J. Ecol. Field Biol. 31 (2): 89～95, 2008

〈Review〉

Integration of Optimality, Neural Networks, and Physiology for Field Studies of the Evolution of Visually-elicited Escape Behaviors of Orthoptera: A Minireview and Prospects

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ABSTRACT: Sensing the approach of a predator is critical to the survival of prey, especially when the prey has no choice but to escape at a precisely timed moment. Escape behavior has been approached from both proximate and ultimate perspectives. On the proximate level, empirical research about electrophysiological mechanisms for detecting predators has focused on vision, an important modality that helps prey to sense approaching danger. Studies of looming-sensitive neurons in locusts are a good example of how the selective sensitivity of nervous systems towards specific targets, especially approaching objects, has been understood and realistically modeled in software and robotic systems. On the ultimate level, general optimality models have provided an evolutionary framework by considering costs and benefits of visually elicited escape responses. A recent paper showed how neural network models can be used to understand the evolution of visually mediated antipredatory behaviors. We discuss this new trend towards integration of these relatively disparate approaches, the proximate and the ultimate perspectives, for understanding of the evolution of behavior of predators and prey. Focusing on one of the best-studied escape pathway models, the Orthopteran LGMD/DCMD pathway, we discuss how ultimate-level optimality modeling can be integrated with proximate-level studies of escape behaviors in animals.

Key words: *Antipredatory behavior, Escape, Locusts, Movement detecting neurons, Neural networks, Optimality model*

INTRODUCTION

Antipredator behavior plays a vital role in predator-prey relationships. When a predator’s attack is imminent, prey lacking special defensive weapons or effective crypsis can only survive by escaping. From the proximate viewpoint, the physiological properties of the neurons that trigger escape responses have been extensively investigated in arthropods such like locusts and grasshoppers (e.g., *Locusta migratoria*; Simmons and Rind 1992, Hatsopoulos 1995, Gray 2005, *Schistocerca americana*; Gabbiani et al. 2002), flies (Holmqvist and Srinivasan 1991, Trimarchi and Schneiderman 1993), cockroaches (Fouad et al. 1996), crabs (Medan et al. 2007, Oliva et al. 2007), and crayfish (Zucker 1972), as well as vertebrates (Gahtan et al. 2002, Hale et al. 2002). Among arthropods, the brain and nervous system of locusts have features that make them particularly useful for studies of the relationship between neuronal responses to visual stimuli and escape behaviors (Burrows 1996). Therefore orthoperan species such as grasshoppers have been used most often as models for electrophysiological studies. Accordingly, we restrict our discussion to researches conducted on Orthoptera. Visual cues are important for prey because they can provide information allowing predator recognition at a relatively safe distance from the approaching predator. Several decades of neurophysiological studies have demonstrated that specific identifiable neurons in the locust visual system are tuned to objects approaching on a collision trajectory (e.g. Rind and Simmons 1992). These neurons respond to angular size and angular velocity (Hatsopoulos et al. 1995) or angular acceleration (Rind and Simmons 1992) of the images of approaching objects as projected on the retina. The electrophysiological properties of the neurons are known so well that they are employed in robotic systems (Blanchard et al. 2000, Stafford et al. 2006, Stafford et al. 2007) designed for avoiding obstacles.

Visually elicited escapes have also been approached from evolutionary perspective. In this ultimate level of analysis, graphical (Ydenberg and Dill 1986) and mathematical (Broom and Ruxton 2005, Cooper Jr. and Frederick 2007) models of the costs and benefits of escape responses have been used to explain selection factors that shape (optimize) prey escape behavior (typically defined as a distance between predator and prey at the moment of escape initiation) without considering the underlying properties of sensory and neural networks. Only recently, an evolutionary model combining

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proximate mechanisms, from a very simple computer-generated neural network, with evolutionary mechanisms has been used to interpret variation in escape behavior among populations (Blumstein et al. 2006). Here, we predict further integration between research of proximate mechanisms and evolutionary cost/benefit analyses of visually-elicited escape behaviors using Orthoptera as examples. We restrict this review to electrophysiological research on locust visual sensory neurons used in escape behavior and general modeling studies of the costs and benefits of prey escape responses.

