Psychology of Learning

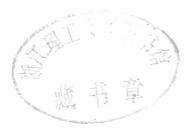
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PSYCHOLOGY OF LEARNING

VOLUME V

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Part 4: Practical Aspects of Learning (Continued)

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Fears, Phobias, and Preparedness: Toward an Evolved Module of Fear and Fear Learning

Arne Öhman and Susan Mineka

ammalian evolution has required the successful development of defense systems to cope with dangers that threatened to disrupt the transport of genes between generations. In the early mammalian environment of evolutionary adaptiveness (Tooby & Cosmides, 1990), disaster could strike fast and without warning, primarily through hunting predators but also through aggressive conspecifics and from physical events such as falling objects, floods, thunder and lightning, and sudden lack of oxygen. Escape and avoidance were common strategies designed by evolution to deal with such exigencies. At a minimum, they required a perceptual system to identify threats and a reflexively wired motor system to move the organism away from the danger. With more sophisticated nervous systems, the effectiveness could be expanded both at the sensory and the motor ends, and the relation between stimulus and response could be rendered less stereotyped, by inserting a central motive state between the two. In this way, the motive state could be activated from innate danger stimuli and serve to promote escape through the flexible tailoring of responses to environmental contingencies (e.g., Archer, 1979). For example, depending on circumstances, the animal would freeze, escape, or attack (e.g., Blanchard & Blanchard, 1988). It is this central motive state that we commonly identify as fear (e.g., Mineka, 1979; Öhman, 1993a). An essential characteristic of fear, therefore, is that it motivates avoidance and escape (Epstein, 1972).

Potentially disastrous events sometimes do not strike without notice, however, but may be heralded by subtle cues. For example, to the attentive observer, a predator may announce its presence by faint sounds or odors. By using the contingency between such cues and the potentially deadly consequence, the central motive state of fear could be conditioned to the cue (e.g., Rescorla & Solomon, 1967), which would promote further flexibility in the relationships between stimulus and response. Furthermore, conditioned fear cues could recruit defensive responses in anticipation of the predator's strike, which provides a decisive edge in the arms race between predator and prey (see Hollis, 1982). From this perspective, it is likely that survivalrelevant relationships between cues and consequences could be used by natural selection to promote their preferential and selective association in the brains of animals (e.g., Bolles, 1970; Seligman, 1970). The emergence of more advanced nervous systems assured that the outcome that evolution selected for, avoidance of potentially deadly events or situations, could be achieved through more sophisticated and selective mechanisms, such as inborn defense responses, Pavlovian conditioning, instrumental learning, and eventually cognition and conscious deliberation (e.g., Razran, 1971).

Viewed from the evolutionary perspective, fear is central to mammalian evolution. As a product of natural selection, it is shaped and constrained by evolutionary contingencies. It is a central thesis of this article that this evolutionary history is obvious in the fear and phobias exhibited and readily learned by humans. We are more likely to fear events and situations that provided threats to the survival of our ancestors, such as potentially deadly predators, heights, and wide open spaces, than to fear the most frequently encountered potentially deadly objects in our contemporary environment, such as weapons or motorcycles (e.g., Marks, 1969; Seligman, 1971).

Purpose and Overview

The purpose of this article is to develop a concept of an evolutionarily evolved fear module (Tooby & Cosmides, 1992) that helps to organize and explain important aspects of human fear and fear learning. The article is organized into eight parts. The first one develops the concept of the fear module. Briefly, a fear module is proposed to be a relatively independent behavioral, mental, and neural system that is specifically tailored to help solve adaptive problems prompted by potentially life-threatening situations in the ecology of our distant forefathers. The second and third parts discuss a central feature of the fear module: its relative selectivity regarding the input to which it responds and preferably enters into associations. In the fourth part, we evaluate two alternatives, one evolutionary but nonassociative and one quasi-associative but nonevolutionary, to evolutionarily shaped selective associations as a basis for fear learning. In the fifth and sixth parts, we analyze the role of cognition in fear learning, particularly with regard to the automaticity with which particular stimuli activate the fear module and with regard to the encapsulation of the module from cognitive input. In the seventh part, we review research that

delineates the neural basis for the fear module. In the eighth part, finally, we develop a levels-of-learning concept to reconcile data from human conditioning with the database from animal research on fear and its neural mechanisms.

