

Although these observations are preliminary, the direct intraphyletic interaction of coral versus coral in the Caribbean seems less modified by predation pressure than on some eastern Pacific coral reefs (18). Space is produced in the Caribbean by slower means, such as the slump or collapse of larger coral heads due to intense boring by sponges and bivalves (19). This might be analogous to the creation of space in highly dense rain forests by tree fall (20) and seems sufficient to offset the slow competitive exclusion which would occur if the system were left totally undisturbed. Elsewhere in the Caribbean, weather disturbances such as hurricanes are probably of major importance to shallow-water coral community organization as well, but Panama does not have such severe disturbances.

In looking at species succession, Pielou (21) found that species diversity increased over time for some small plots of young temperate forest trees. She concluded that natural thinning by interspecific competition caused the decrease in segregation and dominance by single species, the result being an increase in the local diversity. While few data exist for reef succession, most phases of Caribbean coral succession may prove to be similar to this pattern, whereas, without large-scale physical or biological disruptions, eastern Pacific coral succession may prove to be the opposite. In support of this, Grigg and Maragos (22) have shown that, all else being equal, coral communities on the oldest lava flows in Hawaii have the lowest diversities and that the same negative relation between diversity and abundance exists in Hawaii as on the eastern Pacific reefs. They suggest that interspecific competition of the kind outlined above might be the cause for this decrease in diversity over time. Additional support for this hypothesis comes from their observation that in areas exposed to heavy swell and periodic storm damage, abundance remains low and diversity high, regardless of the age of the colonized surface. In Hawaii, where coral fauna and reefs are similar to those of the eastern Pacific, storm and swell damage may act as a diversifying force in the same way as *Acanthaster* predation does in the eastern Pacific.