PROXIMATE LEVEL: ELECTROPHYSIOLOGY OF PREDATOR DETECTION AND ESCAPE INITIATION IN LOCUSTS

Movement Detecting Neurons in Locusts

Certain visual neurons in locusts have selective sensitivity to approaching objects and appear to react to approaching predators with timing properties that are adaptively tuned to promote successful escape from a predator. The nervous system of locusts provides an excellent model system for neurophysiological studies because (a) it consists of a relatively small number of neurons, (b) the majority of neurons have been identified as to function, and have firing patterns that are easy to record and (c) the neuronal response is directly related to insect escape behavior (Burrows 1996). The most widely studied locust visual neurons involved in triggering insect escape responses are: the lobula giant movement detector or "LGMD" (O'Shea and Williams 1974) and the descending contralateral movement detector or "DCMD" (Rowell 1971). The LGMD has fan-shaped dendrites and is a point of convergence for retinotopic inputs (O'Shea and Rowell 1976). The postsynaptic connection of the LGMD with the fast-conducting DCMD has the largest diameter of the contralateral nerves. The DCMD has a synapse with other interneurons that forward signals to subsequent motor neurons. These motor neurons evoke jumping and flying behavior (Burrows and Rowell 1973). Intracellular recordings show that the DCMD axon spike comes after the LGMD spike 1:1 with constant latency, which implies highly correlated properties of both neurons. These empirical data indicate that the LGMD/DCMD neurons function as transducing processors in the nervous system of locusts. These neurons are involved in converting visual signals to motor actions so that visual stimuli from approaching predators can evoke escape behavior at an appropriate moment. Because the LGMD/DCMD pathway is believed to be an important component of the escape-triggering pathway, the physiological characteristics of these neurons establish a basis for understanding the mechanisms by which escape behaviors are triggered.

Fine-Tuning to Approaching Objects

Previous studies verified that (a) the DCMD tends to react to approaching objects rather than retrograde or translating figures (Rind and Simmons 1992), (b) the "critical cues" for the DCMD are an increase in the size of edge and a consistent increase in edge velocity (Simmons and Rind 1992), and (c) the neuronal activity can be elicited by multiplying the velocity and the size of an object's image projected onto the retina (Gabbiani et al. 2002, Hatsopoulos et al. 1995) although some of the details are disputed (Gabbiani et al. 1999, Rind and Santer 2004). Gabbiani et al. (2002) claimed that the mathematical product of an exponential function of the size and the velocity of the image predicts the peak spiking frequency. This peak was predicted to occur before the expected moment of collision between the object and the locust. Therefore, they proposed that the peak can be used by locusts to anticipate collision and to trigger the escape. However, Rind and Simmons (1992, 1999) asserted that the angular acceleration of objects is closely associated with the spiking frequency and their simulation model suggests that the peak often occurs after the expected time of collision with an object (Rind and Simmons 1999). They argue that peak therefore cannot be the signal triggering the escape. Instead, they proposed that a threshold value of the spiking frequency, corresponding to the threshold value of the angular speed of expansion of an object image on the locust's retina may trigger the escape. Regardless, the above-mentioned visual variables (angular size, angular speed) can be extracted by a visual system experiencing the approach of e.g., an avian predator. Researchers agree that responses of the neurons are restricted and finely tuned to stimuli associated with such approaching objects. Therefore, it is reasonable to conclude that this fine-tuning, and other properties of the neurons, might be the results of selection for effective escape from predators. Hence, the properties of these neurons in prey might have been shaped by the predators, but research in this area integrating electrophysiology and evolutionary ecology is still in its infancy.