An Evolved Fear Module

The Status of Evolutionary Explanations

From the evolutionary perspective, behavior is more likely to be organized into relatively independent modules than in terms of general-purpose mechanisms (Tooby & Cosmides, 1992). Just as our body is composed of a number of independent organs serving survival and procreation, behavioral and mental systems can be thought of as composed of organs or independent modules (e.g., Fodor, 1983). As a result of natural selection, such modules were tailored to solve specific adaptive problems that were recurrently encountered in the environment of evolutionary adaptiveness (Tooby & Cosmides, 1990).

In our view, evolutionarily based explanations of psychological phenomena have no special status that set them apart from other types of explanations. Although evolutionary hypotheses are not amenable to direct empirical tests in psychological research, basic postulates that are testable only indirectly, in terms of their consequences, are commonplace in science. To take a classic example, Newton's concept of attraction perhaps did not appear to make sense to his contemporaries, but it did make sense of the data on the paths of planets when used in his axiomatic system. In psychology, however, the widespread commitment to "the standard social science model" (Tooby & Cosmides, 1992, pp. 24-34), with its emphasis on learned behavior, collectively known as culture, has planted skepticism among many regarding the role of phylogenetic influences on human behavior (see, e.g., Delprato, 1980, with regard to fear). Partly, the skepticism is nourished by popular misuse of evolutionary arguments, in which virtually any psychological phenomenon can be declared post hoc to represent evolutionarily shaped adaptations. But if hedged by some reasonable caveats, we think that evolutionarily based theorizing provides a fruitful avenue for analyzing psychological phenomena.

A putative evolutionary explanation must, just as any scientific explanation, be open to empirical tests; to be more precise, it must be integrated into a conceptual network with testable consequences. Here, the distinction between theoretical and metatheoretical statements may be helpful (Johnston & Turvey, 1980). The purpose of a scientific theory is to explain a set of empirical phenomena, whereas a "metatheory is concerned with justifying the asking of certain kinds of questions in a particular area of inquiry" (Johnston & Turvey, 1980, p. 149). For example, the questions about fear that we pose in this article are different from those that would be posed by someone inspired by, for example, a social constructivist or psychodynamic metatheory of psychology. The theory of evolution by natural selection is overwhelmingly supported by data from many different fields of science that provide its legitimate testing grounds. Its use in psychology, however, is not motivated by the ambition to subject it to further empirical tests but by its usefulness in posing problems that can be addressed in research, given the methodological constraints of the particular subfield. Merely interpreting something as an evolutionarily shaped adaptation is a dead end unless it stimulates testable ideas that connect the putative adaptation to other concepts in abstract structures known as *scientific theories*.

As a metatheory for psychology, the theory of evolution starts from the premise that humans (as members of an animal species) are part of the biological universe, which implies that not only their anatomy and physiology but also their behavioral capacity have been shaped by evolutionary contingencies. Thus, it is assumed that behavior serves biologically useful functions and that evolutionary processes are helpful in explaining the characteristics of human behavior and human mental life. These statements are broad generalizations that are of little use in accounting for specific phenomena. To analyze specific units of behavior, more circumscribed theoretical statements are needed. First, it must be ascertained that the specific behavior under scrutiny is a meaningful unit in a functional-evolutionary perspective. For example, our argument starts with the premise that fear is anchored in defense systems that are central to evolution. Thus, fear is likely to reflect evolutionary influences. Second, the characteristics of the behavioral units must be specified. For example, what are their response components and activation characteristics? In the case of fear, we argue that it is composed of behavioral, psychophysiological, and verbalcognitive components, that the activation of the system is automatic, and that it is relatively immune to cognitive influences. Third, as in any scientific enterprise, hypotheses must be generated as to the matrix of causal influences that controls the behavior. With regard to specifying both the characteristics and the causal matrix, the evolutionary metatheory is helpful in suggesting questions that should be addressed and in delineating sets of potential causal factors to consider. For example, we argue that the postulated fear module is particularly sensitive to stimuli that are fear relevant in an evolutionary perspective because they were related to threats that had to be coped with for organisms to survive and leave genes to coming generations. Fourth, in empirically evaluating an evolutionarily based theory, the strategy conforms to standard scientific canon: as stringent empirical tests as possible and the successive ruling out of competing interpretations. The product of this endeavor will be a theory that not only specifies the proximal mechanisms controlling (e.g., fear and fear behavior) but also provides some insight into the ultimate causal factors that shaped and characterized the underlying adaptations.