JAMES W. PORTER

School of Natural Resources,
University of Michigan,
Ann Arbor 48104

References and Notes

1. F. C. Whitmore and R. H. Stewart, *Science* **148**, 180 (1965).
2. P. K. Dayton, G. A. Robilliard, R. T. Paine, L. B. Dayton, *Ecol. Monogr.* **44**, 105 (1974).
3. J. W. Porter, in *The Second International Symposium on Coral Reefs*, G. R. Orme, Ed. (Great Barrier Reef Committee, Brisbane, Australia, in press).
4. T. F. Goreau, *Biol. Bull. (Woods Hole)* **116**, 59 (1959); L. Franzisket, *Int. Rev. Hydrobiol.* **55**, 1 (1970).
5. J. W. Porter, cited in H. S. Horn, *The Adaptive Geometry of Trees* (Princeton Univ. Press, Princeton, N.J., 1971), p. 129.
6. J. Lang, *Bull. Mar. Sci.* **23**, 260 (1973).
7. P. W. Glynn, R. H. Stewart, J. E. McCosker, *Geol. Rundsch.* **61**, 598 (1972).
8. J. W. Wells, *Mem. Geol. Soc. Am.* **67**, 609 (1957). Physical control is especially prominent on the eastern Pacific side, which is by far the more physically stressed of the two reef environments. In the Bay of Panama (Pacific) tidal amplitude can exceed 7 m and water temperature ranges from 31° to 15°C, compared to 0.5 m and 30° to 26°C on the Atlantic side [I. Rubinfoff, *Science* **161**, 875 (1968)].
9. D. R. Stoddart, *Biol. Rev.* **44**, 433 (1969).
10. The origin of the modern eastern Pacific coral fauna is unclear. Although they are generically similar to Miocene and Tethyan fossils from the Panama region, they have no species in common with the Caribbean fauna today. Species similarities with the present Indo-Pacific and remote Pacific island corals, as well as the presence of genera without prior fossil representation in the New World, indicate that some of the present eastern Pacific fauna immigrated from the Indo-Pacific recently (11).
11. J. W. Porter, *Bull. Biol. Soc. Wash.* **2**, 89 (1972).
12. Lines 10 m long were laid parallel to reef depth contours. The number and relative abundances of living coral species under the
- transect line were used to calculate the Shannon species diversity (H') and the total abundances (percentage of line covering living coral) [J. W. Porter, *Ecology* **53**, 744 (1972); see also Y. Loya, *Mar. Biol.* **13**, 100 (1972)].
13. P. W. Glynn and R. H. Stewart, *Limnol. Oceanogr.* **18**, 367 (1973).
14. J. W. Porter, *Am. Nat.* **106**, 487 (1972); thesis, Yale University (1973).
15. R. T. Paine, *Am. Nat.* **100**, 65 (1966).
16. P. W. Glynn, *Science* **180**, 504 (1973).
17. T. F. Goreau and N. I. Goreau, *Biol. Bull. (Woods Hole)* **117**, 239 (1959).
18. The outcome of connecting these two oceans with a sea-level canal is problematic, but what little predictive evidence exists is ominous: eastern Pacific *Acanthaster* are capable of eating all of the Caribbean coral species so far fed to them (11). Why should Caribbean species have any resistance to predators with which they have never come in contact? Further, while dominance experiments between eastern Pacific and Caribbean corals have not been tried, analogy with Indo-Pacific and Caribbean species—the Indo-Pacific species killed even the most aggressive Caribbean corals [J. C. Lang, thesis, Yale University (1970)]—is disturbing, considering the close systematic relationship between the eastern Pacific and the Indo-Pacific corals (10, 11).
19. T. F. Goreau and W. D. Hartman, *Science* **151**, 343 (1966).
20. J. H. Vandermeer, unpublished data.
21. E. C. Pielou, *J. Theor. Biol.* **10**, 370 (1966).
22. R. W. Grigg and J. E. Maragos, *Ecology* **55**, 387 (1974).
23. I thank W. D. Hartman, G. E. Hutchinson, R. K. Trench, D. C. Rhoads, and P. W. Glynn for advice and criticism throughout this research. K. G. Porter, D. H. Janzen, S. T. Hubbell, L. Johnson, J. C. Lang, D. S. Wethey, and S. Ohlhorst have provided helpful comments. Supported by a Smithsonian predoctoral fellowship, NSF grant GA-30970, and a grant-in-aid of research from the Society of Sigma Xi.

13 December 1973; revised 4 March 1974

Studies of Squeezing: Handedness, Responding Hand, Response Force, and Asymmetry of Readiness Potential

Abstract. *Eleven subjects squeezed an electronic dynamometer, at each of three force levels, with both their right and left hands. In right-handed subjects the premovement "readiness" potentials were larger over the hemisphere contralateral to the responding hand. Left-handed subjects show contralateral dominance when responding with the right hand but not when responding with the left hand. The data suggest that in the potentials studied there is a component associated with the preparation to perform a specific movement, rather than with generalized preparatory processes.*

Slow cortical potentials that precede self-paced voluntary movement (1-4) have excited much interest. Although they may provide a useful tool for the study of the physiological mechanisms underlying voluntary movement, considerable controversy still remains. Especially prominent have been suggestions that these potentials represent either diffuse arousal mechanisms or, alternately, postresponse proprioceptive activity (3, 4). We present evidence that these potentials are associated with the execution of specific movements, rather than with diffuse, arousing, preparatory processes. This we infer from

the fact that the amplitude, and scalp distribution, of these potentials is strongly determined by parameters of the subject's movement. We also show that the degree of hemispheric asymmetry of these potentials is different in right- and left-handed subjects.

Of the four components of movement-related electrocortical potentials which have been described (1), we are concerned here with a ramp-shaped negative potential that begins to develop 800 to 1000 msec prior to the movement (N1). Vaughan and his co-workers (1, 4) have referred to the entire complex of potentials as the "motor"

potential. Deecke *et al.* (2) consider N1 to be a "readiness" potential. Much of the literature has focused on the degree to which the various components do, or do not, reflect motor commands issued, presumably, by the precentral gyrus. Several investigators (3) have interpreted their own data as suggesting that some of the later components occur after the actual movement.

