Title

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CHAPTER 14

Evolutionary Restraints on Learning: Phylogenetic and Synaptic Interpretations

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INTRODUCTION

The notion that some organisms may have different propensities to learn specific relationships between themselves and their environments—relationships that have been important on the evolutionary time scale—has been emphasized by several of the contributors to this volume, notably Gould (Chapter 11) and Shettleworth (Chapter 13). In keeping with this theme, I shall examine several aspects of evolutionary restraints on learning, emphasizing two types of analysis: (1) correlations of behavioral and situational changes among animals in natural settings and (2) correlations of experiential and neuroanatomical changes generated by varying behavioral activities. Correlations of these disparate types of analyses are likely to reflect the influences of both phylogenetic and ontogenetic processes of adjustment, some of which have been restrained by phylogenetically old and important contexts.

Levels of Analysis in the Laboratory and Field

Some aspects of the notion of evolutionary restraints have been incorporated into the development of general process learning theory, particularly the hypothesis of "preparedness" (Seligman, 1970), and have led to a large number of studies of taste aversion in a variety of taxa (Garcia, McGowan, & Green, 1972; but also see Cooke, Delaney, & Gelperin, Chapter 10, this volume, and Rescorla, Chapter 12, this volume). Theoretical arguments for more research on learning under natural conditions, as opposed to restricted laboratory conditions (see Johnston, 1981; Johnston & Turvey, 1980), have prompted new studies seeking to broaden the generality of experimental findings to both laboratory and field settings. However, problems of interpretation are encountered when laboratory conditions differ markedly from

field conditions. As an example of the problems emerging in the study of food hoarding and recovery by marsh tits, Shettleworth and Krebs (1982) describe the limitations of confined aviaries that restrict the spacing and complexity of storage sites as compared with the high variability of natural habitats. From this perspective, it appears that the gain in experimental precision in laboratory settings may be offset by physical limitations imposed by those settings. Thus, Shettleworth (Chapter 13, this volume) concedes that laboratory studies may reveal little information about how birds store and recover food in the wild. On the other hand, experimental questions about learning and memory can be tailored specifically to the limitations imposed by laboratory setups. These limitations are most apparent in instrumental learning situations in which the availability of changing environmental features is severely restricted. For example, Rescorla (Chapter 12, this volume) discusses the experimental situations in which animals learn a wide range of signal–signal and signal–consequence associations.

In laboratory setups with little environmental variation, it is not surprising that animals learn to organize their behaviors in ways that maximize the processing of any *invariances* in environmental features (e.g., Gibson, 1966, 1979) that emerge from experimental manipulations. Because experience is restricted to these settings, the animal focuses its attention on subtle changes in organism–environment relationships that might be quite apart from those encountered in the wild (Menzel, 1975). The fact that animals born and reared under laboratory conditions almost never experience the ecologically important tasks of finding food in diverse microhabitats, of searching for mates and defending nest sites, and of engaging or avoiding predators, means that detection of minor variation of independent variables could become very important during associative learning in impoverished settings. In many ways, the rich complexity of pairwise associative learning described by Rescorla might represent a fraction of the true learning capabilities that animals exhibit in the wild.

In contrast with the desirability of extending laboratory studies to field conditions, laboratory studies are paramount for examining the neurobiology of learning and memory, particularly those involving invertebrate taxa that show Pavlovian conditioning (e.g., Alkon, Chapter 1, this volume; Cooke, Delaney, & Gelperin, Chapter 10, this volume). As compared with vertebrates and invertebrates that range over large areas while foraging or searching for mates away from nest sites, terrestrial and aquatic mollusks have limited behavioral repertoires that are quite amenable to laboratory study. The choice for laboratory study of the terrestrial slug (*Limax maximus*) has proved to be exceptionally fruitful, especially the documentation that these mollusks exhibit higher order conditioning (see Gelperin, Hopfield, & Tank, 1985). Furthermore, lip–brain preparations of *Limax* can retain for several hours higher order associations learned initially in intact animals.

As in the studies of *Aplysia* (Hawkins, Abrams, Carew, & Kandel, 1983; Walters & Byrne, 1983), however, the continued focus of attention on bio-

physical changes at the synaptic level restricts the range of inferences about how information emerges at the higher levels of functioning neuronal networks. Moreover, there is the ever present risk of treating any one level of analysis, such as synaptic modification (e.g., Kandel & Schwartz, 1982, p. 441), as if it had ontological primacy; that is, there is a tendency to collapse the hierarchy of higher levels of relationships, such as neuronal circuits and behaving organisms, into that one level of causal description (Marr, 1982; Overton, 1976; Rose, 1980). Computer models of neuronal networks with highly deterministic circuits, in which output behavior is modified by adjusting a single variable such as "synaptic strengths," also give primacy to a single level of analysis (e.g., Gelperin *et al.*, 1985). On the other hand, computer models that incorporate more than one level of analysis with probabilistic features, such as growth of new circuits (Pellionisz, Llinás, & Perkel, 1977), provide for more realistic simulations that could prompt further experimentation. Although molluscan neural circuits are often depicted as deterministic, recent findings by Bailey and Chen (1983) suggest that growth of new connections might be involved in modulating habituation and sensitization in *Aplysia*.

To summarize the preceding points, much of my critique has focused on the reductionistic error of giving primacy to any one level of analysis, molar or molecular. My concern here also extends to problems of generating inferences about how learning works from findings obtained under highly restricted circumstances. As I extend this argument further, dropping from one extreme level to the other, I shall concentrate on the integration of learning and instinct as a continuum of the same general phenomena, that is, multilevel adjustments of organisms to varying environmental conditions occurring over phylogenetic, ontogenetic, and proximate time scales (see Coss & Owings, 1985).

LEARNING AS ADJUSTMENT OF INSTINCT

Based on his acute observations of the first behaviors of deprivation-reared chicks, Spalding (1873) was one of the earliest proponents of a hierarchical view that learning capabilities are restrained by instinctive mechanisms shaped over successive generations by natural selection. With birth or hatching, according to Spalding, "animals may be awaking up in a world with which they are, in greater or less degree, already acquainted." In essence, Spalding considered instinct to be a *product* of the process of natural selection, a view that was later elaborated by Lorenz (1950, 1951) and further exemplified by Riedl (1983) with his hierarchical structure of Aristotelian causes.

Gould (Chapter 11, this volume) continues this tradition, extending the ideas of how Pavlovian conditioning shares features in common with the ethological construct of the innate releasing mechanism (IRM). Although Lorenz (1950, 1951) also observed some of these similarities, noting that the

Pavlovian unconditioned response (UR) could be elicited by an IRM, he differs considerably from Gould's notion that the sign stimulus is just a tuned up conditioned stimulus (CS). The IRM, according to both Lorenz (1950, 1951) and Tinbergen (1951) is a receptory apparatus that inhibits the expression of innate activities. Such an apparatus, with peripheral or central filtering properties (Marler, 1961), releases its inhibition with perception of a simple, key stimulus element—the sign stimulus. The IRM was not thought to function at all in a cognitive manner in which a learned Gestalt was built up through successive experiences. In the case of foraging honey bees, an IRM "tuned" to radially symmetric flower forms could direct the circumstances for learning which flowers yielded pollen or nector; that is, the IRM was an adjunct system that complemented the learning process.

