> ₆	
Neurovisceral responses								
Micturition	18	7	10	23	34	13	11	< .05
Defecation	18	63	71	143	181	135	75	< .01
Behavioral responses								
Grooming	18	147	163	139	109	105	98	< .01
Vigilance levels								
Cortical arousal ^b	20	7	5	51	53	46	24	< .001

Note. Mice were synchronized to a photoperiodicity regimen of LD 12:12, light between 0800 and 2000 hr, darkness between 2000 and 0800 hr.

^aNonparametric biometric test of Friedman (Siegel, 1956) permitting the validation of possible differences between the six reference times. ^bAccording to the percentage scored for cortical states of slow-wave sleep (Poirel, 1991).

effect, the classical biometry procedures referring to simple descriptive chronograms (the simple plot of the measurements as a function of time) are insufficient to demonstrate the existence of rhythmometric entities. In that respect, physiological and behavioral time series must be analyzed at a “microscopic level of resolution” (Halberg, 1966, 1969) involving an “approach for objectively resolving quantitative temporal characteristics in biological data (e.g., by testing the fit of mathematical models to time series and estimating parameters of fitted models).” In that heuristic context, the rhythmometry analyses used the cosinor methodology introduced by Halberg in 1966 (“the name ‘cosinor’ was derived from cosine–vector to emphasize the vectorial concept of a rhythm’s acrophase and amplitude”). In that respect, physiological and behavioral rhythms can be described as time variations corresponding to the following cosine model function expressed by the paradigmatic equation: $y = M + A \cos(\omega t + \phi)$, in which ω is the angular frequency (in degrees per time unit) and t = time. The symbols for the circadian parameters represent the Mesor, *M* (midline-estimating statistic of rhythm, a rhythm-adjusted mean); the Amplitude, *A* (a measure of the extent of predictable change around the Mesor); and the Acrophase ϕ (lag time or phase angle of the maximum value, a parameter corresponding to the best fitting cosine curve). For these studies, the period was imposed experimentally by the photoperiodicity regimen, with $\omega = 2\pi/24$. As previously discussed by Reinberg (1971), such chronobiologic methods are especially designed for the study of rhythmic variations in short and sparse series of data.

Considering the validation and comparison problems of chronobiological data, the methods for cosinor-rhythmometry (Nelson, Tong, Lee, & Halberg,

1979), which involve the zero-amplitude test for possible rhythm detection (this statistical procedure involving regression analyses, e.g., F test, refers to the assumption of “no-rhythm,” or $A = 0$ of the cosine function fitted by least-squares to the data), must also be supplemented by mathematical studies for comparing circadian parameters. In this context, to compare several circadian fluctuations in a dynamical perspective, phase displacement of acrophase values can be analyzed by the rhythmometric procedures of the Amplitude–acrophase test (F test), an “inferential statistical test of amplitude and/or acrophase similarity in two or more rhythms” (Bingham, Arbogast, Cornélissen-Guillaume, Lee, & Halberg, 1982; Halberg, Carandente, Cornélissen, & Katinas, 1977). Quantitative comparison of rhythm-adjusted averages can be treated by the statistical analyses of the Mesor-test (t test) or inferential statistical methods similar to that used in rhythm comparison (Halberg et al., 1977).

Thus, brain rhythmicities or behavioral rhythms can be defined as algorithmically-formulatable recurring psychophysiological changes with a waveform validated by inferential statistical procedures (Poirel, 1984; Poirel & Ennaji, 1991a).

If the time correspondences observed do not legitimate, *stricto sensu*, the existence of functional or causal relationships among rhythms considered within a circadian framework, heuristic methods involving rhythm comparisons (Halberg et al., 1977) make it possible to speculate, at least theoretically, about some possible functional relationships regarding the circadian fluctuations that are rhythmometrically detected.

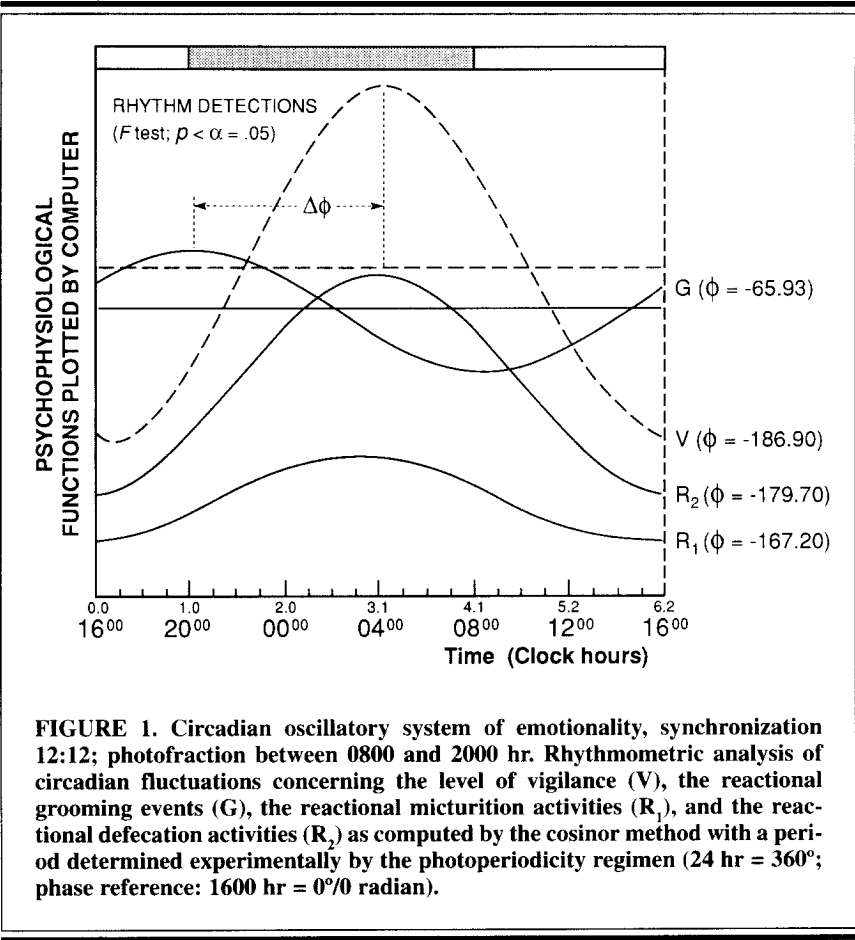
Chronobiological Display of Processes Involved in Stress-Related Events