There is little doubt, however, that the N1 component precedes the movement by several hundred milliseconds. Vaughan *et al.* (4) have reported that the distribution of N1 along the midline of the scalp is consistent with the known distribution of motor centers along the central sulcus (that is, N1 has a "somatotopic distribution"). Such a distribution suggests a strong relation

between motor preparation and N1. Nevertheless, N1 is quite similar in waveform to the contingent negative variation (CNV), originally described by Walter *et al.* (5) as a large, vertex-negative potential shift that can be recorded during preparatory periods, such as those used in the fixed-foreperiod reaction time procedure. The close similarity of N1 to CNV has led to the suggestion that the experimental designs used to elicit the readiness potential are a special case of the general class of situations in which CNV's can be elicited (6), but the evidence is contradictory. The CNV's can be elicited in the absence of a motor response (7), yet the CNV is enhanced when a response is required (8). Although the CNV has been shown to be bilaterally symmetrical irrespective of the responding hand and response effort (6), there are reports of CNV asymmetry as a function of the responding hand (9).

In the present study we try to resolve some of these issues. We felt that Vaughan *et al.*'s (4) demonstration of contralateral dominance of N1 provided the strongest evidence in favor of a specific motor interpretation. However, as Vaughan reported data only for subjects responding with the right hand, it seemed important to determine if the converse results would hold if the subjects responded with their left hand. Moreover, no systematic comparison of the motor potentials has been reported between right- and left-handed subjects. It was also important to determine if the waveform, or amplitude, of the potentials varied with the force with which the subjects responded. We reasoned that, if motor preparation was involved at all, the amplitude should vary with response force. In fact, we suspected that to a large extent the reported failures to observe an asymmetry of the N1 component were due to the relatively weak force requirements in previous studies.

The subjects were 11 male University of Illinois students (7 right-handed and 4 left-handed). Handedness was determined by self-report and subsequently verified by administering the Edinburgh Inventory (10). The electroencephalogram (EEG) was recorded with Beckman electrodes from a vertex (C_z), right sensorimotor (C_1), and left sensorimotor (C_3) placements (11) referred to linked mastoids. The subject was grounded at the forehead. Right supraorbital and canthal electrodes were

