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Antipredator responses and defensive behavior: ecological and ethological approaches for the neurosciences

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Abstract

In nature, animals are exposed to a wide range of threats and dangers with predators being amongst the more prominent and intensely studied of these. The responses of prey to predators and various predator avoidance and antipredator behaviors have been extensively evaluated from ecological and ethological perspectives and more recent ethopharmacological and neuroscience approaches. Unfortunately, there has been relatively little interchange between the ecological–ethological and neuroscience areas with the latter often using responses to predators just simply as another ‘model’ system. There is, however, now a growing realization that integrative approaches incorporating ecological, evolutionary and neurobiological explanations are required for the understanding of behavior and its functions. This necessitates an incorporation of ecological and ethological concepts and validity with neuroscience approaches to the analysis of antipredator responses and defensive behavior. A number of selected ecological approaches that are used for the investigation of predator avoidance mechanisms and antipredator defensive behavior patterns are briefly reviewed here. These include examinations of how predation risk and its variation affect decision making in animals and how learning affects these responses. The trade-offs that are involved, how the risk of predation affects decisions concerning foraging behavior, mating and reproduction, as well as how varying levels of risk affect decisions relative to the type of defensive mechanisms utilized are briefly outlined. The utility of these approaches and their relevance to the design and interpretation of various neuroscience studies is addressed here. © 2002 Elsevier Science Ltd. All rights reserved.

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1. Introduction

In nature, animals are exposed to a broad array of threats and dangers. These dangers include predators, conspecifics, internal and external parasites, bacterial and viral infections, toxins associated with food, and other threatening features of an animal environment. Amongst the most intensely investigated of these threatening factors are predators, with prey animals exhibiting a variety of primary, passive, adaptations to avoid capture as well as secondary mechanisms to actively defend themselves from predators [15,30,32,38,70]. These defensive mechanisms may be morphological (e.g. spines and armor), physiological (e.g. toxins), life historical (e.g. delayed breeding) or behavioral (i.e. predator avoidance and antipredator behaviors).

Changes in behavior such as reduced activity and shelter seeking reduce the probability of an encounter between a predator and prey, whereas morphological defenses reduce

the probability of a successful predatory attack once a prey has been localized. Most commonly, species have evolved a suite of antipredator behavioral adaptations that involve trade-offs and costs. Therefore, these antipredator behavioral responses would be expected to be used only when an animal has an accurate assessment of the current predation risk and, thus, of the benefits of the defense.

The relations between the antipredator and defensive behaviors exhibited by animals and predation risk have been considered from a number of different approaches. Ethologists have been particularly concerned with how prey animals recognize and respond to predator cues [28,30–32,38,53,88,92]. Behavioral ecologists have primarily dealt with the ecological and evolutionary consequences of responses to predator cues [33,39,56,70–73,92,102]. Community ecologists have considered how predatory risk affects the co-existence of, and interactions between, species [17,24,58,104]. Cognitive ecologists have been concerned with information processing and decision-making mechanisms associated with the learned and innate behavioral responses to predators [70,85,103,104] and more recently how these responses reflect fundamental components of cognitive

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mechanisms. (causal knowledge [105,106]). Neuroscientists have emphasized the neurobiological substrates of defensive responses and utilized predator exposures as a means to address the impact of threatening and stressful factors on regional brain activity and plasticity as well as to examine the functioning of various neuromodulatory systems [4,10,47,50,76,79,93,98,99]. At the cellular and molecular level, neuroscientists have used predator exposure as a means of examining the impact of acute and chronic stress on neuronal functioning (e.g. neurogenesis, gene expression [36,93]). At a more behavioral level, ethopharmacological studies have attempted to combine an ethological approach to the understanding of the causes and functions of defensive behavior with pharmacological analyses of the underlying mechanisms [6,11–13,35,40,43,60–64,75,80–83,87]. These latter investigations have also considered the possible relationships between defensive behavior and psychopathologies and used defensive behaviors for testing drugs effective against anxiety and panic.