My own views of the IRM (Coss, 1965, 1968) have changed considerably as a result of more recent experiments on antipredator behavior showing that instinctive processes, such as predator recognition and concomitant orchestration of motor patterns, operate on Gestalt principles with cognitive properties not unlike those observed in associative learning (Coss, 1978a, 1979a). For example, taxa as diverse as newborn humans and newly hatched or isolation-reared African jewel fish (*Hemichromis bimaculatus*) innately recognize the lineamental Gestalt of two facing eyes as facial features (see Coss, 1979a, 1979b; Goren, Sarty, & Wu, 1975). Experience with faces subsequently results in the development of individual recognition that is guided by the salient aspects of two facing eyes. Learning specific facial features is a process of perceptual refinement embedded in the overall innate substrate, which affords the recognition of the Gestalt. This process of individual recognition can be disrupted by cerebral deficits leading to prosopagnosia in autistic children and by prolonged social deprivation in jewel fish (for review, see Coss, 1979a, 1979b; Coss & Globus, 1979). Unlike the higher order cognitive processes underlying individual recognition, which appear labile to developmental anomalies, recognition of two facing eyes persists as a deeply canalized perceptual process (Bateson, 1979; Coss, 1979a; Sæther, 1983; Waddington, 1957) engendering abnormal levels of gaze aversion and flight behavior in autistic children (Richer & Coss, 1976) and deprivation-reared jewel fish.

Because of the highly interactive nature of changing organism–environment relationships during ontogeny, it seems much more appropriate not to treat instinctive behaviors as mediated by isolated mechanistic variables (Pepper, 1942) like IRMs. I must note here that instinctive processes mediating the execution of relatively stereotyped behaviors to changes in highly specific environmental features appear mechanistic because they engage in very brief periods of decision making. Giant Mauthner cells in fish (Diamond, 1971; Eaton, 1983), for example, process sensory input extremely rapidly during the initation of escape behaviors. Similarly, but involving the operation of much more complex neural circuitry, prey-catching behavior by toads

and frogs is thought to be mediated by a classic example of an IRM. Recent studies by Ewert, Burghagen, and Schürg-Pfeiffer (1983) have focused on the ability of this system to extract the Gestalt properties of prey-like visual patterns and engage in goal-oriented decision making. The cognitive, dynamic aspects of this innate system do not fit well with the original model of the IRM with its inhibition releasing properties proposed by Lorenz and Tinbergen. Contemporary use of this term by ethologists and neuroethologists best reflects the inertia of early ethological terminology rather than empirically derived functional interpretations.

Under circumstances in which urgency of correct performance has not received strong natural selection, innate behaviors are much more variable (Schleidt, 1974) and performances can be adjusted by repeated experiences. The learning of song dialect by some birds characterizes a less urgent context in which ontogenetic adjustments refine innate predispositions (Gould, Chapter 11, this volume; Marler, 1976), but even some of these assumptions are being challenged (see Baptista & Petrinovich, 1984). A similar case for ontogenetic adjustments can be made for learning cognitive maps (Menzel, 1978) of patchy food sources, refuge sites, and locations where predatory attacks might occur.

In our own work on the California ground squirrel (*Spermophilus beecheyi*), Leger, Owings, and Coss (1983) found that, under field conditions, the utility of some behaviors varied spatially with respect to the probability of encountering biologically important factors in different microhabitats. Extending this line of argument further, we have noted the numerous occasions in which ground squirrels appear to make cognitive inferences about both present and future contextual properties of these microhabitats (for review, see Coss & Owings, 1985). My use of the term "context" here differs considerably from that described by Rescorla (Chapter 12, this volume) in which context is treated as just another signal to be associated with a CS. I also use the term differently from that appearing in some of the communication literature (e.g., W. J. Smith, 1977), which is more in keeping with the above definition; that is, multiple sources of information outside the organism can be "contextual" to specific communicative events.

From an alternative point of view, context is the *entire set of circumstances*, comprising both the endogenous aspects of the organism, including its expectancies about future events and consequences, and the exogenous features of the locality. Because organisms are dynamic, contextual relationships are constantly in flux. Research by Shalter (1978) provides a clear example of how context is not just a set of adjunct environmental features associated with an important source of information. A stuffed pigmy owl (*Glaucidium passerinum*) was mounted on a pole facing each of the nest holes of seven resident pairs of pied flycatchers (*Ficedula hypoleuca*). These birds were quite disturbed by the presence of the model predator and exhibited mobbing calls that waned over a few minutes. The owl was then removed

and replaced at 15-minute intervals and mobbing calls were again elevated in number. With successive trials, however, the tendency to mob began to habituate. Shalter then moved the owl about 90° relative to their nest holes. The birds were quite disturbed by the owl in its new location, which indicates that habituation had occurred to the nonrealistic, static owl–pied flycatcher relationship and not to the owl model *per se*.

Ground Squirrel Antisnake Behavior

California ground squirrels during interaction with the predators that eat them, adjust their behaviors in ways that reflect the potential risks associated with each type of predator. Fast-moving predators, like eagles and hawks, engender conditions of great urgency after these predators are spotted at a distance. Ground squirrels typically emit single-note alarm calls when startled by the bird's appearance, and they dart toward their home burrows if the bird's trajectory places them at risk (Coss & Owings, 1985; Leger & Owings, 1978). Under less urgent conditions, in which a dog is seen at a distance, ground squirrels emit much more variable alarm calls and may not run to home burrows immediately but may choose to climb rocks to get a better view (Owings & Virginia, 1978).

Rattlesnakes (*Crotalus viridis oreganus*) and gopher snakes (*Pituophis melanoleucus catenifer*) are also important predators of ground squirrels and have been so for several million years. At the San Joaquin Experimental Range in the Sierra Nevada foothills near Fresno, ground squirrels may constitute up to 69% of the diet of rattlesnakes (Fitch, 1948). Unlike their mammalian and avian predators, these slow-moving predators can be approached safely. Ground squirrels will often harass and even attack them, employing behaviors similar to those seen during agonistic encounters among themselves.

Upon detection of rattlesnakes and gopher snakes, ground squirrels exhibit tail hair erection and flag their tails vigorously (see Hennessy, Owings, Rowe, Coss, & Leger, 1981). This activity may attract the attention of other squirrels (Figure 14.1). When snakes are approached cautiously, ground squirrels alternate between elongate investigative postures and crouching, which positions the hind legs for evasive leaping (Coss & Owings, 1985; Owings & Coss, 1981). Jumping back may occur without any apparent provocation by the snake, such as subtle turning of the snake's head or its more salient activities of hissing, rattling, and striking. Ground squirrels readily probe nonmoving snakes into action by their engaging in repeated bouts of substrate throwing (Rowe & Owings, 1978), a variant of the defensive burying behavior seen in rats (e.g., Pinel, Treit, Ladak, & MacLennan, 1980). Because snakes often strike after being hit by detritus, leaves, and twigs, ground squirrels are prepared to leap back and often do so without the snake striking out defensively.

