natural levels of AG are unlikely to inhibit growth of *S. eridania*, although growth might be reduced on plants containing unusually high concentrations of the compound. This result is consistent with the finding that generalists exhibit great variation in growth rate on a range of food-plant species but that growth on some species is comparable to that of specialists feeding on similar plants (*15*, *17*).

The mechanisms of toxicity of allylglucosinolate to *P. polyxenes* and, at higher concentrations, to *S. eridania* remain unknown although toxicity is likely to be a consequence of hydrolysis to allylisothiocyanate (*5*). We found this compound to be present in the gut contents, feces, and various body tissues of *P. polyxenes* larvae that had ingested AG (*18*). The mechanisms of counteradaptation in *P. rapae* and *S. eridania* are likewise unknown, although AG is known to stimulate induction of microsomal mixed-function oxidase enzymes in *S. eridania* larvae (*19*).

Feeny (*20*) has suggested that certain chemical compounds in plants may serve as qualitative barriers to herbivorous insects. Although effective even in small amounts against nonadapted herbivores, they are especially vulnerable to the evolution of counteradaptations and may have little or no dosage-dependent effect on the growth of insect species that are specialists at feeding on plants containing them. Allylglucosinolate seems to be an example of such a barrier.

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11. For the four AG concentrations, measured as 0.04 ± 0.01, 0.74 ± 0.05, 1.83 ± 0.15, and 2.39 ± 0.25 percent (fresh weight of leaf), values of relative consumption rate were, respectively, 1.09 ± 0.08, 1.76 ± 0.11, 1.32 ± 0.10, and 1.58 ± 0.15 mg (dry weight) per milligram of larval biomass (dry weight) per day; values of relative growth rate were, respectively, 0.18 ± 0.01, 0.18 ± 0.01, 0.17 ± 0.01, and 0.15 ± 0.01 mg (dry weight) per milligram of larval biomass (dry weight) per day; values of instar duration were, respectively, 5.0 ± 0.0, 4.6 ± 0.5, 4.7 ± 0.4, and 4.9 ± 0.3 days.
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Prediction of Learning Rate from the Hippocampal Electroencephalogram

Abstract. *Samples of spontaneous electroencephalographic (EEG) activity from the dorsal hippocampus of rabbits were recorded immediately before classical conditioning of the nictitating membrane response. Computer analysis revealed a significant predictive relationship between EEG frequency characteristics and the subsequent rate of learning.*

The hippocampal region of the forebrain has been widely implicated in learning and related processes (*1–3*). In addition to lesion effects on learning (*2*, *4*) and changes in neuronal unit activity during the course of conditioning (*5*, *6*), the frequency characteristics of the hippocampal electroencephalogram (EEG) have been reported to be correlated with acquisition (*7*) or with other behavioral processes accompanying learning, such as attention, arousal, consolidation, or the motor response itself (*8–12*).

In the rabbit, the hippocampal EEG is dominated by rhythmic slow activity (RSA), a large-amplitude, almost sinusoidal waveform of approximately 3 to 7 Hz, which occurs (i) in the waking state, (ii) in response to many forms of stimulation, and (iii) during paradoxical sleep (*9*, *13*). Previous research in our laboratory has demonstrated a significant positive relationship between increases in hippocampal unit activity and the development of classical conditioning of the nictitating membrane (NM) response [tone conditioned stimulus (CS); air puff unconditioned stimulus (UCS)] in the rabbit (*5*), but little is known about the relationship between hippocampal EEG and learning or between the EEG and unit activity under this paradigm. We now present an initial and unexpected result of our investigation of the relations among hippocampal EEG, neuronal unit activity, and learning: a significant and predictive correlation between pretraining frequency characteristics of the EEG in the dorsal hippocampus and the subsequent rate of classical conditioning.

Each of 16 New Zealand White rabbits (*Oryctolagus cuniculus*) was anesthetized with halothane (Fluothane) and implanted with one epoxylite insulated stainless-steel electrode having a recording surface of 5 to 10 μm at the tip and 50 to 60 μm along the shaft. Electrodes were held in place with dental acrylic and skull screws after being localized in the dorsal CA1 of the left hippocampus by a combination of stereotaxis and physiological recording during surgery. One skull screw served as a reference for recording. After at least 1 week of recovery, animals were restrained in the conditioning chamber, and a 2-minute sample of both EEG and multiple-unit activity from the same electrode was recorded on AM-FM tapes. Then conditioning was begun, according to a standard paradigm (*14*). Each animal was given 13 blocks of paired CS-UCS trials per day, each block consisting of eight tone (1 kHz, 85 dB, 350 msec)–air puff (100 msec, 3 pounds per square inch) presentations and one test trial (CS alone). The interstimulus interval was 250 msec (tone and air puff overlapped) and the intertrial interval was randomly 50, 60, or 70 seconds. Daily conditioning sessions were given for a maximum of 4 days (468 trials) or until the animal emitted conditioned responses (CR's) in eight of nine consecutive trials. A CR was defined as an NM movement of greater than ½ mm prior to the onset of the US, or within 500 msec of CS onset on a test trial.