These ecological and neuroscience approaches utilize an array of terms and concepts, e.g. *ecology*: ‘alarm’ [70,71] ‘ecology of fear’, ‘predators frightening prey’ [3,20,21,59]; ‘risk assessment’ [32,70,71] ‘apprehension gradients’ [33]; ‘threat sensitivity’; ‘risk adjustment behavior’ [51,59,70,71]; ‘giving up distance’ [19] ‘vigilance’ [32,59,67,73]: *neuroscience and ethopharmacology*: ‘species specific defense responses’ [15]; ‘risk assessment’ [11,47] ‘fear conditioning’ [16,38,55–57]; ‘fear stimulus’ [98]; ‘defensive distance’ [8,47]; ‘flight’ [16,82,83] ‘freezing’ [15]. All these terms evoke a common underlying currency of ‘fear’ and ‘anxiety’. Despite these similarities, and in some cases even the use of the same terms (e.g. risk assessment and defensive behavior [8,10,42]), there has for the most part been relatively little interchange between the ecological and neurobiological areas.

There is, however, now a growing appreciation of the necessity of having integrative approaches to behavior, which incorporate ecological reality and evolutionary explanations with an understanding of the underlying neurobiological mechanisms. By combining data about an animal’s sensory and neural capabilities with information about its evolution and biological and physical environment one can gain a better understanding about why animals exhibit particular behaviors (i.e. defensive behaviors; perceptual responses) in specific circumstances. This is especially relevant in the interpretation of results that employ animal models for human psychopathologies.

Antipredator responses and defensive behavior require such an integrative approach. This necessitates an incorporation of ecological concepts with neurobiological and ethopharmacological approaches and vice versa. It should be emphasized that using predators or their cues as just another ‘model’ for eliciting fear, anxiety and stress does not by itself provide ‘ecological validity’ or reality to neuroscience studies. Likewise, the measurement of a number of behaviors without knowledge of their evolutionary

and adaptive significance does not render a study of ethological relevance. As a goal of behavioral neuroscience studies is to understand the biological mechanism underlying brain function and behavior, it makes sense to focus on behaviors that are not artificially construed but represent ecologically relevant responses. Ultimately, it is the adaptive nature of behavioral traits, which makes animals fit and not the underlying neurobiological or molecular machinery. As such an appreciation of the ecology and ethology of predator–prey relations and antipredator responses of the species in question is essential for the full understanding of the results of neuroscience studies.

This review briefly considers selected ecological and ethological approaches to antipredator responses and defensive behavior. It is meant to be neither an all-inclusive review of the ecology and ethology of antipredator behaviors nor a detailed description of all the neuroscience and related studies that utilized some aspect of predator exposure. Rather, this brief review highlights a number of selected concepts and questions that we consider of particular interest for our aim of bridging behavioral ecology, ethology and neuroscience.

2. Decision making and trade-offs

When hungry an animal will look for food, when thirsty it will try to drink, when threatened by a predator it will try to avoid being eaten. However, what should the animal do when it is hungry, thirsty and under the risk of predation at the same time? Natural selection has designed animals to choose the behavioral option, which maximizes fitness, often equated with its survival to reproduce. Animals need to make decisions and arrive at compromises for fulfilling various needs. This involves inevitable trade-offs between the benefits of avoiding predation (or other threat) and the costs of doing so in terms of optimization of feeding, reproduction or survival [1,20,71].

2.1. Assessing the risk of predation

To say that an animal makes decisions implies here no conscious intent but merely refers to the fact that at any given time the animal is adopting one behavioral alternative rather than another. Animal decision-making appears to be well adapted for the economic solutions of everyday problems and takes into account differences in the costs and benefits of various alternative options. Although a great deal is known about the predatory stimuli that animals respond to how animals integrate this information on the presence of a predator, along with predator abundance, the likelihood of escape, etc. into some sort of assessment of predation risk is poorly understood. Neuroscience and neurobiological studies are starting to focus on these questions by examining the roles of various brain regions and functions as they may relate to predator exposure [4,50,76,99]. Other neuroscience studies, while not directly

dealing with these questions, could benefit from incorporating antipredator considerations. For example, visual predator recognition often depends on simple cues such as apparent size, shape, speed or the presence of frontally positioned eyes. This permits potential prey to respond to historical predators and evolutionary novel ones [11,23,28,29,32,48,53,95,102]. This should be taken into account in the design and interpretation of studies of stimuli perception and the integration and expression of these responses.