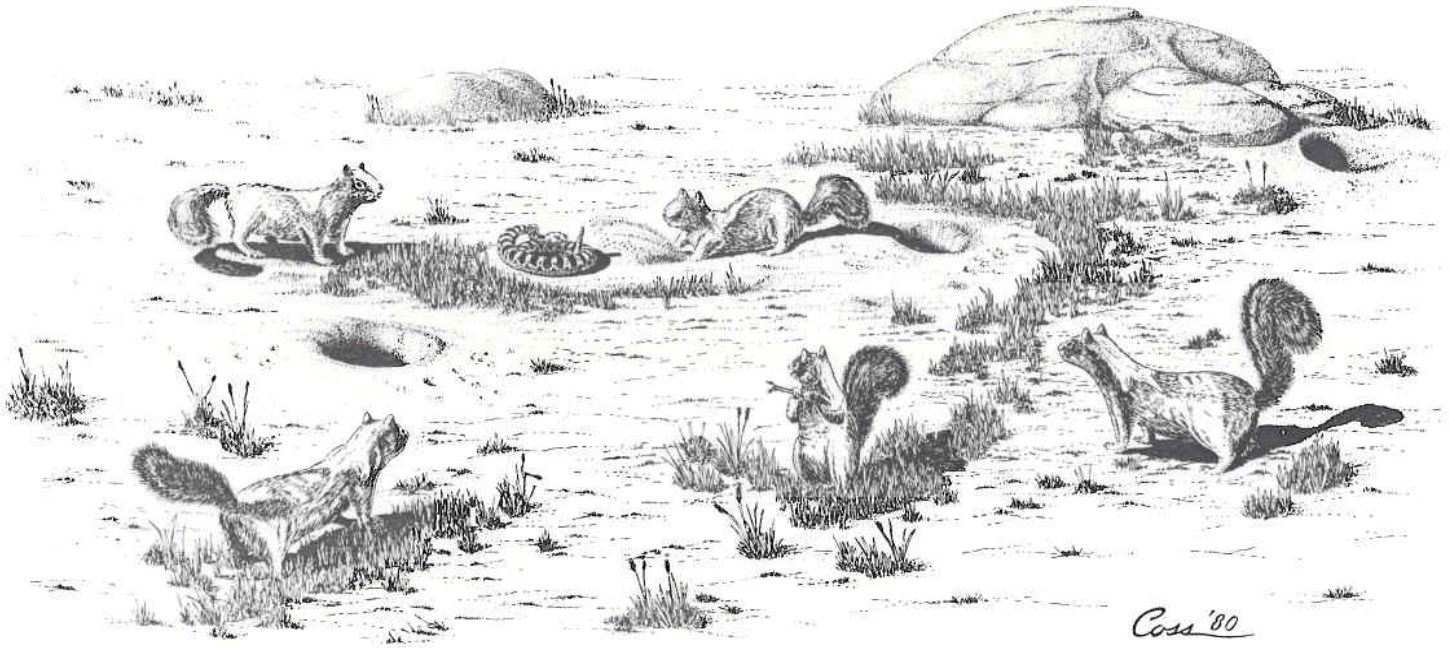


FIGURE 14.1. Reconstruction (from video recordings) of five California ground squirrels harassing a tethered rattlesnake at the San Joaquin Experimental Range in the Sierra Nevada foothills, an area abundant in rattlesnakes. Ground squirrels on the far left and right are tail flagging vigorously and exhibiting cautious, elongate postures. The top middle squirrel is throwing loose substrate at the snake repeatedly. The bottom middle squirrel was first to detect the snake and has now retired from harassing the snake after her activity attracted the other squirrels.

In some circumstances, the squirrel may approach the snake closely and then freeze for several seconds, staring at the snake. This activity seems to intimidate gopher snakes (Coss, 1978b), but with rattlesnakes, this activity invariably leads to the snake striking and the squirrel jumping back dramatically. Analyses of slow-motion video playbacks of encounters between ground squirrels and rattlesnakes in the field have revealed unequivocal bites by striking snakes, but without evidence of serious envenomization. These observations prompted us to study whether ground squirrels had evolved innate immunity to rattlesnake venom. Research in progress using radioimmunoassays, which indicate the amount of binding between rattlesnake venom and ground squirrel serum, has shown that some ground squirrel populations have evolved serum components that are quite effective in neutralizing rattlesnake venom. But further, it must be noted that venom resistance works in concert with the squirrel's ability to regulate venom delivery. Ground squirrels can be killed if they fail to detect rattlesnakes, prepare themselves to leap, and execute jumps that disengage them quickly from embedded fangs.

Extinction of Cognitive Information on the Phylogenetic Time Scale

Douglas ground squirrels (*S. b. douglasii*) living in the Coast Range foothills near Winters and Fisher ground squirrels (*S. b. fisheri*) at the San Joaquin Experimental Range in the Sierra Nevada foothills receive strong predation from both rattlesnakes and gopher snakes. Douglas ground squirrels living on the floor of the Great Valley on and near the University of California (U.C.) campus at Davis encounter only gopher snakes. The antisnake behaviors of these populations were compared during encounters with rattlesnakes, gopher snakes, and garter snakes in seminatural laboratory rooms with sand substrata. Douglas ground squirrels from the rattlesnake-free Davis area were much more likely to approach and harass snakes than were the Douglas and Fisher ground squirrels from habitats with both high rattlesnake and gopher snake densities (Owings & Coss, 1977). Subsequent comparative research has shown a consistent pattern of reduced caution toward rattlesnakes among ground squirrels from the Great Valley, which experience relaxed selection from rattlesnakes (Hennessy, 1982).

It was important to consider the possibility that these differences in antisnake behaviors reflected the different experiences with snakes in the wild. However, lab-reared, snake-inexperienced Fisher and Douglas pups, the mothers of which were trapped at the San Joaquin Experimental Range and U.C. Davis campus, respectively, exhibited marked differences in the way they treated a garter snake, which is a nonpredatory threat. First of all, the Douglas and Fisher pups recognized the snake on first encounter and applied the same general classes of antisnake behavior seen in their wild-caught adult counterparts, such as cautious, investigative approaches and substrate throwing, which agitated the snake (Owings & Coss, 1977).

Second, like the less cautious behavior of adults from the rattlesnake-free Davis area, Douglas pups treated the garter snake with much less caution than did the Fisher pups, the parents of which came from a rattlesnake habitat. Such adaptive variation in antisnake behavior, roughly correlated with relative rattlesnake and gopher snake abundance, afforded a paradigm for generating a phylogenetic time scale for extinction of the cognitive aspects of antisnake behavior.