The theoretical structure that we end up with, the fear module, comprises four characteristics: *selectivity* with regard to input, *automaticity*, *encapsulation*, and a *specialized neural circuitry* (see Fodor, 1983). Each of these characteristics is assumed to be shaped by evolutionary contingencies. The selectivity results to a large extent from the evolutionary history of deadly threats that have plagued mammals. The automaticity is a consequence of the survival premium of rapid defense recruitment. Encapsulation reflects the need to rely on time-

proven strategies rather than recently evolved cognitions to deal with rapidly emerging and potentially deadly threats. The underlying neural circuitry, of course, has been crystallized in evolution to give the module the characteristics that it has. Thus, even though most of the research has addressed the first characteristic of the module, its theoretical validity as well as the fruitfulness of its origin in evolutionary theory should be judged from the complete set of statements that it generates.

Judging the status of the claim that the fear module represents an evolutionary adaptation is formally similar to the diagnosing of medical conditions. The diagnostic signs of an evolved module that we discuss (relative selectivity to input, automaticity, encapsulation, and dedicated neural circuitry) are not independent, and not one in itself is sufficient to allow the conclusion that the system it characterizes is an "evolutionary adaptation. The odds for this inference improve if the system shows all these features, and they can be further improved by considering the functionality of the system in a likely ecology of evolutionary adaptiveness (Tooby & Cosmides, 1990) and by comparative analyses across related species and families. The characteristics, therefore, should be regarded as diagnostic signs; each in itself is insufficient for diagnosing adaptations. Nevertheless, a particular configuration of signs may eventually provide a compelling case for such a diagnosis.

Characteristics of the Fear Module

Selectivity. Basically, the fear module is a device for activating defensive behavior (e.g., immobility or fight-flight) and associated psychophysiological responses and emotional feelings to threatening stimuli. A common requirement of evolutionarily shaped behavioral systems is their relative selectivity with regard to the input to which they respond. Rather than being open to any stimulus, the fear module is assumed to be particularly sensitive to stimuli that have been correlated with threatening encounters in the evolutionary past. By limiting the set of effective stimuli, readymade neural mechanisms could be devised for identifying critical events after only minimal neural processing, which would serve to facilitate rapid initiation of defense maneuvers. The module may be selectively sensitized to respond to evolutionarily primed stimuli by aversive stimuli or aversive states. Less evolutionarily primed events, on the other hand, would require more extensive neural processing to activate the module and would be less sensitized by aversive states. The range of stimuli that can activate the fear module can be vastly expanded through Pavlovian conditioning, which may give stimuli that happen to predict and coincide with the activation of the module power to activate it by themselves. But rather than positing a general associative apparatus that is independent of the specific to-be-associated events, an evolutionary approach expects constraints on associative learning depending on the specific contexts in which the events have typically been encountered during evolution (Domjan, 1983; Garcia, McGowan, & Green, 1972; Revusky, 1977; Seligman, 1970; Seligman & Hager, 1972). When it comes to fear learning, the context involves situations of recurrent survival

threats, and the presupposition would be that events defining such contexts are particularly easy to associate in the interest of promoting effective avoidance of danger. Thus, even though evolutionary fear stimuli would have an advantage, associations between arbitrary cues and fear are by no means precluded but would be more difficult to learn or would be less resistant to extinction.