In behavioral ecological analyses how an animal weighs or assesses the information and arrives at a responses has been considered to be carried out by a ‘rule of thumb’ [18]. The distance that an animal forages from a refuge has been used as a rule of thumb (by both the investigator and by implication the animal) to assess its likelihood to be susceptible to predation. For example, many mammals not only move to safe habitats in response to predation but also possess different behavioral strategies that may minimize risk in areas far from refuges [54,70,94]. By making behavioral responses appropriate for a specific context (e.g. presence or absence of cover) or motivational state (e.g. level of hunger), a prey may be able to significantly reduce the risk of predation. For example, sticklebacks forage on the more exposed and ‘riskier’ denser portions of zooplanktonic swarms when either energetically stressed or safe from attack [67]. Likewise, many small rodents tend to feed closer to refuges and in more central areas when predators are present, with the distance from the refuge again depending on the hunger level and nature of the predator [5,59,70].

2.2. Threat sensitive predation avoidance

Predation carries a much higher risk than that of temporarily losing food, water or a mate. A single predator–prey interaction can have considerable influence on the fitness of a prey individual—one mistake and the prey animal may be eliminated. As such, the avoidance of predators and the exact evaluation of predatory risk are highly favored by natural selection. Therefore, one expects that there would be strong selection pressure on risk assessment and the ability to distinguish between predator cues that indicate a high risk of threat and those that do not [1,2,11,18,94].

Direct cues (visual, tactile, auditory) are produced by a predator that is immediately present. Indirect cues (i.e. odor) do not necessarily indicate that a predator is still present and that the prey has encountered or will actually encounter a predator. Such indirect cues do, however, provide an underestimation of risk if a predator is present and an overestimation if it is absent [2,70,71,94]. The hypothesis that prey species assess and behave flexibly in response to different degrees of predation threat is known as the ‘threat-sensitive predation avoidance hypothesis’ [51]. This concept was originally derived from studies with fishes in which it was shown that the avoidance and defensive responses of prey

species are dependent on the nature of the predator cues present, with visual cues eliciting the greatest avoidance responses and odor cues eliciting decreased responsiveness with a declining intensity of the chemical stimulus [59].

2.3. Predator apprehension and vigilance

The concepts of antipredator ‘apprehension’ and vigilance are widely used in ecological and behavioral ecological studies. Apprehension, which is considered here to reflect a motivational state, is defined as any reduction in attention to other activities (e.g. foraging, mate seeking) as a result of increasing the allocation of attention to detecting and/or responding to potential predators [21,33,44,67]. Vigilance on the other hand is considered as a behavioral state involving alertness and scanning for prey. This results in an ‘apprehension gradient’ ranging from no interest in a predator to total preoccupation with a predator, passing through a phase of reduction in ongoing activities and increased predator directed attention. A good example with gerbils shows how their behavior changes from ‘blind foraging’ to no feeding and total vigilance, through a phase of low feeding and increased scanning behavior [33]. An animal’s normally observed behavior is a compromise between predator avoidance (cost) and the benefit of an alternative activity (e.g. foraging, mating). In general, when the risk is high, animals should adopt safer tactics while when the risk is low animals should be more flexible in their behavior. This ‘apprehension continuum’ is reminiscent of the concepts of defensive distance, predatory imminence continuum, and risk associated suppression of competing motivational systems proposed in the neuroscience related literature [11,15,16,38].

