HOW DO ACOUSTIC INPUTS TO THE CENTRAL NERVOUS SYSTEM OF THE BOLLWORM MOTH CONTROL ITS BEHAVIOR?

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ABSTRACT

The nervous system of the bollworm moth, *Heliothis zea* (Boddie), a noctuid moth that is a major pest of cotton, corn, and tomatoes, is served by two pairs of acoustic sense cells. The moths use the acoustic receptors to detect the ultrasonic cries of predatory bats that feed on these moths. Bats use pulsed high frequency sounds to echolocate and capture moths for food. The moths have developed an avoidance behavioral reaction that protects them from predatory bat capture when they detect the echolocating cries of the bats.

A pair of acoustic receptors are located in each tympanic organ located on the lateral wall of the metathorax on each side of the moth. A1 receptor, the most sensitive unit, can detect 20 kilohertz frequencies at sound pressure levels of 35 dB (0 dB re 20 µPa). The A2 receptor is about 20 dB less sensitive and is also tuned to be most sensitive to 20 kHz sounds. Pulse rates of 10/sec and pulse durations of 10 msec were most effective for eliciting evasive reactions in the bollworm moth.

In field and laboratory behavior tests, we have determined that the moths can detect 85 dB pulses of ultrasound (20 kHz) at a distance of 50-80 feet from the moth and after detection the moths make evasive reactions.

My recent research has focused on identification of the neural circuits from the acoustic receptors to and through the central nervous system (meso-metathoracic ganglia and prothoracic ganglion and brain) to the motor nerves responsible for executing the evasive reactions. The structure of the various parts of the circuits responsible for the behavioral reactions have been identified using histochemical techniques (cobalt chloride and lucifer yellow) that mark only the axons carrying the acoustic information (action potentials) and the motor nerve commands from these nerves to the muscles responsible for directed flight.

Electrophysiological techniques were used to monitor the information flow in the acoustic axons that feed the moth coded information on the high frequency sounds in its environment. If the information is from the A1 receptor, it is processed in the brain to produce behavior commands that are transmitted by the motor nerves to generate a behavioral reactions that produce turn reactions. The information from the A2 receptor is transmitted to neurons in the mesothoracic ganglion directly and produces rapid unpredictable evasive reactions (spirals, dives, and cessation of flight) and do not require "brain" processing. The anatomical circuits, behavioral reaction times, and electrophysiological monitoring of neural activities confirm these findings. These and other studies have demonstrated that the behavior of the moth is influenced or controlled by sensory inputs that can have positive and negative effects on the moth behavior. When the flying moth is attracted to an ultraviolet light and a sound source at the light source generates a pulses of high frequency sound, the moth will make an evasive reaction to the sound stimuli in preference to the continued attraction to the visual stimuli. In other instances, another nocturnal moth species that is attracted to a sex pheromone (an olfactory attractant) can be terminated (behavior turned off) if the trap containing the pheromone is constructed of specific colors that cause an avoidance reaction to the visual stimuli that are dominant over the attractive odor.

These model acoustic studies are establishing the boundaries and conditions that must be met in the neural circuits of the central nervous system of the moth for specific sensory stimuli to be functionally effective. Normal or usual behaviors can be turned
on and off when the proper sensory stimuli are presented according to specific “criterion” conditions. To obtain maximum benefits from the use of non-insecticidal technologies to control insects, a full understanding of the levels of neural processing of sensory stimuli is needed, as is an understanding of the spheres and levels of dominance that specific sensory stimuli exert in the control of the behavior of the insect pest.

RESUMEN

El sistema nervioso de Heliothis zea (Boddie), que es una alevilla noctuida y una plaga mayor del algodón, maíz y tomates, es asistido por un par de células del sentido acústico. Las alevillas usan los receptores acústicos para detectar el grito ultrasónico de los murciélagos predadores de estas alevillas. Los murciélagos usan pulsaciones de sonido de alta frecuencia para localizar por el eco y capturar las alevillas como comida. Las alevillas han desarrollado una reacción en su comportamiento donde evitan la captura cuando detectan el grito localizador de eco de los murciélagos.

Un par de receptores acústicos están localizados en cada órgano timpánico que se encuentran en la pared lateral del metatorax a cada lado de la alevilla. El receptor A1 que es la unidad más sensible, puede detectar frecuencias de 20 kilohertz a niveles de presión de sonido de 35 dB (0 dB re 20 µPa). El receptor A2 es como 20 dB menos sensitivo y también es el más afínado y sensitivo a los sonidos de 20 kHz. Pulsaciones a razón de 10/segundo y pulsaciones durando 10 megasegundos fueron los más efectivos en educir reacciones evasivas en las alevillas.

Hemos determinado en pruebas de comportamiento en el campo y en el laboratorio, que las alevillas pueden detectar pulsaciones de 85 dB de ultrasónidos (20 kHz) a una distancia de 50-80 pies, y que después de detectadas, las alevillas reaccionan evasivamente.