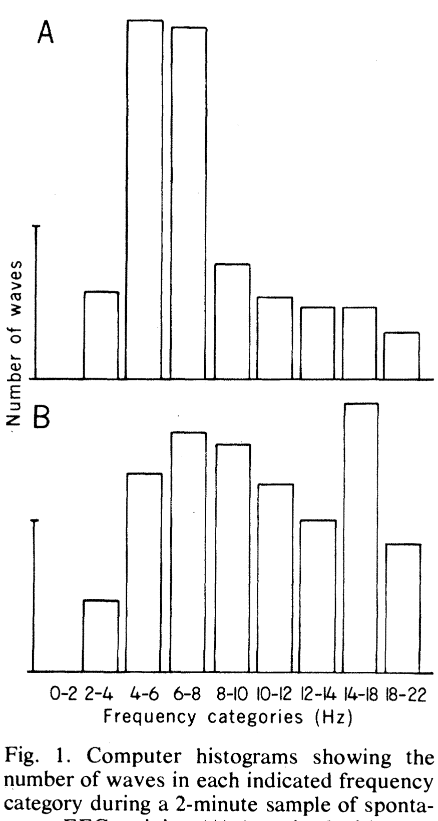

Fig. 1. Computer histograms showing the number of waves in each indicated frequency category during a 2-minute sample of spontaneous EEG activity. (A) An animal with a relatively rapid rate of conditioning. (B) An animal that failed to reach criterion in the 4 days of conditioning. The calibration mark on the ordinate represents 100 waves.

Multiple-unit neuronal records from the tapes were band-pass filtered (500 to 5000 Hz) and analyzed on a PDP-12 computer (*5*). Multiple-unit responses recorded during conditioning from the pyramidal-cell layer of the hippocampus were essentially identical to those reported before—a rapid and substantial increase in the UCS period and subsequently in the CS period as behavioral learning developed (*5*). The EEG records were low-pass filtered (0 to 25 Hz) and analyzed by a zero-crossing program, which measured the waveform period to the nearest 1 msec, converted the period to a frequency, and accumulated the number of waves in each of nine frequency categories: 0 to 14 Hz in 2-Hz increments; 14 to 22 Hz in 4-Hz increments (*10*, *15*). Figure 1 shows the histogram output resulting from the spontaneous activity before training of an animal with a relatively fast conditioning rate [(A) 84 trials to criterion] and one with a slow rate of conditioning [(B) 468 trials, no criterion met]. Relatively more activity was seen in the higher-frequency categories on the part of the slow-learning animal and in the lower frequencies in the case of the rapid-learning animal.

Pearson product-moment correlation coefficients were computed between the amount of time (*16*) in each frequency category and the number of trials to reach the behavioral criterion for conditioning. The time score in each frequency category higher than 8 Hz was positively correlated with trials to criterion; overall, the time spent in higher-frequency activity (8 to 22 Hz, inclusive) was correlated with trials ($r = +.69$, d.f. = 14, $P < .01$). In contrast, the amount of low-frequency RSA (2 to 8 Hz) was negatively correlated ($r = -.66$, d.f. = 14, $P < .01$) with trials to criterion. The coefficients for each separate category below 8 Hz were all negative. The cutoff between positive and negative correlations with rate of acquisition on this task, at about 8 Hz, corresponds to pharmacological and behavioral data indicating that low- and high-frequency RSA may be generated by differing neural mechanisms and may be correlated with different overt behaviors of the rabbit (*12*, *17*). In addition, electrical stimulation studies have localized brainstem and hypothalamic sites that produce contrasting effects on hippocampal EEG activity and that appear to correspond to different monoamine pathways (*11*, *18*).

In order to characterize the overall (2- to 22-Hz) EEG in terms of this low-high frequency dichotomy, a ratio of the percentage of 8- to 22-Hz activity to that of 2- to 8-Hz activity was computed. The ratio for the values in Fig. 1A was 0.40, while that for Fig. 1B was 1.33. The correlation between this measure and trials to criterion was significant ($r = +.72$, d.f. = 14, $P < .01$). The trend of the correlation was linear (Fig. 2). This EEG difference between animals that learned rapidly and those that learned slowly was reflected in the unit activity as well. Standard scores were computed (*5*) to quantify the change in unit activity during the UCS period in the first block of eight paired trials. In the three rabbits that learned fastest (with the most 2- to 8-Hz activity in the EEG), hippocampal unit activity substantially increased during the first trial block (median standard score = 11.2); in the three slowest animals, activity was either slightly suppressed or unchanged (median standard score = −1.2).