It is proposed that when prey have imperfect information on a predator’s whereabouts, they adopt some baseline level of apprehension [3]. This baseline level responds to the number of prey individuals, their individual state, and feeding rate as well as the numbers and characteristics of the predators or predator associated cues. The various levels of apprehension lead prey to select a certain optimal level of vigilance, that is staying alert (i.e. scanning behavior, head up) so as to detect an approaching enemy, in response to their perceptions of a predator’s whereabouts [20,21,23]. It is the baseline of apprehension that determines the prey’s level of vigilance in the absence of any tangible evidence of a predator’s presence. If prey set their level of apprehension too high, they may miss valuable feeding or mating opportunities, while if they set it too low they are likely to be killed by the predator. Gain and risk must trade off so that the largest gain comes at the expense of the lowest risk. The mechanisms and stimuli that determine this level of apprehension are amenable to neurobiological investigations and are of relevance to the understanding of how various other threatening stimuli may be integrated and processed.

Within populations there can also be individual differences in response to predators and other threats. Wilson et

al. [101] defined a shyness–boldness continuum which they based on the ‘propensity to take risks’. An individual that performs more risky behaviors in a particular situation (i.e. decreased avoidance of a predator) is considered bold whereas one which avoids risk is called shy. This is reminiscent of the differences in the activation of the ‘behavioural inhibition system’ and responses to ‘conflict’ and threatening situations proposed in the neuroscience literature [47].

2.4. Foraging and vigilance

Several models predict how foraging animals should balance the conflicting demands for food and safety [20,21,45,71,72]. Animals need to consider choice of food patch, time spent in the food patch, choice of overall foraging location, and selection of a metabolically appropriate diet in relation to overall predation risk. Giving-up-densities of food (GUD, i.e. density of food at which animal stops feeding or searching for food) have been devised as a simple index of the perceived risk of predation, with the GUD of animals increasing with higher predator risk [19]. When foraging under predation risk, individuals sacrifice food availability, food quality and feeding rate for safety either by differentially allocating time among safe and risky habitats or by using vigilance while active within a habitat [5,21]. It was originally considered that vigilance slowed down feeding [71]. It is now becoming evident that vigilant animals can forage (i.e. handle food) and that ‘head down’ foragers can detect predatory attack [73]. Overall, the results of a variety of investigations and theoretical determinations established that foragers always behave as if a predator was present [70,73]. It is better to be too cautious than too bold, with erring on the side of caution being selected for. Animals likely adaptively overestimate the risk of predation to avoid the relatively high cost of underestimation. How this information is assessed and integrated is a question that should be of interest to cognitive neuroscience.

2.5. Refuge use

Prey often respond to a predator’s presence by increasing their use of refuges (e.g. rats and small rodents going into burrows in the presence of cats and foxes; [11,13,35,38,71]). However, refuge use may have some costs (e.g. loss of time for foraging or mating) and physiological constraints (e.g. hypoxia) that should be minimized [2,58,89,90]. Animals should optimize the decision of when to come out of a refuge after a predator exposure by balancing antipredator and other demands [104]. Risks and costs are balanced in determining both when to flee to a refuge and when to emerge from it.

Utilizing the antipredator responses exhibited by various aquatic invertebrates Sih [89,90] modeled the effects of a prey’s uncertainty about predation risk on its refuge use. He showed that refuge use increases with (i) increasing vulnerability to a predator; (ii) decreasing hunger level or

increasing physiological status; (iii) increasing predation risk outside the refuge; (iv) decreasing costs of lost opportunities (e.g. decreased quality of mates or food); and (v) decreasing certainty about the level of predation risk outside the refuge. Similarly, under predation risk Indian crested porcupines in the Negev desert become strongly selective in their choice of habitat and food patches such that porcupines have an actual risk of predation approaching zero [71]. Likewise, Schaller [88] indicated that the presence of lions on the Serengeti caused wildebeest and zebras to be more vigilant and shift their activity towards safer habitats or refuges.

2.6. Predator facilitation

In nature most animals are exposed to more than one type of predator and need to balance the often conflicting responses to different predators. Predator facilitation occurs when prey face two or more predator species and cannot forage and be safe from both types of predators simultaneously: avoiding one predator necessarily leads to exposure to the other [40,68]. In the Negev desert, gerbils face conflicting demands from vipers and owls. Gerbils respond to owls by reducing foraging activity, avoiding open areas, and exploiting patches less. Conversely, vipers in the covered areas lead the gerbils to spend more time in the open; “The fangs of snakes are driving gerbils into the talons of owls” [68]. These types of trade-offs and the relatively complex decision making involved are just beginning to receive attention and are again amenable to cognitive neuroscience analyses of decision-making processes.