A time scale for population divergence throughout California was developed by examining the genetic variation of Douglas and Beechey (*S. b. beecheyi*) ground squirrel subspecies distributed just north and south of the San Francisco Bay and Sacramento–San Joaquin Delta region (D. G. Smith & Coss, 1984). Nei's model for estimating the genetic distance (D_v) of two populations, in units that are linear in time (Nei, 1972, 1978), was calibrated on a .725-million-years-ago event in which the Sacramento and San Joaquin rivers began to drain through the San Francisco Bay. This sudden event, effectively blocking gene flow, initiated Douglas and Beechey subspeciation. The accuracy of this model has been corroborated using recent and ancient geological and fossil time markers (see Coss & Owings, 1985; D. G. Smith & Coss, 1984). Along with the use of this calibrated molecular clock and paleoclimatological evidence, we examined the differential venom resistance of 18 ground squirrel populations in California, selecting for behavioral study three populations with different histories of selection from rattlesnakes and gopher snakes (Coss, Poran, & Smith, in preparation).

Fisher ground squirrels were trapped at the snake-free campgrounds of the Folsom State Park in the Sierra Nevada foothills. Rattlesnakes are abundant within 3 kilometers of the trapping site, but gopher snakes are relatively rare. These Fisher squirrels have the highest venom resistance among the populations surveyed. Sierra ground squirrels (*S. b. sierrae*) were trapped in the Lake Tahoe Basin, an area totally free of rattlesnakes and gopher snakes. According to the molecular clock, these Fisher and Sierra populations diverged about 35 thousand years ago, but geological and paleoclimatological evidence, combined with evidence of moderate rattlesnake venom resistance in squirrels from the Lake Tahoe Basin and an adjacent population at Boca Reservoir, indicates that selection from rattlesnakes has been absent for only a few thousand years. Ground squirrels with very low venom resistance were trapped in the Sacramento Delta on Ryer Island and Little Holland Tract. These populations have been isolated for about 80–90 thousand years from their closest relative, the Fisher ground squirrel in the Sierra Nevada foothills. Although rattlesnakes are not found in the Delta, gopher snakes are found occasionally. Because the Delta was once a tidal marsh prior to land reclamation, a habitat relatively unsuitable to gopher snakes, the presence of these snakes may be a recent phenomenon.

Prior to testing, the animals were maintained under laboratory conditions for 9 months to equilibrate recent experiences among the groups. Unlike previous procedures in which ground squirrels and snakes interacted freely

in 2.5 by 2.4 meter laboratory rooms with sand substrata, the procedure was changed so that a rattlesnake or gopher snake was confined by a 28 by 28 by 28 centimeter compartment with transparent top and 8-millimeter flexible wire mesh on the sides and bottom to prevent injury to either animal. View of the snake was not obstructed by the wire mesh, which is analogous in appearance to that of a grassy barrier. With the compartment centered in the rooms, video recordings were made in plan view from adjacent rooms via overhead and one-way mirrors. After the squirrels spent several weeks in the laboratory rooms in burrow-like nest boxes, the experiment was started by temporarily removing all animals and equipment except the subject squirrel ($n = 8$ per group) and its nest box. Snake presentation was made by raising this remaining nest box remotely. Ground squirrels denied this refuge typically approached the compartment where they discovered the snake. Both a rattlesnake and gopher snake were presented to squirrels in a balanced, repeated, measures design with a 5-day interval between 10-minute trials.

The initial results of this multivariate study provided evidence for the first time that information about former habitats can persist for many thousands of ground squirrel generations. For example, Sierra ground squirrels quickly recognized the snakes, especially the rattlesnake, and treated them as dangerous adversaries. On initial approach or bout of substrate throwing, some squirrels leaped back or sideways from the motionless rattlesnake. Such inference that this motionless form posed a distinct sort of threat suggested that the innate cognitive processes underlying snake recognition in ground squirrels included the expectations of what these snakes can do. Similar inferences of the relative risks of approaching snakes or throwing substrate at them had been noted previously among lab-reared, snake-inexperienced Fisher pups during encounters with a gopher snake in the aforementioned laboratory rooms and in an artificial burrow (Coss & Owings, 1978).

Among the three ground squirrel populations, the Sierra ground squirrels were the most excited during close-range interactions with the snakes as revealed by their tail pilomotor erection, an index of sympathetic nervous system arousal (Fulton, 1955), and persistence in harassing the snakes. In contrast, the rattlesnake-adapted Fisher squirrels tended to engage the snakes more intermittently and several of the squirrels retired after harassing the rattlesnake briefly.

The most important population differences appeared among the Delta ground squirrels, which exhibited the highest interanimal variability. As examples of this variability, some squirrels were slow to initiate their antisnake behaviors, appearing sluggish in their application of substrate throwing. Surprisingly, these particular animals began to habituate to the snakes, jumping back only during the first few snake strikes. Subsequent snake strikes appeared to be ignored. Fewer than one-half of the squirrels behaved

as if the snakes constituted a serious threat; these particular ground squirrels, however, were vigorous in harassing the snakes.

On the whole, the Delta population comprised both highly excitable animals, like those characterizing the Sierra population, and animals that showed much less snake-directed activity in keeping with the Delta population's low venom resistance and rattlesnake-free habitat. Furthermore, the reduction of concern about the gopher snake by the latter group suggests that selection from both types of snake predators has been relaxed for some time, perhaps since the squirrels migrated into the Delta at the beginning of the last ice age.

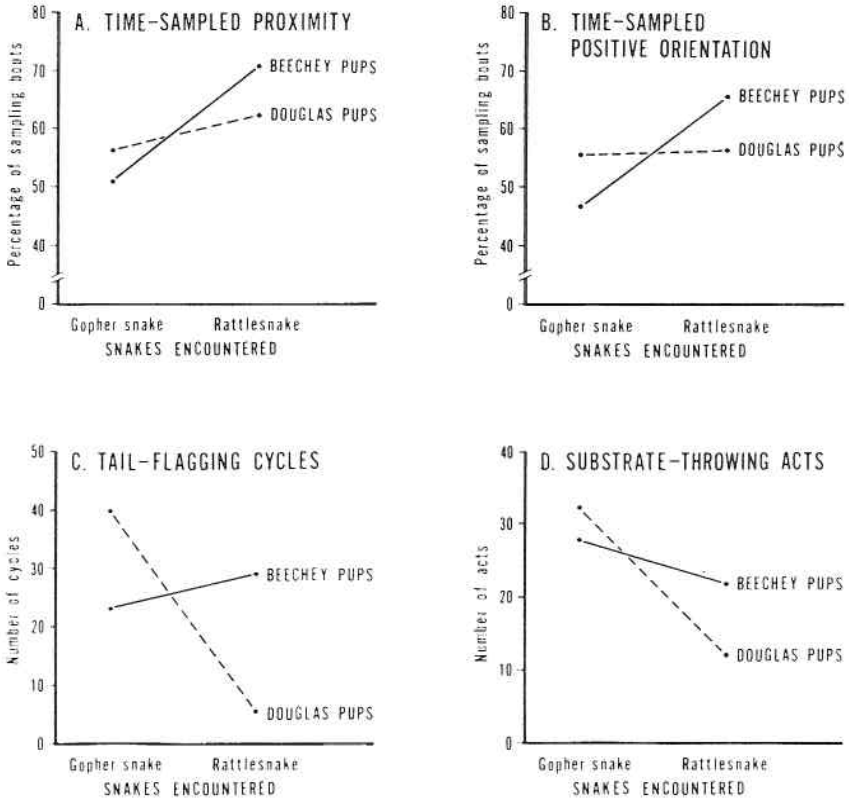
Follow-up research on lab-reared Arctic ground squirrels (*S. parryii ablusus*), a species that has lived in a snake-free habitat for a least 3 million years (Coss & Owings, 1985) and has minimal resistance to rattlesnake venom, provided and important control for the novel aspects of snakes. Using the same snake-presentation protocol, the results of this study revealed that Arctic ground squirrels will treat a rattlesnake and gopher snake as an animate novel object, despite repeated snake strikes accompanied by hissing and rattling. When given the opportunity to interact freely with a gopher snake, however, they may treat the snake defensively as a threatening, novel animate object that bites by throwing substrate weakly at the snake. This behavior is not surprising because defensive burying behavior is seen in other rodents (e.g., Pinel *et al.*, 1980).