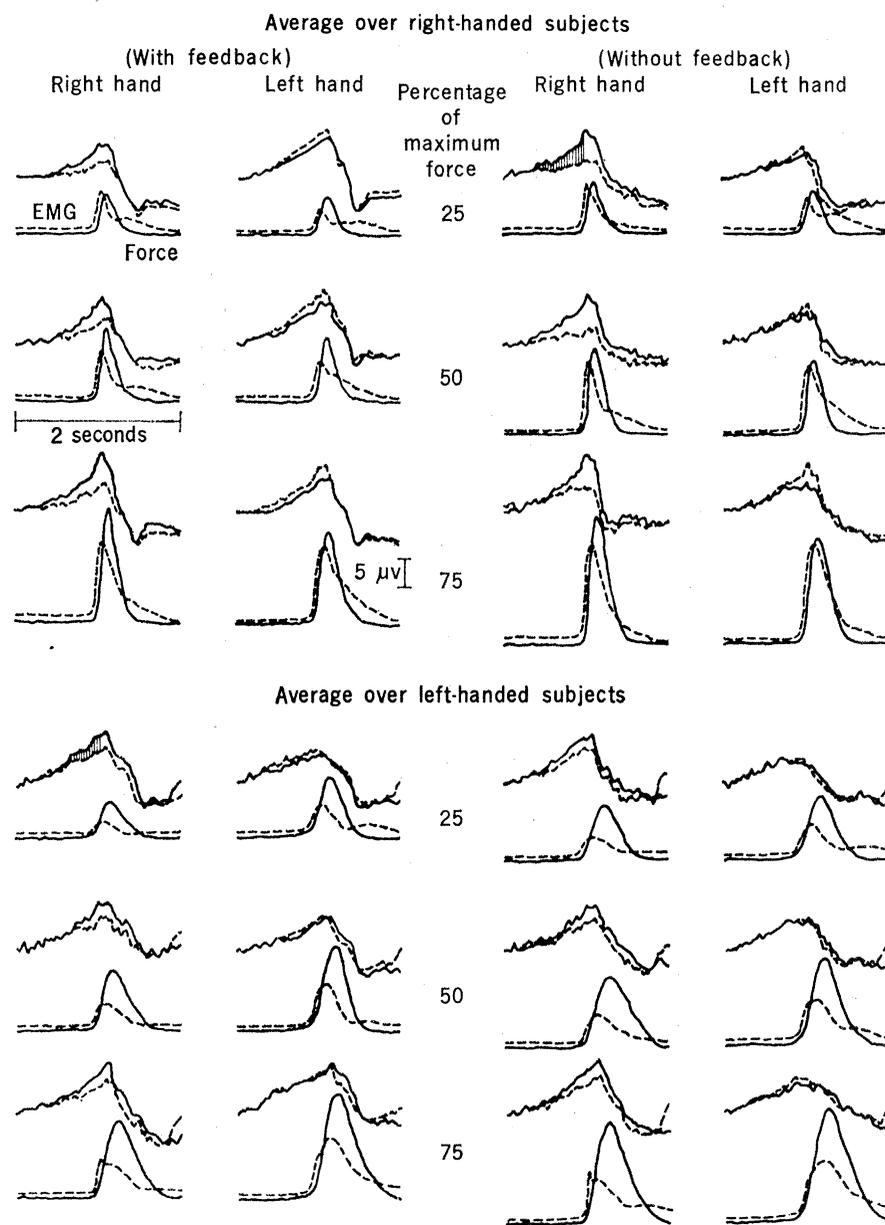


Fig. 1. A comparison of event-related potentials (ERP) recorded at electrodes placed at left central (C_3 , solid line) and right central (C_1 , dashed line) loci during voluntary squeezes. Under each pair of superimposed ERP's we plot the integrated EMG (dashed line) and the output of the force transducer (solid line) averaged over the same trials over which the ERP was averaged. Comparisons are presented as a function of subject's handedness (right versus left), nominal force output (25, 50, and 75 percent of subject's maximal force), responding hand (right versus left), and feedback (with versus without). Averages were obtained over all subjects, after the elimination of trials in which the EEG was contaminated by EOG activity. Number of trials per ERP ranges between 600 and 1050. The polarity convention is "negative up." Hatching in two areas of the comparisons illustrates the areas measured for the purpose of the quantitative data analysis.

used to record the electrooculogram (EOG). The electromyogram (EMG) was recorded from the responding arm (12). The EEG and EOG were amplified with Brush amplifiers (No. 13-4218-00) with bandwidth setting of 0.1 to 30 hertz (6 db per octave roll-off). The EMG was amplified by a Grass model 7P3B preamplifier and integrator combination (½ amp low frequency, 0.3; time constant, 0.02). Data were recorded on FM magnetic tape and averaged off-line with either a PDP8/E or an IBM 1800 computer. No trials in which detectable gross eye movements occurred were used in averaging (13). The averaging was triggered by the initial deflection of the force-transducer output.

Subjects were instructed to rapidly squeeze a dynamometer constructed from a Daytronic linear velocity differential force transducer (model 152A) attached to a handle. The displacement of the dynamometer was 0.025 cm at all applied force levels. At the first session each subject was asked to squeeze the dynamometer several times "as hard as he could." During all subsequent test series the subject squeezed the dynamometer, using three different force levels defined as approximately 25, 50, and 75 percent of the maximal force they had been able to apply during the first session (14). The subject viewed a fixation light upon which a transilluminated circle was superimposed and was told to find the squeeze (that is, force) level that would just extinguish the circle. Subjects were cautioned against overpressing.