3. Temporal patterns of predation

3.1. Risk allocation

Prey animals can both decrease their activity and use different temporal refuges to minimize their vulnerability to predators. Although studies of antipredator behavior have taken advantage of the rapid responses of prey to changes in regimes of risk, few studies have appreciated that these antipredator responses depend on the pattern of risk experienced by the prey. Predators come and go resulting in individual prey experiencing temporal variations in predator risk. Lima and Bednekoff [72] pointed out that by ignoring the importance of temporal variations in risk, investigators might systematically misestimate their actual impact in nature. They devised a ‘risk allocation hypothesis’ based on the notion that prey adaptively allocate their foraging efforts, and thus their exposure to predator risk, across high risk and low risk situations. Optimal prey behavior in any given situation depends on the overall patterns of risks experienced by that individual prey (i.e. whether prey are exposed to a continuous or chronic risk or predation versus those that occasionally experience the threat of predation). If the responses of prey to predators depend on

the proportion of time that prey are exposed to a high risk versus low risk situation, then the usual laboratory procedure that examines the effect of acute predator exposure provides an ecologically relevant assay only if natural predation occurs in relatively infrequent pulses. For example prey that are infrequently exposed to predators display relatively high basal activity and exposure to a pulse of predation (e.g. odor threat) elicits a marked decrease in activity. This could result in an overestimate of the natural responses of the prey to a predator. Conversely, in prey species that in nature are frequently exposed to predators and display a relatively low level of activity, the acute pulse exposure procedures produce minimal changes and underestimate the effects of predation risk. This risk allocation hypothesis reinforces the need to carefully consider the ecological reality that faces a prey species when extrapolating from laboratory experiments to nature. Moreover, the risks faced by prey are not static and can vary according to a variety of factors including, reproductive state, sex, developmental stage and time of day and year. Accordingly, the nature and extent of responses to predator exposure can also vary and need to be taken into account in investigations and interpretation of antipredator behaviors.

3.2. Role of the 'intensity' of the predator threat

In the study of decision making under predation risk, the importance of the intensity of threat has been emphasized several times [2,32,59,70,72]. It has been suggested that if a predator and prey are maintained in very close proximity as done in most laboratory studies, the prey's response may be so strong as to be potentially misleading as to what actually occurs in the wild [70,72]. For example, the marked reduction in gerbil activity seen following exposure to captive owls in close proximity does not reflect the relatively brief reduction in gerbil activity following an encounter with an owl under semifield conditions [3]. Likewise, the large reductions in vole activity following exposure to intense predator odors seen in the laboratory does not always mirror the lowered responsiveness to these odors reported in field studies. Mustelid predators and their odors have been reported to affect the activity levels and spacing patterns of a number of species of voles and other small rodents in laboratory and field studies with relatively small enclosures [34,56,80,81,83]. In contrast, results of studies with large scale enclosures found either no or minimal effects on spacing behavior, activity levels or reproductive behavior of voles exposed to mustelid odors [54,58]. In a study with hedgehogs exposed to badger odor, it was similarly found that while in the laboratory hedgehogs reduced their activity and avoided badger odors for 2–4 days, in a field enclosure their alterations in activity and avoidance lasted for approximately 15–30 min [100]. Likewise, in the laboratory various species of fish show greater amplitude and longer

duration of activity reductions following predator exposures than they do in the wild [45,55].

This apparent lack of a marked effect of the presence of a predator or predator associated cues on the antipredator behaviors of free-ranging animals may be attributed to several factors. In the laboratory individuals are usually presented with a single intense cue (e.g. odor or one chemical component of odor. i.e. anal gland constituent of weasel or fox) to the presence of a predator and thus react strongly. In the wild, however, individuals can assess predation risk via a variety of cues including vision, habitat structure and olfaction and must integrate all these cues to determine the overall risk of predation. As such, responses to experimental manipulations of any single cue, such as predator odor, often may be weaker in the field than in the laboratory.