It is on the basis of such modelization procedures that raw data, taken from individual observations, were analyzed over a 24-hr period. For these rhythmometric studies that refer to individual time series, the mean variation curves and their Cartesian or polar representations were reconstructed from the macroscopic results previously indicated. In this respect, we know that the observation of “systematic circadian occurrence” of an event is a necessary but not sufficient condition to demonstrate an event as a biological rhythm (Webb, 1985, p. 17). That is why classical statistical biometric investigations must be supplemented by rhythmometry analyses, making it possible to characterize the time structure of an event and perhaps to compare circadian parameters of several events.

Rhythmometric Analyses of Reactional Events

Figure 1 refers to the circadian organization of emotionality in mice synchronized to LD 12:12 with a photofraction between 0800 and 2000 hr (see Table 1).

Considering the circadian fluctuations of basic emotional reactivity, rhythmometric variation curves R_1 and R_2 represent the circadian profiles of emotion-



al neurovisceral processes related to micturition and defecation activities. Estimated by linear least squares rhythmometry, the mean variation curves correspond to $y = 0.90 + 0.65 \cos(\omega t - 167.20)$ and $y = 6.25 + 3.23 \cos(\omega t - 179.70)$, respectively. The variation curves R_1 and R_2 are rhythmometrically validated by the zero-amplitude test, $F_{1-\alpha}(2, 16)$, $F_1 = 14.511$, $p < .05$, and $F_2 = 23.853$, $p < .05$. Confirmed by correlation tests ($r' = .56$, $p = .001$), such circadian fluctuations in synchrony tend to show that peaks are located in the dark span (scotofraction) at about 0400 hr ($\phi = -167.20$; $\phi = -179.70$).

Considering the circadian fluctuations of more organized stress-related events, the rhythmometric variation curve G represents the circadian profile of emotional behavioral processes related to psychologically derived activities of grooming. Estimated by linear least-squares rhythmometry, the mean variation

curve corresponds to $y = 6.98 + 1.72 \cos(\omega t - 65.93)$. The variation curve is validated by the zero-amplitude test, $F_{1-\alpha}(2, 16)$, $F = 6.401$, $p < .05$. The circadian fluctuations reached a maximum at approximately 2024 hr ($\phi = -65.93$), with a progressive decrease during the nocturnal span.

Rhythmometric Analysis of Vigilance Levels

With regard to the circadian fluctuations of vigilance, polygraphic recording data were also estimated by linear least squares rhythmometry; the mean variation curve related to vigilance states corresponds to $y = 1.70 + 1.44 \cos(\omega t - 186.90)$. The variation curve is validated by the zero-amplitude test, $F_{1-\alpha}(2, 18)$, $F = 164.000$, $p < .05$. The circadian fluctuations of vigilance expressing the level of central activation reach a maximum at approximately 0400 hr ($\phi = -186.90$), a peak that corresponds statistically to acrophases ($\phi = -167.20$ and $\phi = -179.70$) related to variation curves R_1 and R_2 (statistical association biometrically validated by the Wilcoxon T test (reduced deviation = 4.09, positive relation; $p = .01$), expressing the same directionality of correlation).

Upon comparison of the different circadian rhythms, whose interrelationships were analyzed by correlation tests, a remarkable phase concordance is evident between the temporal periodicities related to vigilance and to indicators of basic emotionality. In contrast, the temporal periodicity for emotional behavior expresses a marked phase dissociation ($\Delta\phi = 121^\circ$) of the circadian bodily pattern of emotionality. This chronobiological dissociation was rhythmometrically validated by the amplitude-acrophase test, $F_{1-\alpha}(2, 35)$, $F = 6.849$, $p < .05$. Moreover, the statistical association studies showed (1) a negative correlation ($r' = -.43$; $p = .01$) between the acrophases of variation curves R_1 (R_2) and G and (2) a negative relation (Wilcoxon T test, reduced deviation = 3.22, $p = .01$) between the acrophases of variation curves V and G .

Rhythmometric Analyses With Circadian Displacement Designs

To verify the temporal pattern of the circadian fluctuations recorded and their possible phase relations, sleep/wakefulness cycles were resynchronized to new photoperiodicity regimens.

Regarding the murine model considered, activity was resynchronized and stabilized after 10 days of exposure to a new circadian photoperiodicity. This was done to confirm the rhythmologic processes in reactional events relative to darkness and light rather than to clock hour, or to estimate these fluctuations relative to vigilance levels rather than to darkness and light.

The new circadian rhythms analyzed were reconstructed from the macroscopic data indicated in Table 2. Figure 2 represents, for instance, the rhythmometric variation curves obtained with a lag phase shift that corresponds to 0800 hr and imposes a photofraction between 1600 and 0400 hr.

TABLE 2
Distribution of Reactional Events and Variation of
Vigilance Levels Over a 24-hr Period

Variable	Observation time (clock hr)							p^a
	N	t_1	t_2	t_3	t_4	t_5	t_6	
Neurovisceral responses								
Micturition	20	24	19	17	16	21	27	< .05
Defecation	20	175	124	129	114	219	205	< .01
Behavioral responses								
Grooming	20	88	110	148	186	119	85	< .02
Vigilance levels								
Cortical arousal ^b	20	57	14	0	7	55	60	< .001

Note. Mice were synchronized to a photoperiodicity regimen of LD 12:12, light between 1600 and 0400 hr, darkness between 0400 and 1600 hr.

^aNonparametric biometric test of Friedman (Siegel, 1956) permitting the validation of possible differences between the six reference times. ^bAccording to the percentage scored for cortical states of slow-wave sleep (Poirel, 1991).