Atomaticity. Evolution may long ago have designed mechanisms to identify stimuli related to recurrent survival threats after a minimum of neural computations and to immediately give them priority (e.g., in terms of efficient attention capture). Because of their origin in animals with primitive brains, behavioral modules that have a deep evolutionary origin typically are not under voluntary control but are directly elicited by stimuli. Thus, the behavior is likely to be elicited whether we want it or not and whether the stimulus has been represented in consciousness. Evolutionarily fear-relevant stimuli, therefore, show characteristics of preconscious automaticity (i.e., they may trigger responses in the absence of any conscious awareness of the stimulus event; Bargh, 1989, p. 11). Automaticity in itself may suggest an evolutionary origin, but it is also clear that automaticity of mental function can be achieved through extensive training (e.g., Shiffrin & Schneider, 1977), even though such automaticity may reflect postconscious rather than preconscious automaticity in Bargh's (1989) terminology. However, rather than pitting evolutionarily derived automaticity against learned automaticity, it is important to realize that evolution frequently uses extensive experience as a means of shaping neural architecture (e.g., Elman et al., 1996).

Encapsulation. A third characteristic of a behavioral module is encapsulation (i.e., that it is relatively impenetrable to other modules with which it lacks direct connections; Fodor, 1983). Thus, once activated, a module tends to run its course with few possibilities for other processes to interfere with or stop it. In particular, evolutionarily shaped modules will be resistant to conscious cognitive influences because their origin typically precedes recent evolutionary events such as the emergence of conscious thought and language. However, even though the module is relatively impenetrable to conscious influences, influences may be possible in the other direction. When such influence is manifested at the level of conscious cognition, it is likely to be distorting, resulting, for example, in exaggerated expectancies of bad outcomes when the fear module is activated to promote persistent coping attempts. Encapsulation may appear closely related to automaticity. However, automaticity is primarily related to the initiating of activity whereas encapsulation refers more to the maintaining of activity over time. For example, behaviors can be automatically elicited yet immediately compensated for by voluntary acts. Electromyographically assessed facial responses, for example, appear to be automatically elicited by certain stimuli, even if the stimulus is not consciously perceived (Dimberg, Elmehed, & Thunberg, 2000). However, this automatic response may be immediately masked by a different facial gesture reflecting culturally determined "display rules" (Ekman, 1972).

Specific neural circuitry. At the neural level, an evolved module is likely to be controlled by a specific neural circuit that has been shaped by evolution because it

mediates the functional relationship between ecological events and behavior. In the case of modules that are of ancient evolutionary origin, such brain circuits are likely to be located in subcortical or even brainstem areas. For fear and fear learning, a neural circuit that appears to be shared by mammals has been delineated through important discoveries by several investigators during the past decade (see reviews by Davis, 1992; Davis & Lee, 1998; Fanselow, 1994; Kapp, Whalen, Supple, & Pascoe, 1992; Lang, Davis, & Öhman, 2001; leDoux, 1996; Rosen & Schulkin, 1998). It is organized around the amygdala, a limbic structure in the medial anterior temporal lobe that mediates input from cortical and thalamic sites to hypothalamic and brain stem nuclei that control various aspects of overt fear behavior. Its sharing among mammals and its subcortical location suggest that it has an ancient evolutionary origin and that it served animals with primitive brains long before more recent biological families with more well developed cortices emerged. In particular, this circuit was firmly established at the base of the brain, which eventually, during relatively recent hominid evolution, became the site of cortical neural networks serving language and advanced cognition. Thus, its ancient origin and location in the brain makes it automatic and relatively impenetrable to cognition (LeDoux, 1996). Indeed, "although the experience of fear can be conscious, the brain mechanisms generating fear and the appraisal of stimuli as fearful are unconscious and automatic, similar to the workings of any other body organ" (Rosen & Schulkin, 1998, p. 326).