Lima [70] has also pointed out that an increasing or very high predatory risk may actually reduce vigilance by eliciting other defensive behaviors, particularly in animals that jointly use time allocations among habitats and vigilance between habitats to mitigate the effects of predation. This has been confirmed by the Blanchards and co-workers [11,13,14] in their elegant studies of the timing and distribution of the antipredator defensive responses displayed by rats in a visible burrow system.

Prey in natural settings can also habituate (i.e. stop responding) rapidly to predators that are not engaged in threatening behavior and are viewed at a safe distance [88]. When in laboratory studies an immobile model of a predator is presented repeatedly, habituation is particularly rapid to models of predators that normally hunt in motion but not for ambush predators that are always potentially threatening [28,32]. There is also virtually no habituation to aerial predators which can be considered to represent a relatively infrequent 'pulse' threat [32]. As well there can be rapid behavioral habituation to predator odors that are not reinforced by the presence of an actual predator [33,34,43,56,81]. In addition, when the cost of lost foraging opportunities is high, animals may also resume foraging and decrease antipredator behaviors soon after predator encounters. Yellow-rumped warblers in migratory disposition (i.e. high energy consumption) resumed foraging significantly sooner after exposure to a mounted hawk than birds in a non-migratory state [78]. Similarly, food-deprived ground squirrels were less vigilant than non-deprived individuals [5].

As indicated previously there are cases of excellent agreements between the results of field studies and of laboratory studies that take into account the ecological validity of the species being examined (e.g. in the patterns of defensive responses) [11–13,40]. This similarity is vividly borne out in studies of the effects of chronic predator exposure. Laboratory rats in the visible burrow system [14] and snowshoe hares in the wild [17] displayed remarkably similar behavioral, physiological, endocrinological (sustained increases in corticosterone and ACTH) and neural changes following chronic predator exposure.

4. Prey signaling to predators

Although in most cases, antipredator defensive behaviors involve avoidance of the predator, there is another category of antipredator responses that involve direct active signaling by the prey to the predator. In vertebrates, these include detection-notification and condition-notification signals, including alarm signals, and predator inspection and mobbing [7,23,31,84]. Predators that stalk their prey rely heavily on surprise. If a prey animal signals in a very obvious manner that it has detected a stalking predator, the predator may give up its current hunt since it is likely to be unsuccessful. Notification of predator detection is provided by the conspicuous white patterns on the posterior ends of a number of species of vertebrates (e.g. some ungulates, rabbits and rodents) that are flashed, flicked or exaggerated by bouncing gaits as they flee a detected predator [23]. Condition-notification signals demonstrate the ability of prey animals to escape pursuit by a predator, e.g. the jumping or stotting gait shown by Thomson's gazelles in response to wild dogs [23]. This detection-notification, again, involves assessment of the nature and levels of risk. Gazelles do not notify and stott for cheetahs which can readily catch the slowed, signaling gazelle. Predator inspection and mobbing signals advertise the location of a stalking predator to all prey in an area causing the predator to move to another area. The neural systems that subserve these apparently paradoxical 'risky' prey signaling responses in highly threatening situation deserve critical examination.

5. Individual and social learning of predator responses

Learning is involved in predator and other threat recognition and the estimation of predation risk in a variety of taxa [15,27,32]. Although many species have certain innate responses to predators (i.e. species specific defensive responses) [15,60] some individual experience may be necessary to access what is the most appropriate antipredator responses. The extent of this varies according to the species and nature of the predator risk. In a classical study, Curio [32] showed that Galapagos finches retain alarm responses to snakes, owls and hawks on islands from which predators are missing. Population differences exist in the responses to snakes in deer mice and ground squirrels, with individuals from habitats in which snakes are absent showing relaxed or modified antisnake behaviors [28,53]. Similarly, adult moose from areas that had been predator-free for 40–75 years displayed lower vigilance and defensive responses to the auditory and olfactory cues of bears and wolves than did moose in areas in which these carnivores were present [9]. However, after some predatory losses the naive prey exhibited enhanced predator responses, thus showing an integration of learned and innate responses.