Estimated by linear squares rhythmometry, the mean variation curves R_1 , R_2 , G , and V correspond to $y = 1.03 + .26 \cos(\omega t + 40.80)$, $y = 8.02 + 2.58 \cos(\omega t + 70.60)$, $y = 6.18 + 2.47 \cos(\omega t - 158.70)$ and $y = 1.65 + 1.72 \cos(\omega t + 52.70)$, respectively.

The variation curves were rhythmometrically validated by the zero-amplitude test. With $F_{1-\alpha}(2, 18)$, F values were 3.132, $p < .05$; 26.069, $p < .05$; 11.985, $p < .05$; and 1621.600, $p < .05$, respectively. Comparison tests of circadian fluctuations on the basis of the comparison of cosinor parameters confirmed the phase concordance of the variation curves R_1 , R_2 , and V , as well as the phase displacement ($\Delta\phi = 106^\circ$) of the variation curve G , $F_{1-\alpha}(2, 35)$; $F = 07.789$, $p < .05$.

The new circadian patterns observed confirm the amplitude, waveform, and phase relations among the emotional circadian rhythms previously analyzed. Correlation studies concerning the new variation curves express the same significant tendencies with a remarkable stability of interrelationship between the two psychophysiological subsystems considered.

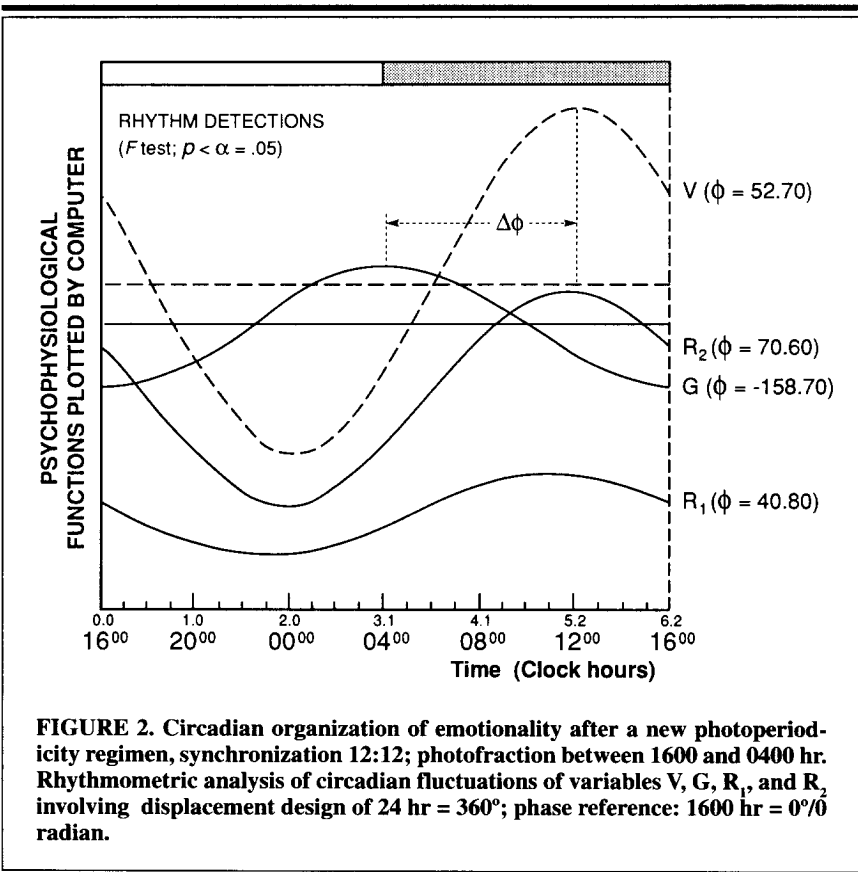
These rhythmometric analyses involving two dissociated subsystems reflect (a) the basic emotional reactivity that fluctuates in synchrony with the level of vigilance and (b) the bodily emotional reactivity that expresses more corticalized integration and fluctuates relatively independently from central activation.

Thus, with phase-shifting experiments, we can observe a recomposition of the circadian organization of emotionality involving the resetting of the two oscillatory subsystems considered.

Lithium as a Research Tool for Behavioral Chronobiology

In a parallel direction from another experimental perspective, the action of lithium salts (i.e., Li^+ ions) upon the circadian organization of emotionality confirmed the chronobiological dissociation between both kinds of emotional reactivity and showed that this psychoactive drug exerts its influence only on the behavioral component of emotionality.

To illustrate the circadian structure of several events comparatively, the results of cosinor analyses may be described in rectangular (see Figures 1 and 2) or polar representations. Considering the variables studied in mice with and without lithium (for more details, see Poirel & Ennaji, 1991b), the circadian data resulting from neurovisceral, behavioral, and vigilance events were plotted on polar coordinates (see Figure 3). In the polar cosinor display, a circular scale is used to represent and compare several circadian processes, with 360° equated to



2400 hr (conventional phase reference $0^\circ = 1600$ hr; photofraction between 0800 and 2000 hr, scotofraction between 2000 and 0800 hr). The amplitude (A) and the acrophase of the fitted cosine functions are represented by directed lines (vectors), in a fashion similar to the hands of a clock (comparison of several functions in the same polar cosinor display involving the notion of cosine-vector).