Effective Stimuli for Activating and Learning to Activate the Fear Module

Categories of Phobic's Fears

Even though fear may be elicited from many stimuli (e.g., Russell, 1979), intense fears and phobias tend to cluster around objects and situations that are fear relevant in a phylogenetic rather than an ontogenetic perspective (Marks, 1969; Seligman, 1971). Two epidemiological studies (Agras, Sylvester, & Oliveau, 1969; Costello, 1982) established that some stimuli (e.g., thunder, snakes) do indeed become the objects of fears and phobias more often than others. A number of subsequent studies examined this issue in a different way by having raters assess on 5-point scales the evolutionary preparedness of the content and behavior of phobic patients' fears. Ratings of 5 were given to objects or situations that were probably dangerous to pretechnological man under most circumstances, and ratings of I were given to objects or situations that were unlikely to have ever been dangerous to pretechnological man. Three studies conducted in this manner reported that the content of most clinical phobias was rated in the 4 or 5 range (i.e., de Silva, Rachman, & Seligman, 1977, who had 69 cases in London; de Silva, 1988, who had 88 cases in sri Lanka; and Zafiropoulou & McPherson, 1986, who had 49 cases in Scotland). Somewhat different conclusions were reached by Merckelbach, van den Hout, Jansen,

and van der Molen (1988), who used a different methodology. They asked students and biology researchers to rate the survival relevance of a variety of items that had been proposed as evolutionarily relevant in the literature on fears and phobias. However, given that survival relevance was not restricted to survival promoted by fear-activated defense, the results are not relevant in the present context. For example, poisonous mushrooms no doubt have threatened survival, but the relevant defense system here is taste aversion, not fear.

To organize the large range of stimuli and situations that may serve as objects of fears and phobias in humans, Öhman, Dimberg, and Öst (1985; see also Öhman, 1986) used an evolutionarily based categorization of behavior proposed by Mayr (1974). First, he distinguished between behavior directed toward the living and the nonliving world, called communicative and noncommunicative behavior, respectively, because only the former would elicit active responses from the environment. Second, within the communicative category, Mayr distinguished between behavior directed toward members of one's own and other species (intraspecific and interspecific fears, respectively). In this way, Öhman et al. (1985) distinguished between fears of physical objects or events (e.g., heights, thunder; noncommunicative fears), fears of other humans (social fears; communicative intraspecific fears), and fears of animals (communicative interspecific fears), noting that these classes of fear corresponded to three important classes of human phobia: nature phobias, social phobia, and animal phobias (cf. Diagnostic and Statistical Manual of Mental Disorders, fourth edition; DSM-IV; American Psychiatric Association [APA], 1994).

The Evolutionary Origin of Fear Systems

Predation has provided an important force in moving the evolutionary frontier, from the enormous proliferation of species in the Cambrian era to the emergence first of mammals and eventually of primates several hundreds of millions of years later (Allman, 1999). Where there is predation, there is by evolutionary necessity its complement, predatory defense. These two processes were tied together in an evolutionary arms race in which the emergence of more effective hunting strategies of predators forced potential prey animals to evolve more effective predatory defense and vice versa (Dawkins & Krebs, 1979). Thus, the need for effective predatory defense systems was the likely origin of the fear module, which has shaped its characteristics and explains the prominent role of animals in human fears (e.g., Arrindell, Pickersgill, Merckelbach, Ardon, & Cornet, 1991).

Early and reliable recognition of the predator is a prerequisite for effective defense. For example, Öhman, Flykt, and Esteves (in press) reported a preattentively controlled bias for picking out threatening animals (snakes and spiders) from complex visual displays and that this bias was specifically exaggerated in participants who were fearful of one of the animal categories. Öhman et al. (1985) suggested that the predatory defense system has its evolutionary origin in a prototypical fear of reptiles in early mammals who were targets for predation by the then dominant dinosaurs. Thus, because of this system, contemporary snakes and lizards remain powerful actual fear stimuli (e.g., Agras et al., 1969; Costello, 1982), and for the same reason, dragons have served as mythical embodiments of fear-arousing creatures throughout the history of mankind (Öhman, 1986; Sagan, 1977).