Although mammals are usually quite adept at the

acquisition of anti predator responses and conditioned fear, the necessity for individual learning can place animals in potentially non-adaptive situations. Social learning on the other hand allows an individual to 'exploit the expertise of others' [86], thus circumventing the disadvantages associated with individual learning. Through social learning animals can avoid hazardous trials and/or reduce time spent on either unprofitable or deleterious activities. If another individual, a 'demonstrator' has already acquired vital skills or information, such as an appropriate diet or the ability to recognize or avoid predators or other threatening factors, an 'observer' that can socially acquire such information will be in an advantageous situation [25,52]. Socially learned predator recognition has been most extensively studied in fishes where social transmission of predator recognition was first reported [97]. Recent studies have clearly demonstrated that individual fishes which socially learned to recognize predators gained survival benefits during staged encounters with a predator [77]. Predator-naive individuals of several species of birds have also been shown to learn to recognize and mob predators by observing the mobbing of others [31]. Similarly, recognition and fear of a snake was shown to be socially acquired in primates in both the wild and in the laboratory [7,27,91]. It was speculated that social learning may also play a role in the enhanced antipredator responses displayed in naive moose witnessing predatory losses [9].

Biting and blood feeding flies are amongst the most prevalent and biologically important of natural stressors. They can be considered as a major threat akin to 'micro-predators' with a broad behavioral and neural impact. Defensive responses to and avoidance of biting flies were shown to be rapidly acquired by mice through both individual and social learning [63–65]. The neuromodulatory processes involved here were indicated to be similar to those involved in laboratory studies of fear conditioning involving electric shock [41,63,64]. This further supports not only the involvement of learning in determining antipredator responses, but also shows the utility of predator avoidance behaviors for the investigation of learning in an ecologically appropriate context.

There are also data showing that prey can learn about a predator's strategies and consequently alter their defensive and escape behaviors. Fenn and Macdonald [42] found that wild rats in the field shifted from nocturnal to diurnal feeding in response to variation in predator activity pattern. Results of elegant studies with Diana monkeys showed a rapid learning of, and adaptation to, the hunting tactics of their predators [22]. Normally these monkeys react to their natural predators, eagles and leopards, with high calling rates and approach. In Tai National Park, Ivory Coast, humans with guns hunt monkeys for their meat with the poachers imitating animal calls to feign the presence of eagles and leopards. In the presence of humans the monkeys quickly learned to become silent and move on. In a small part of the park in which the poachers have been excluded,

the monkeys react to the calls, but not when humans are present. These results showed that adaptation to changes in predation could rapidly occur. In related studies, it has been further indicated that Diana monkeys are able to quickly learn to form mental representations of different predator categories when hearing conspecific or heterospecific alarm calls [105,106].

6. Predation, reproduction and mating responses

There is evidence that various environmental factors affect mate preferences and mate selection. Mate choice and sexual behaviors are costly in many species and, as such, they are condition and context dependent [57]. Predation risk has received attention as a cost of reproduction. Reproducing animals are often exposed to increased predation risk owing to either an increased conspicuousness to predators, a decreased possibility of escape, or more frequent predator encounters [26,32,70]. Consequently, animals, and in particular females, should balance their reproductive decisions (i.e. when, where and how to reproduce) against predation risk so that their lifetime reproductive success is maximized. This suggests a greater sensitivity or responsiveness to predators in females than males, which is consistent with the results of a number of laboratory and field investigations [12,26,80,83].

The risk of predation is, however, not constant but varies in time and space during an individual's lifetime. Individuals should therefore assess short-term changes in predation risk and adjust their reproductive decisions accordingly. There is evidence that females can suppress reproduction under increased predation risk by refraining from reproducing or decreasing investment into reproduction e.g. amount of eggs produced by fish [26]. Predators or their odors have been reported to inhibit estrous, breeding, foetal development, growth of young, sexual maturation and to reduce litter size in microtine rodents in the laboratory and within outdoor enclosures [59]. In the field chronic predator exposure reduced litter size in snowshoe hares [17].