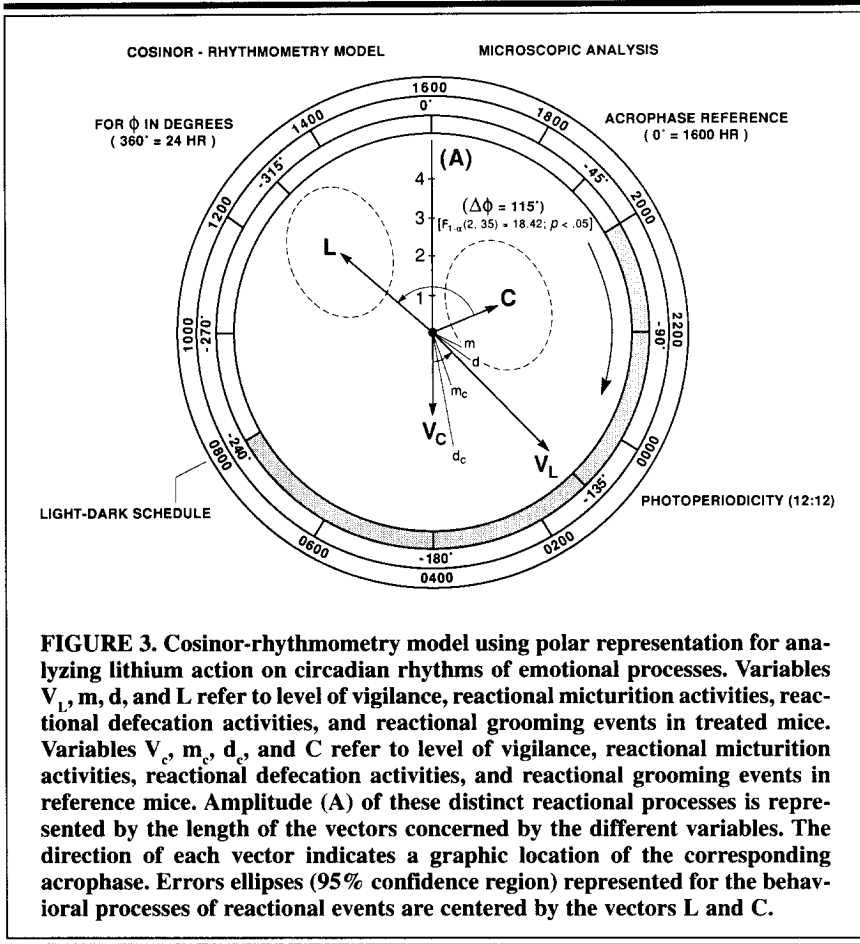
Amplitudes of these different circadian processes are represented by the length of the vectors **L** (reactional behavioral responses under lithium), **C** (reactional behavioral responses for the reference group), **V_L** (vigilance level under drug treatment), and **V_c** (vigilance level for the reference group). The vectors **m**, **d**, **m_c**, and **d_c** refer to reactional micturition and defecation activities under lithium, and to reactional micturition and defecation activities without the drug. The direction of each vector indicates a graphic location of the corresponding acrophase. The key to the ellipse concerning reactional behavioral responses under lithium corresponds to mesor ($M = 9.25 \pm 3.71$), amplitude ($A = 3.08 \pm 2.26$), and acrophase ($\phi = -312.87^\circ (-283.27^\circ; -337.26^\circ)$). The key to the ellipse concerning reactional behavioral responses for the reference group corresponds to mesor ($M = 7.08 \pm 1.46$), amplitude ($A = 1.76 \pm 2.13$), and acrophase ($\phi = -67.24^\circ (-122.56^\circ; -17.31^\circ)$). The clock hours for **L**, **C**, **V_L**, and **V_c** were 1248, 2028, 0100, and 0400 hr, respectively. For **L** and **C**, circadian acrophases differed significantly by 115° (0740 hr). The difference between these two circadian processes was rhythmometrically validated by the amplitude–acrophase test (see Figure 3); the comparison between the two mesors ($M = 9.25$; $M = 7.08$) revealed a statistically significant difference (Mesor test, $t = 2.37$; $p < .05$). For **V_L**, **V_c**, **m**, **d**, **m_c**, and **d_c**, the acrophases did not differ significantly: their graphic locations corresponded to the second third of scotofraction.

Thus, such rhythmologic events and their phase relations remain in accordance with the implication of two distinct oscillatory processes within the circadian framework of emotionality.

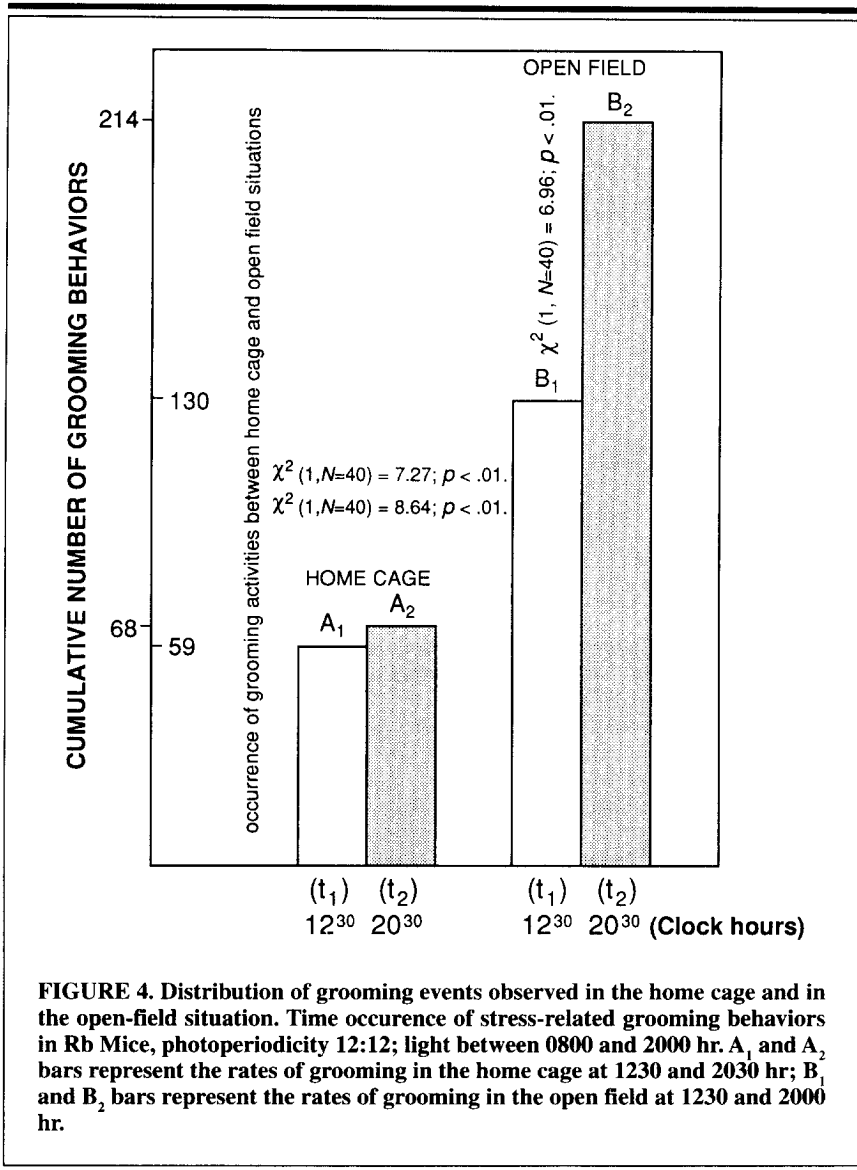
Comments Regarding the Circadian Studies of Stress-Related Events