Neural Network Models at the Proximate Level

Simulations that faithfully mimic the natural neural network used in insect escape behavior create stepping stones towards future optimality models that may focus on the evolution of such networks (and hence the evolution of neural structures in animals). The neural network model of the orthopteran escape pathway imitates the electrophysiological properties of the LGMD/DCMD neurons in locusts in a collision-detecting neural network (Rind and Bramwell 1996). The neurophysiological activity simulated in the model matches the activity of the real system in locusts. This model was subsequently used by Stafford et al. (2006) to devise a computer-based robotic system that was able to perform a variety of tasks such as avoiding approaching objects. The robotic system used the hypothetical threshold mechanism deduced from studies of locust electrophysiology to successfully avoid objects on a collision trajectory, which might be viewed as equivalent to escaping from predators that are directly approaching the prey. All of the results suggested that a good approximation of realistic collision-avoidance behaviors of animals and their underlying mechanisms has been artificially created in research laboratories. We propose that evolutionary biologists can exploit the situation by adding evolutionary and optimality mechanisms to the existing neural networks models based on real systems in order to study evolution of escape mechanisms in prey and adaptations of predators that trigger escapes. With this idea in mind, we will briefly review recent models used to understand the evolution of escape behaviors.

ULTIMATE LEVEL: OPTIMALITY MODELS AND EVOLUTIONARY SIMULATIONS

The dynamics of predator-prey relationships and the evolutionary history of escape responses have been studied for many years (Beddington et al. 1975, Berryman 1992, Yoshida et al. 2003). Optimal escape timing or optimal distance to the predator at the moment of escape can be found that maximize the benefits to costs ratio for the prey (or meet any other criterion). The major costs of escape are energy and time used for escape that otherwise might have been used for other vital activities such as mating, feeding, parental care, etc. Additionally, escape from one predator may make the prey visible and susceptible to predation by another type of predator. The benefit of escape behavior is, clearly, avoidance of death (due to predation) at a success rate that may depend on the properties of the predator and the distance between the prey and the predator at the moment of escape initiation. Therefore, the ratio between costs and benefits and the optimal escape timing are affected by the characteristics of predators and their behavior (e.g., speed, directedness, repetitive representation). Accordingly, Cooper Jr. (2006) found that grasshoppers initiate their escapes at a larger “flight initiation distance” (the distance from the predator when prey starts to escape upon detection of a predator) in response to a predator approaching more directly and at a faster speed. In addition to the costs and benefits of escape and their effects on prey fitness, a prey animal’s ability to detect a predator in the first place will also play a vital role in the evolution of antipredatory behavior. The effects of predator detection on response behaviors have been illustrated in previous studies. For example, according to Blumstein (2003), flight initiation distance in prey increases with “starting distance”, defined as the distance between the prey and the potential predator at the moment when the predator first spots the prey. Broom and Ruxton (2005) included prey “wariness” and ability to detect predators in their evolutionary model of predator strategies (e.g., chasing) and prey escape behavior. They found that the optimal escape strategy in prey can be affected by characteristics of the predator (e.g., speed, detection, success at chasing) and the prey (e.g., costs of escape, benefits of escape). Models can also predict optimal escape behaviors by including factors known to affect the escape behaviors, including variables resulting from the sensory properties of prey (“wariness”, “detection ability”). However, such models do not explicitly include and model evolution of sensory structures and their properties in prey.

Graphical Models

Ydenberg and Dill (1986) first designed a theoretical model that distinguished predator detection from the response to predator detection. They predicted that prey would not escape if the benefit of remaining in place exceed the costs. Escape behavior prevents prey from spending time on other behaviors such as mating, foraging, nesting etc. Consequently, frequent escapes are detrimental to prey, reducing their chance of successful reproduction (Magnhagen 1991). Hence, prey benefit from mechanisms that allow them to only initiate the escape response if the predator poses an imminent threat. Ydenberg and Dill (1986) focused on this aspect of the escape response and developed a simple qualitative model predicting that prey will increase their flight distance in response to increased risk of capture. This model is supported by empirical data; the distance that a prey animal (a grasshopper) flees increases in response to increases in the speed or increases in the directness and repetitiveness of approaches by predators (Cooper Jr. 2006).