Within each session there were two separate runs. In the first, the subjects were instructed to generate a series of 50 to 100 identical squeezes, each momentarily extinguishing the feedback circle. In the second run, they were instructed to continue squeezing the dynamometer at the same level that had previously extinguished the light. There was no visual feedback in this run. In any one session voluntary movements were performed, with only one hand at each of the three force levels, always in the order 25, 50, and 75 percent. Each subject participated in a minimum of six experimental sessions, three with each hand. The order of hand usage was counterbalanced across different subjects.

The data are summarized in Fig. 1, which shows event-related potentials (ERP) averaged over the seven right-

handed subjects, and the four left-handed ones. These grand averages are representative of the ERP's of the individual subjects. When right-handed subjects perform a self-paced voluntary movement with either hand, N1 is consistently larger over the sensorimotor location *contralateral* to the hand used. This asymmetry is evident as early as 500 msec before initiation of movement, defined by the onset of the EMG curve. Although somewhat diminished when the left hand was used, the *contralateral* dominance of N1 appeared consistently in all right-handed subjects. *Contralateral* dominance was also apparent (though reduced) in our left-handed subjects when they responded with their right hand. This, however, is not the case when left-handed subjects respond with their left hand. Whereas the left-handed subjects show *contralateral* dominance when using their right hand, they produced bilaterally *symmetrical* waveforms when performing with their left hand. Some of the left-handers showed a slight inconsistent degree of *contralateral* dominance for left-hand movements in some conditions. The waveforms generated by left-handed subjects were more variable and somewhat less similar to the "classic" motor potential than were the ERP's generated by the right-handed subjects.

As a measure of hemispheric asymmetry we performed a point-by-point subtraction of the curves recorded at C₃ and C₄ and then integrated the resultant difference-curve over the 500 msec preceding the onset of the EMG deflection. These values were obtained for all subjects under all experimental conditions. We computed an analysis of variance (15) of these values, the main factors being the subjects' handedness, the responding hand, and the force level used. Statistically significant effects were obtained for the responding hand, where asymmetry is larger for the right- than for the left-hand movement, independent of the subjects' handedness ($F = 48.61$, d.f. = 1/9, and $P = .00007$). The means for right- and left-handed subjects are also quite different with the interhemispheric asymmetry being larger for right- than left-handed subjects; significance, however, is not obtained because of variability between subjects. Whenever asymmetry is obtained, the *contralateral* amplitude is larger than the *ipsilateral* amplitude. We analyzed in a similar way the effect of response force on the area un-

der the *contralateral* ERP curves for the 500 msec just preceding the stimulus. Force of response does have a statistically significant effect on the area of the ERP at the *contralateral* electrode ($F = 5.83$, d.f. = 2/18, and $P < .05$).

These results confirm and extend the earlier reports (1, 4) suggesting that the N1 component of the premovement potential is associated with the processes initiating the movement in question. It is hard to see how a diffuse, generalized arousal process could be so specific to the hemisphere involved in the control of the movement and so much affected by the force of response. Eccles (16) has recently stated that "we can assume that the readiness potential is generated by complex patterns of neuronal discharges that eventually project to the pyramidal cells of the motor cortex and synaptically excite them to discharge, so generating the waves just preceding the movement . . . [the readiness potential] can be regarded as the neuronal counterpart of the voluntary command." We believe that the data we present here provide strong support for this hypothesis. It is, perhaps, useful to state explicitly that these conclusions pertain only to the asymmetric component of premovement potentials. This component may be superimposed, on occasion, on a symmetrical, nonmotor CNV.

There have been several previous reports (17) that left-handedness is associated with a reduced degree of cerebral asymmetry. The present study provides confirming evidence for this hypothesis. The right-handers showed *contralateral* dominance with striking consistency. The left-handers presented a more heterogeneous picture. Yet in all left-handed subjects the readiness potentials recorded over both hemispheres were of equal amplitude when these subjects responded with their left hand. The data show a substantial measure of hemispheric asymmetry when they responded with their right hand. In short, we find that the readiness potential is *contralaterally* dominant, except in the case of left-handed subjects responding with their left hand. These data suggest that ERP's might provide a direct, and novel, approach to the determination of cerebral dominance.