Considering the Motivational States of Reactional Grooming Activities

If the murine models of emotionality have been discussed exhaustively since the first studies on micturition and defecation reactional activities by Hall (1934), the reference to emotional grooming events was more recently approached on the bases of ethology and behavioral physiology. The biological significance and the psychological dimensions of grooming behavior vary considerably with the situational contexts (Colbern & Gipsen, 1983; Fentress & Stilwell, 1973); this complex kind of reactional behavior must be operationally interpreted as a function of experimental situations involving distinct motivational states (Miliaressis & Poirel, 1972; Poirel, 1975, 1983), or be considered simply as a conclusion to a consummatory activity (Bolles, 1960). If these behavioral responses occur in



novel environments (e.g., transitional activities in uncertain situations), in conflictual situations (e.g., adjunctive phenomena, time-sharing activities; McFarland & Houston, 1981), and in adaptive processes of derivation (Tinbergen, 1952), these reactional events (see Figure 4) also should occur in anxiogenic situations such as those classically realized in open field conditions (e.g., stress-related events considered in comparative psychology as displacement activities; Armstrong, 1950; or transitory psychosomatic disorders; Barnett, 1955). For instance, from a group of 80 female mice reared and studied according to the same standardized conditions previously described, 40 subjects were individually analyzed in a home cage situation (control group) and 40 subjects were analyzed in the open field situation (experimental group). The occurrence of grooming events was recorded for 30 min at the same times of day (i.e., 1200 and 2000



hr). From these comparisons, the increasing occurrence of grooming responses in the open field situation expresses the reactional dimension of these behavioral responses as stress-related events; these results also demonstrate the significant incidence of these behavioral responses at 2030 hr. The reactional modalities linked to such stressful conditions can be reduced in intensity, frequency, and

sequential organization by previous treatment with psychotropic drugs (tranquilizers such as haloperidol and fluphenazine, or anxiolytics such as meprobamate and diazepam). For instance, chlorpromazine tends to decrease the reactional grooming level in rats significantly (Miliaressis & Poirel, 1973).

According to Gellhorn (1968), the cerebral hemispheres that are preferentially involved in motivational processes add two important features to the subcortical integration of emotionality: namely, differentiation (e.g., grooming events are arranged in a hierarchical sequence with "the progressive organization pattern of face washing to fur licking" (Gellhorn, p. 151); this behavioral grammar, however, is not observed in decerebrate animals that present fragmentary or poorly directed grooming activities), and sensitization (e.g., increase in the occurrence of reactional behaviors in a stressful situation such as, for instance, experiments with the open field test). Together with the criteria for testing the motivational events of emotionality, another feature deserves to be mentioned: the diachronic increase in grooming. During an observation in an open-field situation, the duration of the experiment is very crucial to result validity (Poirel, cited in Waysse & Medioni, 1982). For instance, from 1 to 5 min, neurovisceral responses of emotionality are predominant with few grooming activities; after 5 min, micturition and defecation reactional activities are progressively replaced by stereotypic grooming behaviors. Thus, psychologically induced activities of grooming tend to increase at a far slower rate during the initial state of overarousal, which facilitates the expression of basic emotional reactivity.* In contrast, a more adaptively complex activity (e.g., psychological defense mechanisms) is facilitated at moderate increases of central activation until a critical time threshold is reached. Considering delayed occurrence of grooming, complex organizational psychological events appear to be incompatible with overarousal states (Poirel, cited in Brown & Graeber, 1982).

The Problem of Emotionality as a Circadian Process

In 1967, Charles Stroebel began to study some emotional chronograms in rats (e.g., emotional conditioning and time of day). However, as previously indicated, "the establishment of a systematic circadian occurrence of an event is a necessary but not sufficient condition to establish an event as a biological rhythm" (Webb, 1985, p. 17). In this respect, "to determine the interrelationship between two systems within a circadian framework" (Webb, p. 18), displacement designs involving several photoperiodicity regimens may be used to establish murine circadian patterns of behavioral processes (Poirel, 1975, 1984) and to confirm, for instance, the circadian fluctuations of emotional reactivity relative to vigilance

*From a chronobiological perspective and from this diachronic aspect, such dissociations tend to confirm the action of ergotropic and trophotropic subsystems of emotionality in brain neurophysiology as described by Gellhorn (1968).

level rather than to clock hour. If one considers the circadian organization of emotionality through the perspective of phase displacement studies, basic emotional reactivity does not seem to be an independent circadian process. The oscillation of this kind of emotional reactivity seems to be directly induced by circadian fluctuations of vigilance.

From an ethological perspective, indirect psychological designs may be used for testing stress-related behaviors as circadian rhythms (for instance, the change in behavioral variables responding to same or similar emotional motivational factors). These include repetitive behavioral activities such as spontaneous oral movements or anarchical escape behaviors in an open-field situation and stereotypic exploratory behaviors observed in the classical psychopharmacological test measuring mouse exploratory activity (i.e., the "hole board test," Boissier & Simon, 1962). In this respect, the rhythms of the new stress-related variables under consideration must correspond to the same time characteristics.