The finding that cognitive information about snakes under conditions of relaxed selection can persist for perhaps 100,000 years, but not 3 million years, prompted the examination of whether relatively recent relaxed selection from one type of snake predator would differentially affect the antisnake behaviors during encounters with both types of snake predators (Coss & Poran, in preparation). Lab-reared pups, the mothers of which were trapped on the U.C. Davis campus, were compared with lab-reared pups, the mothers of which were trapped at Sunol Regional Park in the Coast Range mountains southwest of Livermore. Genetic distance analysis calibrated to time suggests that Douglas ground squirrels from Davis experienced relaxed selection from rattlesnakes beginning about 3000 years ago when they migrated onto the floor of the Great Valley, an area abundant with gopher snakes. Beechey ground squirrels live in a habitat that has been a relatively stable refugium for both species of snakes. Snake-inexperienced Douglas and Beechey pups (n = 8 per group) were tested at 60–70 days of age using the same protocol described earlier, with the exception that 5-minute rather than 10-minute trials were used.

The results of this study of the effects of relaxed selection from one type of snake predator, the rattlesnake, but not both types as in the previous study, indicates that ground squirrels can evolve relatively discrete patterns of information unique to each type of predator. Beechey pups, for example, appeared to differentiate the rattlesnake and gopher snake on a gradient of

risk; they spent significantly more time-sampled bouts within striking range of the rattlesnake (Figure 14.2A), maintaining more time-sampled bouts of positive orientation that afforded better surveillance of the rattlesnake's activities (Figure 14.2B). In contrast, Douglas pups were equally vigilant toward both snakes, but they were less aroused by the rattlesnake, as compared with arousal by the gopher snake, exhibiting significantly fewer cycles of tail flagging (Figure 14.2C) and significantly fewer substrate throwing acts (Figure 14.2D).

FIGURE 14.2. Antisnake behavior of eight young snake-inexperienced Douglas and Beechey ground squirrel pups during 5-minute encounters alternately with a rattlesnake and gopher snake in seminatural laboratory settings with sand substrata. Each snake is confined by a wire-screened compartment resembling a grassy barrier. The Beechey pups, the parents of which came from a rattlesnake and gopher snake habitat, investigated the rattlesnake more intensely than they did the gopher snake, exhibiting significantly more time-sampled bouts within the rattlesnake's striking range (A, $p < .01$) and, within this range, a positive orientation (B, $p < .005$). Douglas pups harassed their natural enemy, the gopher snake, with significantly more tail-flagging cycles (C, $p < .005$) and substrate-throwing acts (D, $p < .05$) than they did the rattlesnake, a predator that has not provided the circumstances for selection for about 3000 years.



In short, Beechey and Douglas pups engaged in differential behaviors toward each predator for entirely different reasons. For Beechey pups, the intense selection from rattlesnakes engendered greater concern for keeping track of what the rattlesnake was doing throughout the trial even though they harassed both snakes with about equal intensity. Douglas pups, on the other hand, differentiated the snakes as a result of about 3000 years of relaxed selection from rattlesnakes, exhibiting a markedly reduced tendency to harass the rattlesnake as compared with the gopher snake.

Although these studies of adaptive variation in ground squirrel antisnake behaviors did not focus on the examination of learning *per se*, a number of field and laboratory observations provided ideas about how learning enhanced the effectiveness of these behaviors. Clearly, rapid learning goes on about specific features of *that* particular predator in *that* particular microhabitat, such as change in the predator's movement, orientation, size, and distance relative to the perceiver in its own microhabitat (see Coss & Owings, 1978; Leger *et al.*, 1983; Owings & Owings, 1979). Learning is thus congruent with the innate processes of predator recognition and concomitant inferences about the predator's capabilities vis-à-vis the perceiver; that is, the context for organizing and executing appropriate antipredator behavior emerges immediately upon perception of these variables.

In confined laboratory settings, wild-caught adult ground squirrels, presumably with snake experience (Owings & Coss, 1977), are less likely to exhibit the intense snake-directed behavior observed in snake-inexperienced pups. Changes in the adult's propensity to engage snakes in laboratory settings may well reflect differences in the context engendered by laboratory and field conditions as well as any previous snake experience. From this theoretical perspective, learning cannot be extricated as a separate entity from instinct, but could be considered as proximate and ontogenetic adjustments of a genetically orchestrated substrate, itself adjustable on the phylogenetic time scale (see Coss & Owings, 1985).

NEUROBIOLOGICAL IMPLICATIONS

What are the neurobiological implications of the viewpoint that learning is part of a continuum of adjustment over phylogenetic, ontogenetic, and proximate time scales? First, rapid and cumulative experiences resulting from changing organism–environment relationships add supplemental information during ontogeny to a network of processes already roughly organized through phylogeny. In this view, these processes are restrained, not only by their adaptation to the environment, but also by their adaptation to each other (see Lewontin & Levins, 1978; Webster & Goodwin, 1982). Second, with intense persistent selection over phylogenetic time, genetic and epigenetic processes construct nervous systems with organizational properties and expectancies about specific types of habitat variation, but

only approximately so. Learning thus provides the details about the organism–environment circumstances that are too variable to act as reliable sources of selection.