This model also proposed that flight distances of prey should become shorter when the cost of escape increased, and that the distance would change when prey animals possess special defensive weapons such as venom, thorns, stench, or cryptic body figures. The fitness benefits gained from living in groups may also affect the distance covered during escape. However, these aspects of the graphical model have not yet been quantitatively tested.

Mathematical Models

Broom and Ruxton (2005) designed a mathematical model of optimal escape strategies for inconspicuous prey. The underlying assumptions of this model are (a) that prey is cryptic to some extent, (b) that the predator-prey relationship starts at the moment when prey detects predator, (c) that unless the prey is discovered, the predator does not head towards the prey, regardless of whether the prey detects the predator, and (d) that the benefit of escape to prey is directly related to its survival. Differences between this model and that of Ydenberg and Dill (1986) are summarized in

Table 1. Broom and Ruxton's model concentrates on both the prey and the predator and describes escape behavior in detail, including interactions between prey and predator such as chasing and ambush. The two models make different predictions about the importance of costs of escape to the prey. Ydenberg and Dill predict that the cost of escape is significant, whereas Broom and Ruxton predict that escape happens relatively infrequently and prey may return to feeding quickly, leading to minimal costs. Clearly, further empirical studies are still required.

Cooper Jr. and Frederick (2007) designed a mathematical version of Ydenberg and Dill model (1986) to clarify the predictions of the previous model. Their model accentuates the benefits that can be maintained even after prey death (e.g., considering contributions to inclusive fitness and the fact that external fertilization is not associated with the need for parental care in orthopterans). This model is based on the assumption that prey behave in such a way as to maximize their average fitness when facing predators. Thus, the model of Cooper Jr. and Frederick (2007) considers the long-term effects of escape on prey fitness, rather than focusing on short-term and immediate results of predator-prey encounters (Broom and Ruxton 2005).

TOWARDS INTEGRATIVE STUDIES

Evolutionary Simulations of Neural Network Models

The graphical and mathematical models discussed above define escape in terms of timing of escape in relation to the approaching predator. These models ignored sensory processes in the prey's brain and its sensory and nervous systems. The nervous system is treated as a "black box" that produces observable behaviors. It is surprising that despite over 40 years of neuroethological and neurophysiological studies on escape systems, there remains a conspicuous absence of optimality analyses of the evolution of the "interior" of the "black box", while theoretical analyses of the resulting behaviors are well developed. The brain of an animal is a complex network of neurons and synapses, all of which are under natural selection just like the behaviors resulting from the activities of the "black box". Studies in neuroethology have already proved that a nervous system can evolutionarily adapt to a particular lifestyle or function (e.g., locust flight systems and escape behavior in crayfish; Dumont and Robertson 1986, mate calling in crickets; Fullard and Yack 1993, learning in songbirds; Marler 1991, prey location in barn owls; Konishi 1986).

Software-based neural networks reflect the biological properties of nervous systems and therefore can in principle be applied to simulate evolutionary adaptive changes in biological neural structures (biological neural networks). Neural network models employ mathematical formulas and computational algorithms for the purpose of understanding the proximal mechanisms of neural processing. Only recently, neural network modeling has been employed to ask evolutionary questions in the context of predator-prey relationships: Blumstein et al. (2006) used a simple artificial neural network and a genetic algorithm to devise a virtual environment for prey and predators. Genetic algorithms linked with neural network properties allows evolution of neural processing during the simulation so that the adapted traits of the eprey neural network can be selected and inherited using this model. Blumstein et al. investigated the effect of the presence of a specific predator on predator recognition abilities in prey. A simple, two-layer neural network was designed to mimic prey escape decisions in response to visual images. The images represented matrices (n × n pixels) of two different shapes, representing two different types of predators. This model is valuable