For instance, we can demonstrate chronobiologically that the stereotypic exploratory processes fluctuate in synchrony with the circadian fluctuations of stress-related grooming events (Poirel, 1975). Where the circadian rhythms of adaptive behaviors responding to exploratory motivations are concerned, there exists a systematic phase displacement of several hours between the maxima of spontaneous exploratory activities and of stereotypic exploratory activities. These maxima tend to fluctuate in close phase with the circadian peak of reactional grooming.

With respect to the behavioral variables expressing emotional reactivity states (e.g., reactional grooming events, stereotypic exploratory activities), there exists a phase displacement of approximately 8 hr between the acrophase corresponding to neurovisceral expression of central activation and the acrophase corresponding to the behavioral expression of more corticalized emotional integration.

The problem of emotionality as a circadian process involving central regulation and several levels of brain integration may also be approached on the basis of relationships between neurosecretion rhythms and time fluctuations of emotional reactivity. With special reference to the murine model already considered, some time correspondences may be observed. For instance, the hypothalamic secretion of corticotrophic releasing factor (CRF), which experimentally induces grooming events in rodents (Colbern & Gipsen, 1988), and the behavioral events of emotionality, previously analyzed, exhibit similar circadian fluctuations with a peak toward 2000 hr (under the synchronization regimen with light onset at 0800 hr). The brain secretion of norepinephrine, which is linked to the nocturnal expression of central activation, also fluctuates in synchrony with the emotional neurovisceral reactivity. Thus, such circadian neuroendocrine activities would be dissociated in parallel with the distinct rhythms of behavioral and neurovisceral responses of emotionality.

Considering the circadian regulations inherited in the course of evolutionary

ecology, phylogenetically it may be observed that physiological, then behavioral, activities are hormonally controlled (Becker, Breedlove, & Crews, 1992; Bennett, 1974; Rusak, 1981, 1989). If behavioral rhythmicities in mammals are modulated by numerous neuropeptides (e.g., vasopressin, somatostatin, vasoactive intestinal polypeptide [VIP], enkephalin) localized in the suprachiasmatic nuclei, in birds and in inferior vertebrates temporal regulation mechanisms are also hormonally influenced. The pineal gland secreting melatonin appears to play a key role in circadian behavioral rhythmicities. For instance, in lizards, frogs, and sharks, the third eye receives light stimuli responsible for behavioral circadian entrainments. As regards the circadian fluctuations of basic emotionality presumably governed by the suprachiasmatic dominant pacemaker in mammals, the N-acetyltransferase enzyme is regulated by norepinephrine from the sympathetic nervous system whose fibers innervate the vestigial pineal tissue.

When considering the primary pacemaking structures in vertebrates, Menaker and Binkley (1981) compared the avian pineal organ to the mammalian suprachiasmatic nuclei. Concerning the nonmammalian systems, as recalled by Epstein (1980) and Shepherd (1988), the question of whether vertebrates "lower" than mammals express differentiated emotional responses is very difficult to evaluate. In the context of the circadian studies presented, we may assume that the circadian systems of emotionality studied are only concerned with the second type of emotional events (Shepherd, 1988) that involve in mammals (or in superior vertebrates) (a) neurovisceral responses and (b) specialized motor actions. The problem is all the more complex in invertebrates, in which possible emotional expressions are not directly visible. In this respect, considering possible emotional actions referring to primitive motivational processes (e.g., escape or aggressive behavior), neuroendocrine controls of rhythmic locomotor activity were suggested for invertebrates (Page, 1981).

In the field of comparative zoology, we may, with Shepherd (1988), conclude that "a complex innervation of the internal viscera, and a complex set of muscles which can independently signal autonomic and other internal states, are two components that are necessary for the expression of emotion in animals. These two components are almost entirely lacking in invertebrates and lower vertebrates" (p. 572).

On the basis of comparative ethological studies (Poirel, 1988; Sechter & Poirel, 1985), we could take into consideration, at least theoretically in mammals, the notion of a circadian paradigm of emotionality linked to reactional grooming activities and also to other kinds of behavioral responses that fluctuate in synchrony and exhibit similar rhythmometric characteristics (Poirel, cited in Brown & Graeber, 1982).

More generally speaking, in the descriptive context of dual organization of emotional life, and assuming that the marked circadian dissociation between two peaks of emotionality reflects two integrative levels in the brain, we may go further and venture the hypothesis of a functional dissociation between the neuro-

visceral and behavioral modalities of emotionality. Such a chronobiological dissociation suggests the existence of two parallel circadian devices that are functionally complementary: (a) a subsystem regulating basic emotional reactivity under subcortical mechanisms and (b) a second subsystem regulating emotional behavioral events under cortical control. If time correspondences observed do not legitimate, *stricto sensu*, the existence of causal relationships among rhythms considered within a circadian framework, such time correlations lead the way to the study of certain possible functional phase relations involving hierarchical levels of emotional integration.

Theoretical Aspects of Psychophysiology and Behavioral Chronobiology

On the basis of these rhythmometric investigations, the description of two asynchronous circadian systems of emotionality renders it possible to discuss new concepts of mental life and the epistemology of time: For instance, the reconsideration of the classical law of a "continuum of vigilance" formulated by Lindsley (1951) and the concept of comparative chronopsychology (Poirel, 1975) approached in light of Prigogine (Prigogine & Nicolis, 1977) and Thom's (1990) ideas.

Emerging Concepts in Psychophysiology and Comparative Psychopathology

On the functional relations between vigilance and emotionality. The phase relations among the circadian fluctuations bring into question the conceptualization of a "continuum of vigilance" involving a functional linear relationship among vigilance, overarousal, and emotionality.

If the rhythms of basic emotionality in synchrony with the fluctuations of vigilance confirm the notion of a functional continuum for the directly physiological forms of emotional reactivity, then the dissociated behavioral rhythms involving more corticalized integration do not satisfy this classical psychological law (Lindsley, 1951) in their chronobiological expression.

Considering the contexts of both chronobiology and psychology in a neo-Jacksonian neurological perspective, the highly integrated organization of emotional events, as portrayed by motivationally derived activities, may be elicited by certain moderate vigilance levels, but they would be incompatible with circadian overarousal states.