A high : low ratio of frequencies was also computed from a 2-minute sample of spontaneous EEG recorded after the session in which each animal reached behavioral learning criterion. The difference between this ratio and the pretraining ratio was also correlated with trials to criterion ($r = -.865$, $N = 16$, $P < .01$), indicating reliable frequency changes during learning.

The major finding of this study is that a brief time sample of hippocampal EEG taken before the onset of training predicts subsequent learning rate, even over a period of days. A higher proportion of hippocampal RSA in the 2- to 8-Hz range predicts faster rates of conditioning,

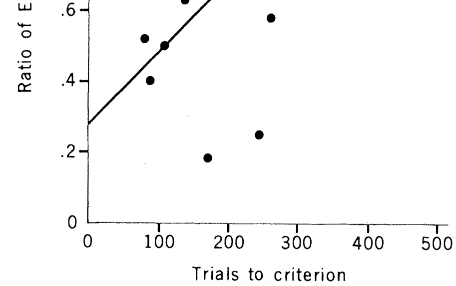

Fig. 2. Scatterplot and best-fitting regression line for the relationship between trials to criterion and the EEG frequency ratio (the percentage of 8- to 22-Hz activity divided by the percentage of 2- to 8-Hz activity).

while a greater proportion of higher frequencies (8- to 22-Hz) predicts slower rates of learning. To our knowledge, this is the first demonstration that a neurophysiological measure taken before training can predict the subsequent behavioral rate of learning. The result is consistent with consolidation studies showing a positive relationship between amount of theta in the posttraining EEG and subsequent retention performance (*10, 15*), and with studies reporting changes in hippocampal frequency during training that are correlated with the degree of learning (*7*). This result also seems relevant in the context of mathematical learning theories (*19*), in that a physiological measure can increase precision in estimating acquisition rate parameters. Our data support the hypothesis that the hippocampus has a critically important role in learning and raise the possibility of manipulating learning with independent variables influencing hippocampal RSA. Although some studies have indicated that massive lesions of either the hippocampus or the septum do not impair NM conditioning (*20*), more selective disruption of hippocampal activity by stimulation or making lesions of discrete afferent pathways significantly retards the rate of learning (*21*). Finally, the data presented here support the general notions that "behavioral state" plays an important role in learning (*22*) and that hippocampal EEG is a potentially powerful index of behavioral state (*3, 22*).

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Mating Behavior and Related Morphological Specialization in the Uropodine Mite, *Caminella peraphora*

Abstract. *Sperm transfer in* Caminella peraphora *is closely associated with secretion and construction of a female-associated structure, the signet ring. The ventral portion of the ring serves as an external spermatheca early in mating. Although sperm assimilation occurs prior to development of the dorsal ring elements, male participation is instrumental in successful ring completion.*

Caminella peraphora Krantz and Ainscough (*1*) is a nematophagous uropodine mite that has been recovered only in moist to semiaquatic habitats on two neighboring mountains in the Coastal Range of western Oregon. Unlike other known acarines, females of *C. peraphora* carry a large, noncellular, saclike structure dorsally, fused to a ring of similar material which girdles the body behind coxae IV (Fig. 1, D to F). It was suggested (*1*) that this "signet ring" might be a flotation mechanism which aided in dispersal of eggs or larvae, and that formation of the ring probably occurred prior to the last nymphal molt. Later, Ainscough (*2*) speculated that the ring was an external spermatheca, and observed that it developed after ecdysis.

As with most uropodines, the life cycle of *C. peraphora* includes egg, larval, protonymphal, deutonymphal, and adult stages. Oviposition is sporadic under laboratory conditions (*3*), but viable eggs are produced throughout the life of the female. An average of 68 days was required for newly oviposited eggs ($N = 3$) to reach the deutonymphal instar. Laboratory-cultured deutonymphs failed to attain adulthood, although specimens survived for up to 37 days in this stage. Field-collected deutonymphs occasionally would molt successfully and mate, but often only after several weeks in captivity. The average developmental time observed for each life stage was: egg to larva, 22 days (21 to 23, $N = 5$); larva to protonymph, 24 days (22 to 32, $N = 5$); protonymph to deutonymph, 21 days (19 to 25, $N = 3$).

Female deutonymphs of *C. peraphora* are attractive to males shortly before female ecdysis. A single male "courts" each deutonymph, remaining by her side until she molts. In those instances where other males attempt to intervene, a brief, nonaggressive contact between the defending male and encroaching individuals is sufficient to disperse would-be suitors. Mating proceeds soon after female emergence, with the male approaching the female from the posterior and mounting her dorsum. Mounting occurs swiftly, with no further courtship being observed. The female begins a lateral rocking which may persist for 30 minutes or more. After this time, the male reverses his position on the female dorsum so that he is facing posteriorly (Fig. 1A). The male then initiates a later-