Table 1. Comparison of main characteristics in Ydenberg and Dill model (1986) and Broom and Ruxton model (2005)

	Ydenberg and Dill (1986)	Broom and Ruxton (2005)
Type	Graphical (Economic)	Mathematical (Optimal)
Cost to prey due to feeling earlier	Reduced feeding time	Alerting predator
Focus	Prey	Prey and predator
Cost of escape	Significant	Relatively variable
Effect of fleeing	Prey loses invested food and time	Prey quickly returns to feeding
Factors	Cost of flight Risk of capture Defense tactics of prey Group size	Cost of flight Success rate of chase Predator speed Effect of initiating escape Probability of detecting predator in advance by prey spotting prey by predator

because the evolutionary mechanism linked prey fitness with the network's properties. The model is therefore important for making the point that evolutionary changes in neural networks to optimize recognition of one predator may interact with the optimization of recognition of another type of predator. However, the extreme simplicity of this neural network (i.e., simple two-layer system) that was not based on neural structures in real prey makes the model predictions not testable with respect to the evolution of neural structures in biological organisms. Nevertheless, this model showed how, in the future, more realistic neural network models (already constructed with proximate questions in mind, such as the model by Rind and Bramwell 1996) can be modified to address evolutionary questions and to produce predictions testable in biological systems.

CONCLUSIONS AND PROSPECTS

The preceding examples of physiological, theoretical, and ecological studies show research across a wide range of topics related to predator escape, including investigations of the signal-transmitting mechanisms of risk-sensing neurons, applications of models imitating decision-making processes, and reconstructing evolutionary histories of escape behavior. These diverse fields of study have not yet been linked to each other and no attempt to fully integrate proximate and ultimate approaches has been made. The first step in such a study would be to express the behavioral predictions from the ultimate level of analysis (e.g., Santer et al. 2005, Cooper Jr. 2006) in terms of electrophysiology and neural network properties