Öhman et al. (1985) proposed that social fears and social phobia originated from a second evolved behavioral system related to conspecific attack and self-defense (see Blanchard & Blanchard, 1988). This system controls the interaction among individuals in a group by defining which group members boss or yield to which others. The resulting dominance hierarchy provides a vehicle for bringing order into the group and for minimizing further aggressive encounters. Because the focus here is on the relevance of this system for fear, Öhman et al. (1985) talked about the defense or submissiveness part of it, relating social fear and anxiety to exaggerated social submissiveness.

Facial expressions of threat and submissiveness provide an important channel of communication in dominance contests among primates, which makes facial threat a powerful fear stimulus (Dimberg & Öhman, 1996; Öhman & Dimberg, 1984). Like animal stimuli (Öhman, Flykt, & Esteves, in press), facial stimuli suggesting threat are powerful attention catchers in humans. Thus, using carefully matched schematic faces, Öhman, Lundqvist, and Esteves (2001) reported that normal nonanxious participants were quicker to detect a discrepant threatening face among neutral and friendly distractors than a friendly face against neutral or threatening distractors.

Even though Öhman et al. (1985) invoked the differential evolutionary background of these two defense systems to understand differences between animal and social phobias, both interspecific defense and intraspecific defense appear to rely on the same neural system (Blanchard & Blanchard, 1988). Thus, the same basic fear module may serve in the different behavioral contexts provided by the predatory defense and the social submissiveness systems (as well as for the much less studied nature fears). For example, antipredator strategies tend to rely on active defenses that tax metabolic resources, thus prompting cardiac accelerations (see Öhman & Wiens, in press), whereas social submissiveness may rest on behavioral immobility and prolonged risk assessment (Blanchard & Blanchard, 1988), putting less demand on the cardiovascular system. The relative balance between these two types of defenses (active, such as fight-flight, vs. passive, such as immobility) is also related to the imminence of the threat (Fanselow, 1994; Fanselow & Lester, 1988).

Perceptual Mechanisms for Activating the Fear Module

Because of the time constraints of predatory-prey encounters, the more rapid the defense recruitment, the more likely the potential prey is to survive the encounter. Thus, the fear module's judgment of the fear relevance of stimuli is likely to rely on a quick and dirty process that rather risks false positives than false negatives (LeDoux, 1996). Because the fear module originates in primitive brains with limbic cortex rather than neocortex at the top of stimulusprocessing hierarchies, recognition of fear-relevant stimuli in limbic structures

may be possible in primates. Thus, there are populations of cells in the primate amygdala that respond selectively to faces (Desimone, 1991; Rolls, 1992), and representations of emotional faces in the amygdala may be accessed directly from midbrain and thalamic nuclei (Morris, Öhman, & Dolan, 1999). Furthermore, there is at least one report of amygdaloid cells in monkeys that respond specifically to spiders (Ono & Nishijo, 1992).

Öhman (1993a) argued that there must be an initial stage of perceptual processing involving feature extraction to allow preliminary identification of stimuli that (innately or because of learning) convey information about threatening circumstances. Thus, identifying simple stimulus features that could access and activate the fear module is an important research priority. They may be simple, such as rapid stimulus onsets (Yantis & Johnson, 1990) or directed movements (e.g., Bernstein, Taylor, Austen, Nathanson, & Scarpelli, 1971). However, they may also include more complex characteristics, such as sinusoidal shapes related to snakes or hairy bodies with many protruding legs such as in spiders. For example, Aronoff, Barclay, and Stevenson (1988) reported that participants rated curved lines converging on a joint point, suggesting the legs and body of a spider, as more negative and active than when the same curved lines were regularly arranged in parallel with no point of convergence. Similarly, Lundqvist, Esteves, and Öhman (1999) reported that frowned eyebrows composed of diagonal V-shaped lines provided decisive information for the negative evaluation of schematic faces. Following up on these findings, Öhman et al. (2001) reported that such faces were rapidly and accurately detected among distractor faces in visual search tasks. Further work to identify features or configurations of features that can activate the fear module is important because it would promote understanding of the psychological information-processing mechanisms that control the fear module.