Gould (Chapter 11, this volume) describes the various properties of honey bee foraging in which certain "preconceptions" about the habitat, including its temporal properties, guide honey bees to appropriate sources of pollen and nectar. Similarly, food-storing birds appear to have expectations about the most suitable microhabitats for storing and recovering seeds as well as dealing with probabilistic factors like seed predation (Shettleworth, Chapter 13, this volume). California ground squirrels also seek suitable microhabitats for foraging and for maintaining vigilance after they have learned that a specific type of predator is in the area (Coss & Owings, 1985). Because such expectancies bias decision making, they are "seen" by selection when organisms fail to organize and execute behaviors with sufficient skill to survive and produce progeny. With prolonged relaxed selection, this innate information undergoes extinction, but as it does, it continues to bias decision making for many thousands of generations.

In the case of Sierra and Delta ground squirrels, gene substitutions, probably at regulatory loci, have undergone sufficient drift (random changes in genetic structure) to alter the functional integration of many genetic loci (Mayr, 1963; McDonald, 1983). Such subtle changes could markedly affect the pattern of neuronal organization, thus altering the *invariances* in the information emergent in interneuronal communication. A surprising aspect of this study, as manifested by the Sierra population, was evidence that during the early phase of relaxed selection from snakes, ground squirrel antisnake behavior becomes more excitable and consistent within members of the population. With more prolonged relaxed selection, however, antisnake behavior begins to dissipate in some of the animals. The sluggish, somewhat erratic application of antisnake behaviors by the least active Delta ground squirrels gives the figurative impression that the underlying cognitive organization has been disrupted, almost as if cloaked by mist.

Adjustments in the Neuronal Substrate

Several types of neurobiological studies have shed some light on the evolutionary restraints discussed earlier. Studies of phenotype, behaviors, and neurotransmitter levels in *Drosophila melanogaster* have documented that single gene mutations can alter learning capabilities (see Byers, Davis, & Kiger, 1981; Quinn & Greenspan, 1984). Studies of homozygous weaver mice (Sotelo, 1975) and chromosome anomalies in humans (Marin-Padilla, 1974; Purpura, 1975; Takashima, Becker, Armstrong, & Chan, 1981) have shown aberrant changes in dendritic structure, especially the presence of unusually long dendritic spines.

The initial outgrowth of dendritic branches seems to be restrained more by endogenous cell processes than by the extrinsic influences of nearby

afferent projections (e.g., Whitehead, 1979). Growth of multiple branch orders, however, can be sculpted by extrinsic factors (see review in Greenough, Chapter 5, this volume; Tieman & Hirsch, 1982; Vaughn, Henrikson, & Grieshaber, 1974). Dendritic growth, even late in life (Connor, Diamond, & Johnson, 1980; Connor, Melone, Yuen, & Diamond, 1981), associated with the organism's differential experience could be considered as an ontogenetic adjustment of a substrate previously organized by more intrinsic regulatory processes (Clark, 1976). It therefore seems reasonable to consider that the previous history of dendritic growth in some cells could restrain subsequent patterns of growth and connectivity.

An important question emerges when one considers the implications of dendritic growth, retraction, and other processes of dendritic remodeling (i.e., Mates & Lund, 1983). When neuronal networks undergo remodeling, how are previous invariances that constitute information preserved? In jewel fish, for example, innate recognition of two facing eyes begins promptly in fry on the 13th postspawning day of age and continues throughout life without disruption (Coss, 1978a, 1979a; Coss & Globus, 1979) even though the apical dendrites of tectal interneurons have elongated dramatically (see Figure 14.3). Preservation of such ecologically relevant information, despite massive neuronal growth, suggests that the information emerges in the proportional relationships among growing neurons rather than in the formation of absolute relationships that could be labile to growth. Because the brains of newly hatched fry are tiny relative to those of adults, fish have not adopted the strategy of synaptic overproduction and competition that is typically found in mammals (see Purves & Lichtman, 1980).

The sources of selection on young fish, such as predation, are probably too intense to permit the adoption of a less reliable process of connectivity during development; although it must be noted that competitive exclusion can be surgically induced in adult fish (Meyer, 1979). In contrast, the overproduction and subsequent stabilization of synapses in mammals (Greenough, Chapter 5, this volume) and in birds (Rausch & Scheich, 1982), probably reflects their overall growth trajectories. The notion that synapses can form "on demand," as proposed by Greenough, is a reasonable candidate for describing the changes in the neural circuitry that provide the potential for new neuronal relationships.

Formation of new synapses, however, is not a necessary component of learning. In short-lived holometabolis insects that emerge from pupation as adults, selection is especially intense for stable and reliable neural circuitry. Newly emerged and forager honey bees show no appreciable differences in spine density on Kenyon cells (see Figure 14.4) in the calyces of the mushroom bodies (Coss, Brandon, & Globus, 1980). At the other end of the developmental spectrum, adult jewel fish readily learn to recognize new mates long after the late juvenile developmental period in which the optic tectum shows little signs of further growth. Most dendritic growth occurs early in jewel fish development (Burgess & Coss, 1980), especially

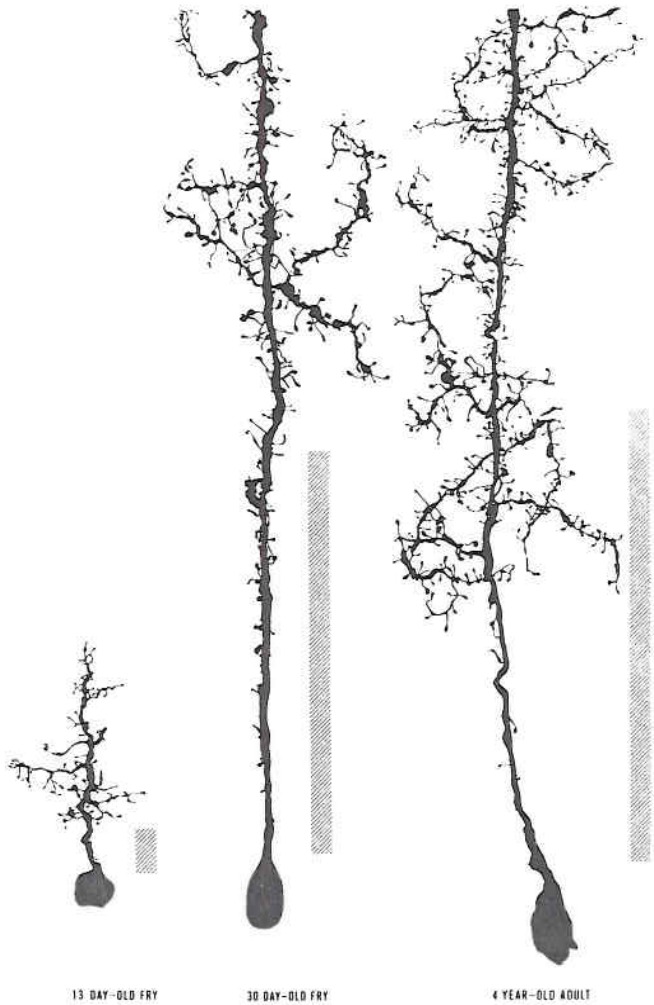


FIGURE 14.3. Camera lucida tracings (1 μm = 6 mm) of spiny pyriform interneurons in the jewel fish optic tectum showing growth-related changes in the lower half of the dendritic trees. For scale, the hatch bars, depicting the stratum album centrale (SAC) plexiform layer are, from left, 7.3, 66.2, and 74.0 μm. At 13 postspawning days of age, all types of tectal neurons observed acquire the general appearance of their adult counterparts. Spines on 13-day-old interneurons are short, averaging 1.17 μm in length (range: .59–2.54 μm). At 30 days of age, spines average 1.85 μm in length (range: .59–3.38 μm), which falls within the adult average of 1.52–1.95 μm in length). Dendritic branches within the SAC of adults are labile to early deprivation rearing. Tectal thickness (basilar edge of SAC-pia) is, from left, 54, 217, and 370 μm.