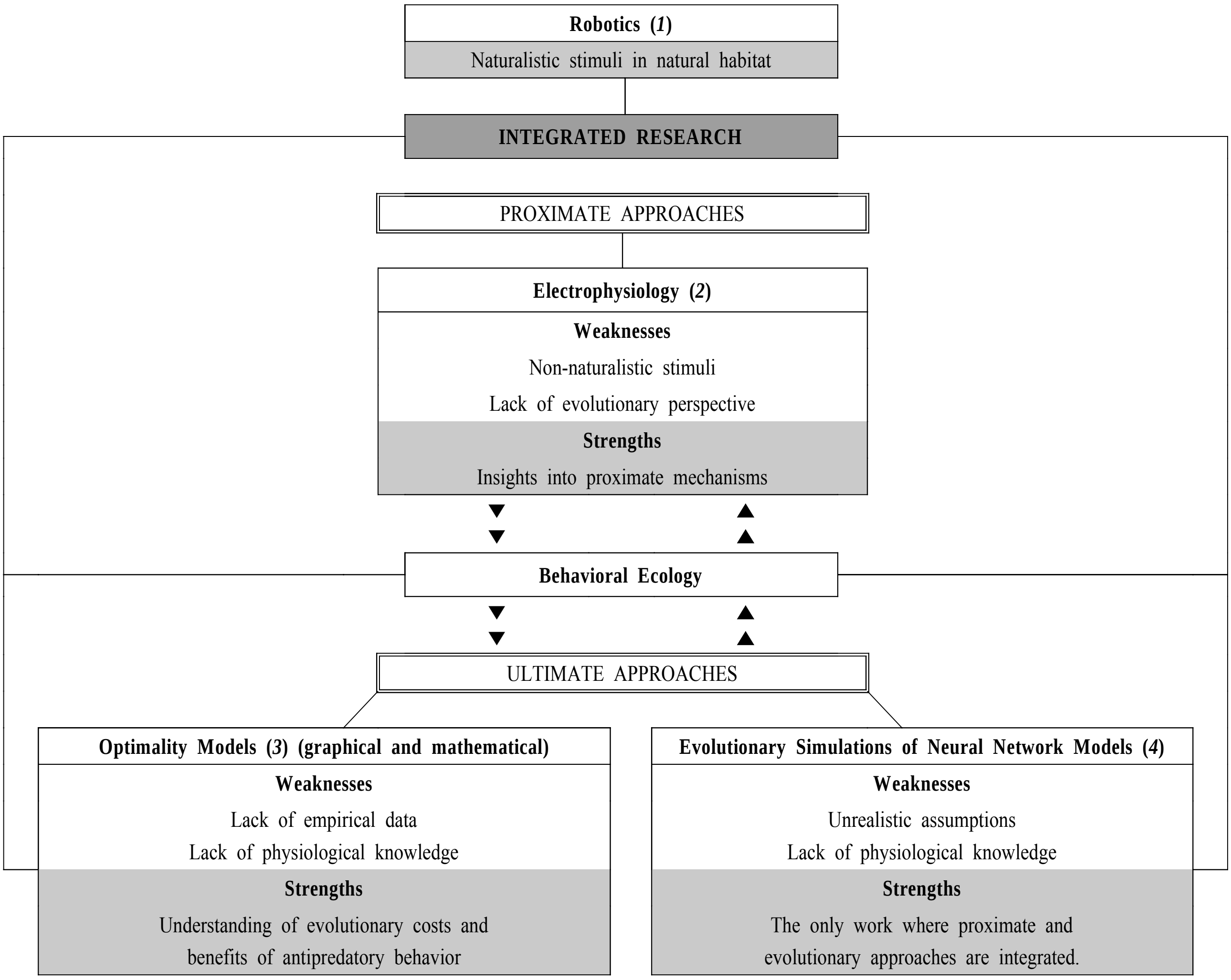

Fig. 1. Schematics of inter-relations between the traditional proximate (1, 2, 4) and ultimate (3) approaches in the study of antipredatory behavioral escape responses ("weaknesses" and "strengths" from the point of view of integrative studies of evolutionary processes are listed in each box). We propose that the gray areas can be integrated into one research program supplemented by input from robotics science to produce naturalistic predator-like stimuli for experimental purposes. The four areas of research are exemplified by papers reviewed in the text; each of four subjects directly corresponds to the title of the part in the text.

in prey (e.g., Broom and Ruxton 2005). This could be done by better representation of the proximate level of mechanisms in the evolutionary modeling. Biomimetic robot models may be used to verify the mechanisms in natural habitats by presenting realistic stimuli rather than the oversimplified, simple geometrical stimuli used in previous studies. Current developments in robotics have already generated realistic wing movement of birds (Wu and Popović 2003). Another promising future research avenue may focus on the evolution of predators is shaped by escape neuron properties in prey. For instance, Jabłoński and Strausfeld (2000) proposed that the neural circuits of insects may result in the evolution of specific traits in predators. This can be demonstrated by physiological studies of the visual neurons of insects and modeling research that employs artificial neural networks and genetic algorithms. The integrated approach (Fig. 1) towards escape behavior is a promising new direction for studies of predator-prey relationships.

ACKNOWLEDGMENTS

This paper has been created for the class of Behavioral Biology at the Seoul National University, taught by P.G. Jabłoński in the Fall semester 2007. H.S. Shin created the initial draft and the text was written under guidance and with an input from P.G. Jabłoński.

The study was supported by the Korean Research Foundation Grant No. C00747.

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(Received February 25, 2008; Accepted May 21, 2008)