MARTA KUTAS

EMANUEL DONCHIN

Department of Psychology, University of Illinois, Champaign 61820

References and Notes

1. L. Gilden, H. G. Vaughan, Jr., L. D. Costa, *Electroencephalogr. Clin. Neurophysiol.* **20**, 433 (1966).
2. H. H. Kornhuber and L. Deecke, *Pfluegers Archiv. Gesamte Physiol. Menschen Tiere* **284**, 1 (1965); L. Deecke, P. Schied, H. Kornhuber, *Exp. Brain Res.* **7**, 158 (1969).
3. L. K. Gerbrandt, W. R. Goff, D. B. Smith, *Electroencephalogr. Clin. Neurophysiol.* **35**, 259 (1973).
4. H. G. Vaughan, Jr., L. D. Costa, W. Ritter, *ibid.* **25**, 1 (1968).
5. W. G. Walter, R. Cooper, V. J. Aldridge, W. C. McCallum, A. L. Winter, *Nature (Lond.)* **203**, 380 (1964).
6. J. J. Tecce, *Psychol. Bull.* **77**, 73 (1972); W. McCallum and J. Knott, Eds., *Event Related Slow Potentials of the Brain* (Elsevier, New York, 1973), pp. 77-131.
7. E. Donchin, L. K. Gerbrandt, L. Leifer, L. Tucker, *Psychophysiology* **9**, 178 (1972).
8. D. A. Irwin, J. R. Knott, D. W. McAdam, C. S. Rebert, *Electroencephalogr. Clin. Neurophysiol.* **21**, 538 (1966); M. E. Low, R. P. Borda, J. D. Frost, Jr., P. Callaway, *Neurology* **16**, 771 (1966).
9. D. A. Otto and L. J. Leifer, in *Event Related Slow Potentials of the Brain*, W. McCallum and J. Knott, Eds. (Elsevier, New York, 1973), pp. 29-37; K. Syndulko, thesis, University of California, Los Angeles (1972).
10. R. C. Oldfield, *Neuropsychologia* **9**, 97 (1971).
11. Electrode labels are according to the "International 10-20 system" described by H. H. Jasper [*Electroencephalogr. Clin. Neurophysiol.* **10**, 371 (1958)].
12. The EMG electrodes were placed on responding arm only—one electrode at a third of the distance from the lateral humeral epicondyle to the styloid process of the ulna, the other electrode approximately 3.8 to 5 cm in the distal direction along the same line.
13. Trials were rejected if the sum of squared digitized values exceeded a criterion value determined by visual inspection of a large sample of EOG traces and their corresponding digital values.
14. For all subjects the nominal force levels of 25, 50, and 75 percent were set within ± 9 newtons the values 49, 98, and 147 newtons, respectively, for the nondominant hand and 68.5, 121.4, and 218 newtons for the dominant hand. The means and standard deviations of the peak force generated were determined for each subject in each of the conditions. Analysis shows that (i) the actual peak force is a monotonically increasing function of the nominal force levels (the distributions of actual force exhibit only minimal overlap), (ii) the mean peak values are consistently smaller for the nondominant hand than for the dominant one, and (iii) in the without-feedback condition response amplitude always exceeded that generated during equivalent feedback condition.
15. Analyzed by SOUPAC program BALANOVA. See *CSO volume 9 (User): Statistical Systems* (Computing Services Office, Univ. of Illinois at Urbana-Champaign, Champaign, 1974).
16. J. Eccles, *Understanding the Brain* (McGraw-Hill, New York, 1973), p. 108.
17. H. Hécaen and J. de Ajuriaguerra, *Left-handedness: Manual Superiority and Cerebral Dominance* (Grune & Stratton, New York, 1964); J. Semmes, *Neuropsychologica* **6**, 11 (1968).
18. Supported by NSF grant GB30999 and contract DAHC-15-73-C-0318 with the Advanced Research Projects Agency, Department of Defense. The electronic dynamometer was purchased with the support of the University of Illinois Research Board. M.K. is supported by NIH training grant 5 T01 MH 10715. A paper based on the same study was read before the Neuroscience Society, 3rd annual convention, San Diego, Calif., November 1973. Evelyn Satinoff, Steven Hillyard, Steven Porges, and Walter Ritter were constructively critical.