Sensitization and Learning of Fear Responses

The predatory defense and social submissiveness systems discussed by Öhman et al. (1985; Öhman, 1986) suggest that there are stimuli (e.g., snakes and threatening faces) that owe part of their potential to activate the fear module to evolutionary contingencies. However, they are not necessarily innate fear stimuli in the sense that they automatically and invariably activate the module in all individuals. Rather, other conditions such as the presence of other aversive stimuli or a preexisting state of fear or anxiety in the organism may enhance the likelihood of an evolutionarily primed stimulus to elicit fear. Accordingly, the fear of such stimuli could be selectively sensitized to be displayed only in aversive contexts (see Gray, 1982, 1987; Lovibond, Siddle, & Bond, 1993).

As traditionally conceived, sensitization would result in a relatively time-limited enhanced responsiveness to evolutionarily relevant fear stimuli when the fear state is already activated (e.g., Groves & Thompson, 1970). More permanent changes in the tendency of a stimulus to elicit fear would require learning. Thus, in contrast to sensitized fear, learned fear denotes a relatively permanent change in response readiness to stimuli that have been

previously encountered in aversive contexts (e.g., Kimble, 1961). Learning is an evolutionarily derived adaptation to cope with environmental changes that occur within the life span of individuals and allows individual organisms to tailor their behavior to the specific environmental niche they occupy (e.g., Öhman & Dimberg, 1984; Plotkin & Odling-Smee, 1981). Learning is costly in terms of the relatively advanced neural circuitry that it requires and in terms of the time needed to get the adaptive response in place (Öhman et al., 1985). For example, if effortful trial-and-error learning was the only learning mechanism available, most animals would be dead before they knew which predators and circumstances to avoid (Bolles, 1970).

The evolutionary cost of learning, however, must be balanced against its potential benefits in solving specific adaptive problems (Johnston, 1982). In general, survival-critical responses to aspects of the environment that remain stable across aeons of time can be efficiently controlled from the gene pool. The panic elicited by choking may be a human case in point (Klein, 1993). But survival threats also vary across time and space, and there is an enormous number of stimuli and stimulus dimensions that have been connected with fear in different species (e.g., Marks, 1987; Russell, 1979). In such circumstances, as long as it occurs rapidly, learning which specific objects and situations to fear may provide a better solution to adaptive problems than inborn fears. It is better in the sense that it allows the organism to deal with relatively rapid environmental changes, such as new predation pressures, and with the selection of which specific stimuli out of many similar ones to fear and avoid. For example, predators may specialize on a particular prey, and so avoidance of those predators by individuals from other species may only provide unnecessary restrictions in those species' foraging behavior.

The Preparedness Theory of Phobias

Organisms are likely to be conservative in their dealing with potentially fatal situations (Hendersen, 1985; Mineka, 1992). Given the lurking deadly consequences of failures to elicit fear responses, the evolutionary perspective makes it likely that organisms quickly (i.e., with minimal training) would learn to fear potentially deadly stimuli. These premises were incorporated into a theory of fear acquisition by Seligman (1970, 1971). This theory combined the insight that intense fear may result from Pavlovian conditioning (e.g., Watson & Rayner, 1920), the evolutionary requirement of survival contingencies, and the empirical fact that phobias primarily occur to stimuli that are survival relevant in an evolutionary perspective (e.g., Marks, 1969). Seligman (1970, 1971) assumed that evolutionary pressures have predisposed primates to condition fear more readily to stimuli related to recurrent survival threats (phylogenetic ally fear-relevant stimuli) than to stimuli that never have threatened survival (fear-irrelevant stimuli) or to fear-relevant stimuli that emerged only recently in our evolutionary history (e.g., ontogenetically fear-relevant stimuli such as guns and electric outlets). Seligman (1970) further proposed that prepared associations not only should be easy to acquire (often in as little as one trial) but