Aside from any chronobiological considerations, experimental stimulations at different functional levels of cerebral integration (Poirel, Gire, & Waysse, 1970) confirmed the relationships suggested by rhythmometry analyses: If basic emotional reactivity varies linearly with the progressive increase of central activation, then more complex kinds of emotionality correspond to preferential levels of vigilance in their derived manifestations. Moreover, hypervigilant states, whether induced by chronobiological fluctuations or by experimental stimulation, tend to disorganize motivational behaviors in the order of their adaptive complexity and of their functional hierarchy.

In this interpretative context, rhythmometric studies tend to confirm the psychological notion of the optimum of motivation regulating adaptive behavior over a 24-hr period (Poirel, 1975).

Toward a possible cortical chronomodulation induced by lithium. The rhythmometric data involving lithium experiments lead to several comments regarding some shifts of temporal variations of stress-related activities in treated mice. Chronobiological results suggest that lithium does not displace the circadian patterns of basic emotionality but does, however, displace, with possible phase delay, the behavioral circadian rhythms associated with more corticalized integrations (i.e., grooming responses as psychologically analyzed for their emotional significance; see Colbern & Gipsen, 1988, and Poirel, 1988). Considering the results obtained, the rhythmometric data tend to be in favor of a preferential telencephalic action of Li^+ ions and of their psychological efficacy on affective disorders. These results are consistent in psychiatry with the clinical action of lithium salts because the ions primarily affect the psychological content of affective disorders (e.g., affective reactions, manic-depressive psychoses); chronobiological comparisons suggest a temporal dissociation between the two kinds of stress-related reactions (visceral and behavioral responses), whose various phases are differentially affected by lithium.

More generally speaking, in biological psychiatry, when considering the possible endogenous mechanisms involved in affective disorders, cerebral subsystems with different circadian frequencies could be implicated in episodes of internal desynchronization (Halberg, 1968). In this respect, we might suggest, at least theoretically, that lithium resynchronizes several brain oscillators, probably at the "centrencephalic" level (i.e., mesodiencephalic subcortical structures), but for the most part this tends to occur at the cortical level.

Proposals involving a possible leading role played by telencephalic structures should be discussed in light of the phase-advance hypothesis and with reference to chronobiological concepts regarding brain circadian pacemakers.

Of the possible endogenous mechanisms involved in those brain structures that regulate the circadian rhythms of vigilance and emotionality, several interconnected modulators appear to be affected by the action of lithium. A functional circadian timing system that includes two separate brain oscillators (the X and Y oscillators, previously described by Moore-Ede, Sulzman, & Fuller in 1982), which are affected by lithium in different ways, tends to drive numerous circadian physiological and psychological functions. The X pacemaker appears to be dominantly involved in the circadian rhythmicity of REM sleep and core body temperature, whereas the Y pacemaker governs the sleep/wakefulness cycle, slow-wave sleep rhythm, skin temperature fluctuations, and the rest/activity cycle. These endogenous regulators, which are interconnected in a functional network, are reflected in a two-oscillator model (Kronauer, Czeisler, Pilato, Moore-Ede, & Weitzman, 1982; Wever, 1979), implying that, functionally, a weak Y

modulator is dominated by a stronger X pacemaker. Although the neural basis of the Y oscillator is associated with the anatomy of the suprachiasmatic nuclei of the hypothalamus (chronobiologic integration linked to the diencephalic level), the location of the X oscillator is still not identified. From a broader theoretical perspective involving neo-Jacksonian principles (Poirel, 1976, 1982) emerges the possible role of the medial forebrain bundle (MFB), which would act as a chronobiologic system in the temporal organization of adaptive behaviors (cf. the notion of a "premotivational activating system," Miliareiss & Poirel, 1972). The diencephalic endogenous regulators would be governed or controlled by cortical oscillators within a circadian framework involving staggered clocklike mechanisms (a metaphoric notion of brain clocks).

Considering the problem of brain oscillators and the circadian rhythm phase-advance hypothesis, although some patients with depression can have phase-advanced sleep/wakefulness cycles, in our lithium studies referring to murine models there are no apparent phase disorders in the sleep/wakefulness cycle organization. From another chronobiological viewpoint, organism rhythms in depression could exhibit lower amplitudes. In our experiments, the rise in amplitude of variation curves concerning the behavioral events (involving possible telencephalic action in our observations) shows that lithium reverses this tendency. This possible additional chronobiologic property would reinforce its therapeutic efficacy on endogenous psychoses.

Moreover, in light of lithium experiments, it appears that this drug would possibly act on the X oscillator rather than on the Y oscillator. Thus, lithium would affect, at least theoretically, the cerebral cortex (telencephalic level of integration), which mediates the occurrence of complex behavioral responses, rather than the hypothalamic suprachiasmatic nuclei (diencephalic level of integration), which drive the rest/activity cycle and the rhythms of slow-wave sleep (Moore-Ede et al., 1982). In addition, the Y pacemaker drives the sleep/wakefulness cycle (i.e., the circadian rhythm of vigilance) as well as related circadian fluctuations (or associated variations) such as basic emotional reactivity rhythms. Thus, lithium would not affect the Y oscillator governing the circadian fluctuations of vigilance, which remain in synchrony with the temporal variations concerning the neurovisceral responses of emotionality. Under lithium, mice maintain their normal circadian timekeeping related to vigilance level and basic emotional reactivity. From another biological perspective, the same conclusions were also reached: that this psychoactive drug could affect the X pacemaker rather than the Y modulator (Engelmann, 1987).

Considering the possible location of the X pacemaker in the medial forebrain bundle, such a suggestion may also be legitimated by the anatomical hypotheses favoring the lateral hypothalamic area as a possible site for the second dominant oscillator (Moore-Ede et al., 1982). In effect, this structure is functionally integrated into the medial forebrain bundle. Moreover, from a neo-Jacksonian perspective regarding the neural basis organization of circadian rhythmicity (Poirel,

1975), the Y oscillator (inferior level) should normally be controlled by the X oscillator (superior level). Previous lithium studies concerned with a selective forebrain electrophysiological activity (Barratt, Creson, & Russell, 1968) tend to legitimate such psychophysiological interpretations.