Females may also change their mating decisions with the levels of risk. It has been suggested that the effort committed to discriminating among possible mates will decrease as predation risk increases. Female guppies exposed to predation risk spend less time near males and tend to associate with less conspicuous males who are less likely to attract predators [74]. Males also face a trade-off regarding sexual traits and the risk of predation. Those male traits that are favored by females (e.g. odors, bright colors, odors) may also be more attractive to predators [107]. For example the chemical signals that male rodents use to establish territories and advertise to females are visible under ultraviolet light and can be detected by avian predators [96].

Males are also affected by the threat of predation becoming less choosy or discriminating in their mate preferences. The presence of a female can, however, modify the anti-

predator responses of males leading to a greater risk taking [37,65]. Male guppies in the presence of a female show greater boldness and willingness to risk approaching and inspecting a predator [46]. The antipredator responses of male mice are also condition or context dependent. Brief pre-exposure to the odors of a novel estrous female shifts the condition or motivational state of a males such that they display greater 'boldness' and lowered avoidance of, and corticosterone responses to, predator odor [65]. This may be associated with an enhanced sexual motivation and responses to a transiently available sexually receptive female. This context dependence needs to be considered in behavioral neuroscience and neurobiological studies when interpreting the expression and modulation of sexually related responses and extrapolating them to naturalistic settings.

7. Parasites and responses to predation threat

Parasites and disease have a major impact on the evolution, ecology and behavior of their hosts. Animals acutely 'sick' from systemic infections display a set of co-ordinated 'sickness behaviors' and defensive responses to facilitate recuperation [49]. These weakened animals display reduced activity and feeding which while facilitating recovery also reduces the threat of predation.

Parasites can also have significant effects on their hosts even when the level of infection is subclinical and the animals do not display any overt signs of illness. The observed altered behavioral responses have been proposed to either benefit the parasite (parasite 'manipulation'), benefit the host, or simply arise as side-effects of the infection [66]. Studies with parasitized rodents have revealed alterations in a variety of behaviors that might directly or indirectly increase vulnerability to predation, facilitating parasite transmission to a definitive host [66,69]. Mice and rats that are infected with protozoan parasite, *Toxoplasma gondii*, display reduced antipredator responses and decreased avoidance of predators [8]. Even species that serve as single host systems may reveal significant changes in the responses to predator threat when infected [62]. The reduction in sensitivity to predator threat here may be part of a general reduction in fearfulness and anxiety in the infected individuals, decreasing avoidance of conspecifics and increasing interactions between infected and uninfected individuals, thereby facilitating parasite transmission in single host systems [66]. This again illustrates the context and condition dependency of the expression of antipredator responses and defensive behaviors. This is of special importance when comparing the results of laboratory and field studies as most natural populations of small rodents are infected with parasites which use predators of rodents as final hosts [66,69]. In studying animals that live in 'aseptic' laboratory environments, it is easy to forget that animals have evolved and thrive in environments with an array of parasites.

8. Conclusions

Ecological and ethological studies have extensively dealt with antipredator responses and defensive behavior. This review has focused on a number of findings and questions addressed in those studies that are of interest to, and worthy of consideration by, investigators in the neurosciences. This includes, but is not limited to, questions such as: (i) How do predation risk and variation in predation risk affect decision making and which factors are of importance in an individual's decision making processes? (ii) How do varying levels of risk affect decisions relative to the types of defense mechanisms employed? (iii) What roles do individual and social learning play in the determination of antipredator responses? (iv) How does the risk of predation affect foraging, courtship and mating decision? (v) How does the presence of potential mates affect responses to predators? (vi) How do parasites impact on predator responses? These questions are not only of relevance to studies of antipredator behaviors *per se* but also to various neuroscience and ethopharmacological investigations of how various stimuli are perceived and integrated in an ecologically meaningful manner. Understanding brain and behavior relationships in the context of natural conditions and constraints is essential if we are to understand the neurobiological basis of behavior.

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