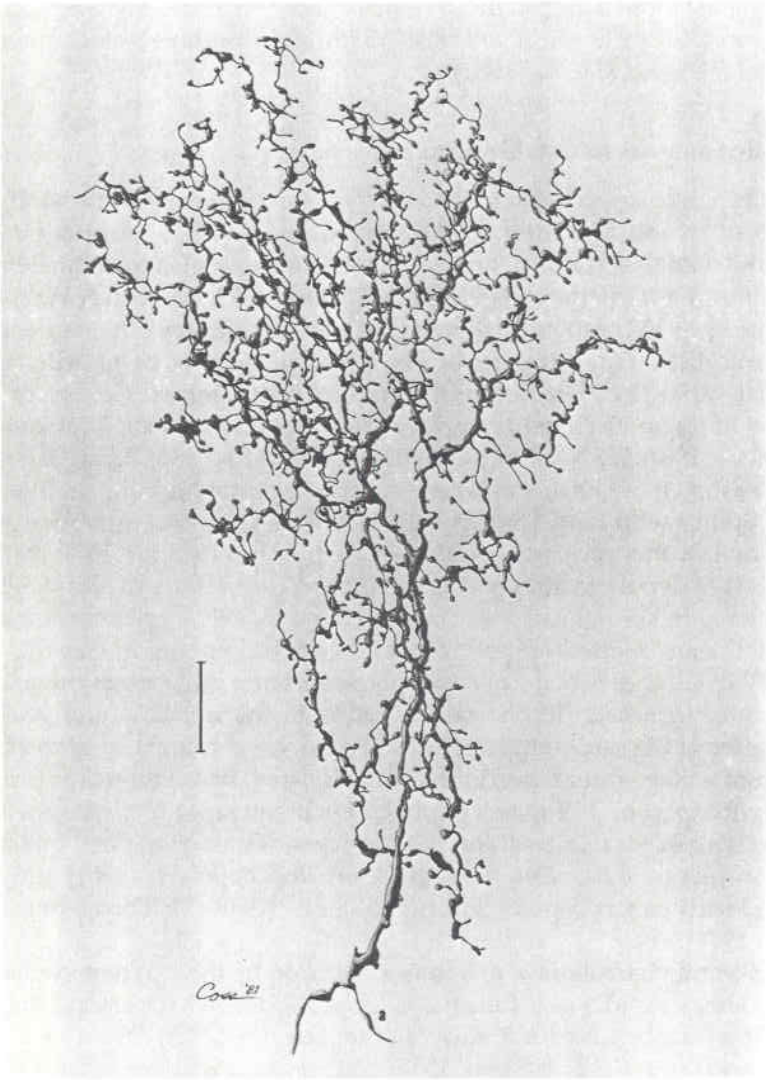


FIGURE 14.4. Spiny Kenyon cell (type II) in the calyces of the honey bee corpora pedunculata. Illustration was made from a camera lucida tracing (1 μm = 6 mm); scale bar represents 10 μm. On this type of interneuron, spine density per unit length of dendrite is stable in newly emerged, nurse, and forager honey bees. After honey bees take their first orientation flights lasting a few minutes, spine stems are found to be shorter on only the longest spines as a result of a process of elongated dilation of spine heads.

among newly formed cells in the germinal zones. Spine density is remarkably stable after 160 days of age at dendritic loci formerly sensitive to environmental variation (Burgess & Coss, 1982).

Dendritic Spines as Adjustable Regulators

The probabilistic aspects of synaptic activity, as characterized by the stochastic process of neurotransmitter release, saturation of ionic channel binding sites, and variable channel opening time constants (Gage & McBurney, 1975; Kuno, 1964; Matthews-Bellinger & Salpeter, 1978; Redman & Walmsley, 1983), are likely to contribute to the already considerable noise in interneuronal communication. One function of dendritic spines may be to reduce this potential variance by restricting the amount of ion influx. Computer simulations of spine electrical properties (Kawato, Hamaguchi, Murikami, & Tsukahara, 1984; Koch & Poggio, 1983; Perkel, 1982–1983; Perkel & Perkel, 1985; Wilson, 1984) have converged on one important functional interpretation. Spines with long, narrow stems increase the input resistance at the synapse, and this property regulates synaptic conductance by creating a much larger depolarization in the spine head than in the parent dendrite. A rapid rise in spine head membrane voltage quickly approaches reversal potential, thus delimiting ion influx and current generation (see Stevens, 1984). With successive bouts of synaptic conductance, this putative regulatory property of spines could dampen variation in the rise time and peak depolarization at the same dendritic locus, the net effect being a more consistent pattern of voltage integration in the dendritic tree. Based on this argument, one might expect to find spines throughout a broad range of phylogenetically old and distant taxa; in addition to those taxa described earlier, spines are found in marine flatworms (Keenan, Coss, & Koopowitz, 1981) and molluscans, such as gastropods and cephalopods (Bailey & Thompson, 1979; Young, 1971).

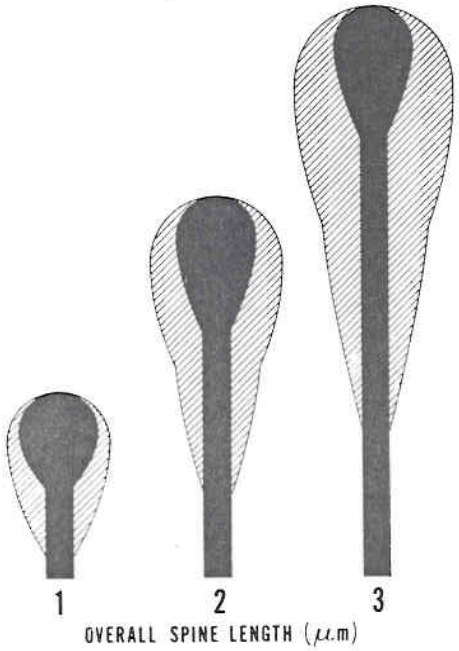
A second characteristic of spines is evinced by their dynamic ability to change shape rapidly as a function of synaptic activity (Desmond & Levy, 1981; Greenough, Chapter 5, this volume; Lee, Schottler, Oliver, & Lynch, 1980; Van Harreveld & Fifkova, 1975) and under conditions of biologically important behavioral activity (Brandon & Coss, 1982; Burgess & Coss, 1983). Quantification of large numbers of spines in young and old honey bees and jewel fish has shown a consistent change in spine morphology. Spine stems are shortened successively by elongated dilation of spine heads without appreciable change in overall spine lengths (Brandon & Coss, 1982; Burgess & Coss, 1983; Coss *et al.*, 1980). Rapid and long-lasting unidirectional shortening of the spine stem is thought to lower the input resistance, and this factor changes two spine properties: (1) Lowering the input resistance also lowers peak spine head voltage, and this could affect synaptic conductance mediated by any appreciable number of voltage-dependent ion channels

