

ered by the theta rhythm in the cat is lower (3 to 7 hz).

To get a quantitative evaluation of the effects of reward and nonreward on theta frequency, we used an automatic wave-count device (pass-band, 3 to 50 hz) constructed in the laboratory. This counted the number of times per second the hippocampal record rose above the zero-volt base line set by the resting position of the EEG pen. It was set into operation when the rat crossed the final photobeam in the runway and printed out the wave-count for each of the 5 seconds the animal remained in the goalbox. The mean goalbox wave-count for seven rats during an initial series of rewarded trials was 7.03 (S.D. = 0.64); on a subsequent series of nonrewarded trials it was 7.70 (S.D. = 0.77) the difference being significant at $P = .01$ (t for correlated means = 5.45, d.f. = 6). Similar differences between rewarded and nonrewarded trials appeared in animals trained on a sequence of mixed reward and nonreward.

That these small but highly consistent frequency shifts have some functional significance is strongly suggested by the results of a second experiment in which we examined the effects of sodium amobarbital on the threshold for septal driving of the hippocampal theta rhythm. Stimulation (pulse duration, 0.5 msec) was applied to the septal electrode by a constant-current square-wave generator constructed in the laboratory. In agreement with observations on rabbits reviewed by Stumpf (5), low-frequency stimulation drove the hippocampal theta rhythm, as judged by synchrony between the stimulus trace and the hippocampal EEG displayed on the cathode ray oscilloscope. Stimulation at 1-hz steps within the range 6 to 10 hz caused a driven wave to appear in the hippocampus at the corresponding frequency (Fig. 2). An excellent driven response could also be obtained at 30 hz (Fig. 2). Using the runway already described, and a dose of 20 mg/kg injected intraperitoneally, we determined the effect of sodium amobarbital on the threshold for septal driving of the hippocampus at approximately 2-minute intervals for 10 to 40 minutes after injection, the period over which the behavioral effects of this drug have usually been noted (3). Control experiments with saline injections showed that these had no effect on driving thresholds.

The effects of amobarbital on driving thresholds in two groups of five rats tested, in one case, at approximately 1-hz steps over the range 5.9 to 10.0 hz and, in the other, at 7.7 and 29.4 hz are shown in Fig. 2 as a function of driving frequency. Within the theta range, the threshold for a driven response at 7.7 hz is considerably lower than at any other frequency investigated ($P < .001$). Amobarbital completely eliminates the advantage of this frequency for driving within the theta range. This selective effect of amobarbital on 7.7 hz is further emphasized by the fact that the drug fails to alter the threshold for driving 29.4 hz, a frequency that can be driven at about the same threshold as 7.7 hz when no drug is given. Over the two groups of rats taken together, amobarbital raised the 7.7-hz driving threshold by about 70 percent ($P < .01$). These results of the driving experiment are consistent with the changes produced in hippocampal electrical activity by amobarbital: there is a shift from the dominant 7.5 to 8.5 hz theta of the normal record to a lower-frequency theta of about 6 to 7 hz together with an increase in fast-wave activity [(5) and Fig. 1].

Thus, the effects of amobarbital on septal driving of the theta rhythm are disproportionately great precisely for that frequency (7.5 to 8.5 hz) which is spontaneously displayed in the hip-

poampal record when the rat is exposed to novelty or frustrative nonreward, while frequencies spontaneously displayed when the rat is running toward an expected reward or consuming a reward are unaffected. These results suggest that a hippocampal theta rhythm at a frequency of about 7.7 hz plays an important role in the control of behavioral responses to frustrative nonreward, and that injections of amobarbital (3), medial septal lesions (2), and hippocampal lesions (1) all affect this kind of behavior by disrupting the hippocampal theta rhythm.

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Antarctic Pelecypod Faunal Peculiarities

The living antarctic pelecypod fauna does not fit all of the postulates on cold-water marine bivalve faunas as proposed by Stehli *et al.* (1). Some of their assertions concerning the general characteristics of cold-water marine pelecypod faunas are these: (i) Cold-water pelecypod faunas virtually lack endemic families and consist of families that are cosmopolitan in distribution. Unfortunately, the authors do not state what they consider an endemic family to be. (ii) Cosmopolitan families, which comprise nearly all of the cold-water pelecypod faunas, are relatively old and include few families that evolved within the past 50 million years. In other words Stehli *et al.* claim that, at least as a general rule, endemic families are young families and cosmopolitan families are old families. This is simply the Willis theory of age and area,

which was proposed in 1922 and which was ably reviewed by Lotka (2). Applied to living pelecypod families, this is generally true, but there are some exceptions such as trigoniids and astartids. Also, a few old families are today confined to warm water, such as the pteriids and the pinnids.