3 May 1974

Circadian Oscillations in Rodents: A Systematic Increase of Their Frequency with Age

Abstract. *The circadian activity rhythms of golden hamsters and two species of deermouse, when released from a light-dark cycle of 12 hours light and 12 hours of darkness into constant darkness, had progressively shorter periods as the animals became older. A possible bearing of this fact on the aging process is briefly outlined.*

In the course of analyzing data accumulated over many years on the properties of free-running and entrained circadian pacemakers in rodents (1) we have encountered a previously unrecognized phenomenon. The period (τ) of the free-running circadian activity cycle in golden hamsters (*Mesocricetus auratus*) and two species of deermouse (*Peromyscus maniculatus* and *P. leucopus*) becomes continuously shorter as the animals age. Since these are the only species for which we have the relevant data and the effect occurs in all three, it is an interesting possibility that the phenomenon will prove to be more general. If so, it merits attention, not only as a significant variable to be controlled in the study of circadian pacemakers, but as a previously undetected aspect of the aging process.

Our experiments (2) on the circadian rhythm of activity in these rodents involved about 200 animals. The experiments included many different protocols designed primarily (i) to elucidate the stability and lability of free-running circadian pacemakers, (ii) to investigate inter- and intraspecific differences in their phase-response curves, and (iii) to relate their entrainability by light-dark cycles to these phase-response curves with the use of a model (3) based on the behavior of the circadian pacemaker in *Drosophila*.

Because of (i) the complexity in the succession of experimental treatments each animal experienced and (ii) the fact, already known and extensively further documented by the experiments themselves (1), that τ is subject to small but significant change traceable

to the oscillator's immediately previous experience, we had not thought to look in the data for systematic changes in τ attributable to the animals' ages. Indeed, the effect was initially detected in *M. auratus* and *P. maniculatus* when we sought evidence on the reproducibility of an individual animal's period (τ) in two prolonged (~ 3 months) free runs in constant darkness (DD) 9 months apart, each following an identical, and prolonged (~ 4 months) period of entrainment to the same (LD 12:12) light cycle (Fig. 1): τ was shorter when the animals were older.

The identity of the prior light cycle eliminates the possibility that this difference in τ was caused by differences in the pacemaker's previous experience (a so-called "aftereffect"). Aftereffects on τ have so far been recognized as a consequence of previous exposure to constant light, single light pulses, different photoperiods, and LD cycles with a period (T) different from 24 hours (5-7). Even the standard LD 12:12 ($T = 24$ hours) light cycle has an often significant effect in bringing τ to a value closer to 24 hours than it eventually assumes when allowed to free run for a long time (Fig. 1) (1). It follows, therefore, if one wishes to assay the effect on some variable, like age, on the frequency of a circadian rhythm (i) that the experience prior to the free run must be identical and (ii) that the effect will be better detected in a long free run when the aftereffect of that prior experience has decayed.

Figure 2 summarizes the two τ -estimates (8) obtained, 9 months apart, for each of the 17 animals in the initial comparison. In all eight hamsters and in all but one of the ten *P. maniculatus*, the τ value was smaller at age 14 to 16 months than at age 5 to 7 months.

Our data for *P. leucopus* involve eight animals which experienced a short (15 days) DD-free run (following LD 12:12) at ages 10 to 14 months, and a long (77 days) DD-free run (following LD 12:12) at ages 24 to 28 months. Seven of these eight animals also had a shorter circadian period when they were older (Fig. 2).

In hamsters an estimate of the age effect can be made over a wider range of ages than Fig. 2 covers. Figure 3 shows all the available (51) τ -estimates from long free runs (> 30 days) in hamsters of known age. The changes are small, but nevertheless statistically significant, as demonstrated by Pear-