From Chronobiological Fluctuations to Chronopsychology

On the concept of comparative chronopsychology. The concept of chronopsychology was introduced to comparative ethology (Poirel, 1975) and to human psychology (Folkard, 1977; Fraisse, 1980; Monk & Folkard, 1978) to reflect some circadian behavioral fluctuations modulated by psychogenic motivations. This field study devoted to mental rhythmicities derived from investigations into behavioral chronobiology (Poirel, 1968) and from clinical observations concerning the diurnality of human performance (Halberg, 1973).*

Regarding the heuristic concept of comparative chronopsychology from the rhythmometrically analyzed circadian modalities of emotionality, the notion of biological or psychological time series may refer to structuralistic concepts (Piaget, 1968; Poirel, in Ceriani, 1992). Considered as dynamic structures, the intermodulated circadian rhythms of emotional life form a very complex functional system, with several devices that have interlocking control. These circadian rhythms express continuous transformation systems including autoregulation phenomena. In this respect, the circadian fluctuations observed satisfy the three criteria of totality, transformation, and autoregulation, as defined by the laws of structuralism. In theoretical psychiatry, this is a possible transition between the phenomenological notion of temporality (Straus, 1967) and the structuralistic concept of chronopsychology (Poirel, 1990).

Considering the new notion of a nonlinear continuum of vigilance derived from our observations and the working hypotheses presented by chronobiology, the concepts of "order by fluctuation" discussed by Ilya Prigogine (1967) and René Thom (1990) may be approached on the basis of the dynamic organization of the oscillatory system of emotionality.

Emotional life in the perspective of chaotic systems. If the notion of "active desynchronization" expresses a concept referring to chaotic systems in chronobiology, the desynchronization processes refer to a "state of two or more previously synchronized rhythmic variables that have ceased to exhibit the same frequency and/or the same acrophase relationships and show changing time relations" (Halberg et al., 1977, p. 79). These rhythmologic transformations involving several desynchronization modalities were studied by Glass and Mackey (1988) in physiology, and they could well apply to the field of psychology.

*The term chronopsychophysiology has also been used for approaching physiological aspects of behavioral chronobiology (Stroebel, 1975).

Considering the psychological time arrow throughout biological evolutionary time and the asynchronous structure of emotionality, in the context of chaotic systems we might consider the progressive existence of a separation between the dynamic organization of basic emotional reactivity and the dynamic organization of behavioral events of emotionality, anticipating bifurcation processes from these emotional orderly states.

If psychological components of emotionality refer to complex fluctuations and chaotic dynamics arising in a deterministic system of biological reactivity, then some routes to chaos would involve progressive "active desynchronization" states of biological vigilance over evolutionary time.

According to our interpretation, founded on Prigogine's theories, from primitive biological vigilance to mental reactivity (so-called mental alertness), the function of chaos would evolve, in theory, in three stages involving active desynchronization processes. In this evolutionary context, circadian rhythmicities that are built into organisms result from interwoven linkages between endogenous and exogenous factors whose time-keeping processes are progressively inherited through biological evolution.

Considering the problem of the mental evolution of emotional integration, the reactivity would first be characterized by homogeneous rhythmic aspects of emotionality initially involving a continuum of vigilance with equilibrium states and functional linearity processes (i.e., intricate oscillations of emotional reactivity corresponding within this primitive stage to steady states that refer to homeostasis).

Progressively, states of equilibrium would be dissociated in response to the increasing complexity of adaptive functions during evolution. In this new context, the dynamic trajectory of emotional systems would lead to the emergence of heterogeneous rhythmic aspects of reactivity involving distinct coherent fluctuations with a predictable self-organization of emotionality in nonequilibrium systems of vigilance (circadian dissociations suggesting functional dissociations; oscillations associated with possible periodic solutions that are more directly concerned with the chronobiological domain of rhythmometry); as a result, these systematic temporal variations bring into question the classically held physiological concept of homeostasis discussed in chronobiology, as well as the reference principle of the linearity of time.*

The most recent evolutionary stage is concerned with the psychology of time and its subjective dimension in humans. In this respect, chaotic time series of emotionality referring to the highest mental activities must be considered, aspects

*In an analogy to thermodynamics applied to living processes (Prigogine, 1967), a new order of emotional rhythmicity occurs within the mental life: This new distinct fluctuation (e.g., the variation curve G) tends to correspond to more complex adaptive functions (e.g., derived activities manifesting neurotic defense mechanisms, psychologically induced stress-related behavioral events).

of which were recently addressed by Deleuze & Guattari (1991) as well as by Gillett (1991), regarding the controversial notion of the “mind-body problem” in the psychological perspective of the *endoconsistent* and *self-referential* contents of thought. Such circadian emotional fluctuations could display, at least biologically, both oscillatory and chaotic dynamics, the keys to which may be found in a deterministic system of reactivity (a possible chronopsychological domain of the nonlinear dynamics of mental life).

Concluding Remarks and Research Perspectives for Psychology

From these chronobiological and chronopsychological findings, which tend to demonstrate the existence of several systematic emotional oscillations measurable in organisms, we now have a rhythmometric model and a circadian paradigm for a possible temporal organization of emotional life in vertebrates. Such rhythmologic emotional entities tend to foster the principle of a predictable time structure of emotionality in comparative psychology. Rhythmometric investigations into brain activities suggest that chronobiology should be considered when searching for possible mechanisms regulating emotional processes. Such rhythmologic studies tend to express the heuristic power of chronobiology more generally for experimental or theoretical research into the fields of behavioral neuroscience and comparative psychopathology. Thus, the chronobiological studies presented, and their chronopsychological perspectives referring to the circadian framework of emotionality, are concerned with epistemological considerations regarding the semantic depth of time and the Euclidean principle of the linearity of time, as well as the conceptualization of biological rhythms within psychological time.

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