(see Miller, Rall, & Rinzel, 1985; Perkel & Perkel, 1985); (2) If synaptic conductance still matches the lowered input resistance, that is, if spine head voltage still approaches the reversal potential (Kawato *et al.*, 1984; Koch & Poggio, 1983), this lowered input resistance will enhance the transfer of electrical charge from the spine head to the parent dendrite. In short, spines seem capable of adjusting their regulatory properties in keeping with differential patterns of synaptic activity (for review, see Coss & Perkel, 1985).

A final important implication of spine-stem shortening takes us back into the theoretical realm of learning as adjustment of instinct. Clearly, long spines exhibit a greater potential range of stem shortening than do shorter spines (see Figure 14.5).

During jewel fish development, short spines appear earliest in fry and are followed by more variable spine lengths as fry disperse from parents, a developmental period in which learning is important (compare the 13- and 30-day-old interneurons depicted in Figure 14.3). Spine density becomes labile after this period, and developmentally deprived jewel fish have fewer,

FIGURE 14.5. Range of variation in spine morphology on Kenyon cells in 3- to 5-week-old forager honey bees. Black and hatched spine profiles are adapted from standard deviations of mean values. Note the overlap of stem shortening in spines 2 and 3 μm long. Between the newly emerged and forager stages of honey bee behavioral development, spines 2–3 μm long show progressive stem shortening, a process that culminates in foragers having a residual plasticity of about 16% narrow-headed spines (black profiles).



but longer spines (see Berard, Burgess, & Coss, 1981; Burgess & Coss, 1982; Coss & Globus, 1978). Similar findings of fewer, but longer spines appear in mammalian studies with experimental intervention (Berry & Bradley, 1976; Chen & Hillman, 1982; Tavares, Paula-Barbosa, & Gray, 1983) and genetic anomalies (Sotelo, 1975, 1978; Takashima *et al.*, 1981). Such observations have led to the "search and capture" hypothesis in which overall spine length is regulated by endogenous growth processes and extrinsic stabilization processes with synaptogenesis (see Llinás, Hillman, & Precht, 1973; Marin-Padilla, 1974), albeit, some long spines can be "naked" (Hirano & Dembitzer, 1975). In effect, the distribution of long and short spines in fish and mammals could reflect one genetic–epigenetic restraint on the overall adjustability of the neuron (Coss & Brandon, 1982), a restraint that combines both deterministic (genetic) and probabilistic (labile) attributes (Berard *et al.*, 1981).

As discussed earlier, honey bees exhibit stable spine densities on Kenyon cells after emergence from pupation, but overall spine length appears to be stable as well (Coss *et al.*, 1980). During the newly emerged to nurse stages of development, in which honey bees adjust many of their innate hive maintenance and brood care activities to match variable hive conditions, the shorter spines show acceleration in stem shortening. Conversely, during their first orientation flight when honey bees learn terrain landmarks and under the complex conditions of foraging (see Gould, Chapter 11, this volume), the longer spines undergo marked stem shortening (Brandon & Coss, 1982; Coss *et al.*, 1980). But also across an enormous phyletic gulf, jewel fish hatch with short spines when instinct predominates and the shorter spines show the most reliable stem shortening (Coss & Perkel, 1985) in older juveniles exhibiting prolonged escape behaviors requiring reliable behavioral expression (Burgess & Coss, 1983). Like that of honey bees engaging in complex behavioral activities requiring adjustments to varying environmental conditions, jewel fish which explore and control their physical and social environment (Coss & Globus, 1979) also show the most reliable stem shortening among their longest spines (see Coss & Globus, 1978).

Although spine stem adjustability, as a function of overall spine length, and the ecological requirements for behavioral adjustability are only roughly correlated in these taxa, any correlation at all provides ideas of how instinct and learning might reflect a continuum of the same cellular process. Furthermore, once spine-stem shortening has reached a stable asymptote in the long spines through elongated dilation of the spine head, a process that might occur rapidly (Lynch & Baudry, 1984; Robinson & Koch, 1984) and relatively early in development (Curcio & Hinds, 1983), the input resistance and regulatory properties of these long spines could approximate those of much shorter spines which have yet to undergo as much stem shortening (see Figure 14.5). If the stability of overall spine length seen in honey bees and jewel fish is similar to that of other taxa, a point that is still equivocal (see Lund, Boothe, & Lund, 1977), spines with short and shortened stems

could be less plastic in their regulatory properties. The reciprocal of this reduction in plasticity at specific neural loci would likely manifest itself in the ability of an organism to now deal with environmental aspects only partly specified by selection on the phylogenetic time scale.

CONCLUSION

I have presented a view of evolutionary restraints on learning, selecting two types of analysis for discussion—phylogenetic and synaptic. These two types of analyses could be considered part of a three-dimensional matrix characterizing processes of adjustment. Two of the axes represent phylogenetic and ontogenetic time scales, and the third axis could be viewed as a structural scale representing hierarchical levels of description. I treated organism–environment relationships as the highest level in the hierarchy and relationships of synaptic processes as the lowest level, both of which are interpretations embedded in the matrix of phylogenetic and ontogenetic time scales of adjustment. When viewed from the perspective of this three-dimensional matrix, learning could be considered as an adjustment of instinct at the level of organism–environment relationships. As evinced by behavior, instinct itself is restrained by all the processes constituting lower levels. My discussion of the synaptic level focused on the idea that invariances in interneuronal communication constitute information; and for information to be preserved, stable regulatory processes must emerge from initially adjustable processes. The dendritic spine was emphasized as a structural component of the synapse with putative voltage regulating properties. Dendritic spines of different overall lengths provide the potential for gradations of low and high adjustability by shortening their spine stems. Such changes are roughly correlated with the ecological demands for behavioral adjustability in members of two phyla. In light of the discussion of the probabilistic aspects of growth and connectivity in neural circuits and preservation of information, it seems remarkable that the mammalian nervous system can retain information about former habitats for thousands of generations. From the neurobiological perspective, slow extinction of information on the phylogenetic time scale means that neurons and neuronal circuits have histories that should not be ignored. Perhaps the most important implication is that learning and instinct might be mediated by the differential adjustability of the same neuronal processes. The variation of plasticity detected at one level may simply be the reciprocal of restraint engendered at the level by previous adjustments of plasticity over phylogeny.

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