Among shallow-water marine pelecypod faunas, that of the antarctic has several peculiar aspects. There is an uncommonly high percentage of small-sized species. Sixty-one percent of the antarctic pelecypod species are no more than 10.0 mm in height or length; the fauna with the next highest percentage of small-sized species is the South Australian with 38 percent (3). The antarctic has an uncommonly low percentage of infaunal species—59 percent as compared to the arctic, which is about average with 73 percent (4).

Table 1. Percentage of old families and percentages of species belonging to old families in seven marine pelecypod faunas. Data from (6).

Region	Old families (%)	Species in old families (%)
Abyssal	30	43
Arctic	30	52
Antarctic	30	26
South Australia	19	21
West Africa	23	19
Caribbean	20	23
Northern Panamic	19	22

There are no species of deposit-feeding tellinaceans in the antarctic; all other marine pelecypod faunas have at least a few species of deposit-feeding tellinaceans (5).

In terms of the families and the amount of diversity within them, the arctic fauna includes more numerous cosmopolitan groups than does the antarctic fauna, for example, the abundance of the Mytilidae, Cardiidae, Tellinidae, and the presence of the Veneridae in the arctic. The diversity of the Philobryidae and Cyamiidae in the antarctic gives that pelecypod fauna a much more provincial aspect (6). To further emphasize the biological differences between the two polar pelecypod faunas, no species, only 28 percent of the genera, and only 43 percent of the families occur in both polar regions (6).

The antarctic pelecypod fauna is dominated by three families—the Limopsidae, Philobryidae, and Cyamiidae. These three have more than one-third of the species of antarctic pelecypods, and none of these families is found living in arctic waters. The Limopsidae are also absent from many shallow-water tropical faunas and could hardly be considered a cosmopolitan family. The Limopsidae are found in strata as old as Jurassic but could not be considered a truly old family of pelecypods. The Philobryidae, which are so common in cold and temperate waters of the Southern Hemisphere, are represented by only one species in the Northern Hemisphere, *Philobrya setosa* (Carpenter), which is found from Lower California to the Gulf of Alaska. Therefore, this family is not cosmopolitan, and it is not known in the fossil record before the Tertiary. The Cyamiidae are a fami-

ly with most of their species found in the cold and temperate water of the Southern Hemisphere. Like the Philobryidae, this family is unknown before the Tertiary and would certainly be considered a young noncosmopolitan family.

Apparently Stehli *et al.* counted only the families in the various faunas and paid no attention to the number of species in each family. This can result in an inaccurate picture of the total pelecypod fauna of a region. For example, should one give as much weight to the presence of one rare species of astartid in a fauna as to 12 species of philobryids? The astartids and mytilids, both ancient stocks, are represented by only one species each in antarctic waters.

In Table 1 I show how differences can arise when data are used in different ways. Only the abyssal, arctic, and antarctic are cold-water faunas. I have included the following families in the Paleozoic or old category: Nuculidae, Nuculanidae, Solemyidae, Arcidae, Pectinidae, Mytilidae, Pteriidae, Trigonidae, Pinnidae, Limidae, and Astartidae. Perhaps some others should be included, such as the Isognomonidae, Ostreidae, Carditidae, and Crassatellidae, but at least some of these families may be doubtfully Paleozoic; and only the Carditidae, with two species in each polar region, are found in cold water. I believe, therefore, that I am showing no bias.

There are higher percentages of old families in the cold-water faunas (Table 1). However, when species belonging to the old families were counted, the results are considerably different. The antarctic has only a slightly higher percentage of species belonging to primitive families than do the warm-water faunas. The arctic fauna, on the other hand, has an astoundingly high percentage of species belonging to old families, being twice as high as the antarctic. I noted this marked primitive aspect of the arctic pelecypod fauna in 1955 (7). This great difference in percentage of species belonging to old families exemplifies another basic difference between the two polar faunas.

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Intermodal Equivalence of Stimuli in Apes

Davenport and Rogers (1) incorrectly cite a report of mine (2) as suggesting that "symbolic language may be essential in the mediation of certain cross-modal phenomena." In both that cited report and in others I not only gave detailed arguments against this view, but also argued strongly for an explicitly opposed thesis. I stated that "*it cannot be argued that the ability to form cross-modal associations depends on already having speech*, rather we must say that the ability to acquire speech has as a prerequisite the ability to form cross-modal associations. An important area of research which remains to be studied extensively is that of the course of acquisition of cross-modal learning in childhood before speech is fully developed" (italicized as in original report) (2, p. 275).

My argument was therefore that the ability to form cross-modal linkages was a necessary (although not a sufficient) condition for the acquisition of language. In view of the recent studies of the Gardners and Premack (3), which appear to show that chimpanzees do have some linguistic abilities, the finding of Davenport and Rogers that these animals can carry out certain cross-modal tasks is in conformity with my views.

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