Mis investigaciones reciente se han enfocado en la identificación de los circuitos neurales de los receptores acústicos hacia y a través de del sistema nervioso central (ganglio meso-metatorácico y ganglio protoráctico y el cerebro).

The nervous system of the bollworm moth, Heliothis zea (Boddie), a noctuid moth that is a major pest of cotton, corn, and tomatoes, is served by two pair of acoustic sense cells (Agee 1967, Roeder & Treat 1957). The moths use the acoustic receptors to detect the ultrasonic cries of predatory bats that feed on these moths (Agee 1969a). The bats use pulsed high frequency sounds to echolocate and capture moths for food. The moths have developed an avoidance behavioral reaction which protects them from predatory bat capture when they detect the echolocating cries of the bats.

A pair of acoustic receptors is located in each tympanic organ located on the lateral wall of the metathorax on each side of the moth. The A1 receptor, the most sensitive unit, can detect 20 kilohertz frequencies at sound pressure levels of 35 dB (Agee 1967). The A2 receptor is about 20 dB less sensitive than the A1 receptor and is most sensitive at 20 kHz. Pulse rates of 10/sec and pulse durations of 10 mssec were most effective for eliciting evasive reactions in the bollworm moth (Agee 1969a, 1969b, Agee & Webb 1969). In response to bat cries or electronically generated pulses of ultrasound, the acoustic receptors generate action potentials that are transmitted to the central nervous system. In the flying moths, this information causes evasive reactions that include directed turns, unpredictable dives, and falls to the ground. The behavior of non-flying moths is less affected by pulses of ultrasound (Agee 1969b).

In field and laboratory behavior tests, we have determined that the moths can detect ultrasounds at an SPL of 85 dB at a distance of 50-80 feet and make evasive reactions (Agee 1969a,b) after detecting this sound.

Recent research has focused on identification of the neural circuits from the acoustic receptors to and through the central nervous system (meso- metathoracic ganglia and
prothoracic ganglion and brain) to the motor nerves responsible of executing the evasive reactions.

A special electronic data acquisition and analysis system was developed to selectively record and analyze the electronic events occurring in the central nervous system in response to pulsed ultrasound (Agge 1986a) (Fig. 1).

The action potential caused by the stimulation of ultrasound can be tracked from the tympanic nerve through the central nervous system using special electrodes. Figure 2 compares the action potentials from the tympanic nerve, the axon in the ganglion, the coded information on a pulse of sound identified as an action potential from a pulse marker neuron and the action potential produced by the non-acoustic B cell in the central nervous system as shown in Figure 1.

The structure of the various parts of the sensory input and motor nerve output circuits responsible for behavioral reactions have been identified using histochemical
Fig. 2. Examples of acoustic responses recorded at (A) the tympanic nerve, (B) repeater neuron in the mesothorax, (C) pulse marker neuron in the prothoracic ganglion, and (D) B cell recorded from position 3 in the prothoracic ganglion. Time scale for A, B, and C indicated on C.

techniques (cobalt chloride and lucifer yellow) that mark only the axons carrying the acoustic information (action potentials) and the motor nerve commands from these nerves to the muscles responsible for directed flight (Fig. 3) (Paul 1973, Orona & and Agee 1987a,b, Tyrer & Altman 1974.

Electrophysiological techniques were used to monitor information flow in the acoustic axons that feed the moth coded information on the high frequency sounds in its environment (Agee 1985a). If the information is from the A1 receptor, it is processed in the brain to produce behavior commands that are transmitted by the motor nerves to generate behavioral reactions that produce coordinated turning. The information from the A2 receptor is transmitted to neurons in the mesothoracic ganglion directly and produce rapid unpredictable evasive reactions (spirals, dives, and cessation of flight) that do not require “brain” processing. The anatomical circuits, behavioral reaction times, and electrophysiological monitoring of neural activities confirm these findings. These and other studies have demonstrated that the behavior of the moth is influenced or controlled by sensory inputs that can have positive and negative effects on the moth
Fig. 3. Representative camera lucida reconstructions of the cells labeled following cobalt infiltration of the tympanic nerves. The A1 and B cells have synaptic terminals scattered throughout the thoracic ganglia. The axonal terminations of the A2 cell are confined to the meso-metathoracic ganglia.

behavior. For example, when the flying moth is attracted to an ultraviolet light and a sound source at the light source generates pulses of high frequency sound, the moth will make an evasive reaction to the sound stimuli in preference to the continued attraction to the visual stimuli (Agee & Webb 1969). In other instances, a nocturnal moth species that is attracted to a sex pheromone (an olfactory attractant) can be terminated (behavior turned off) if the trap containing the pheromone is constructed of specific colors that cause an avoidance reaction. Visual stimuli are dominant over the attractive odor (Mitchell et al., unpublished data). If an olfactory attractant, i.e., sex pheromone, is presented to the moths without a repellent visual or acoustic stimulus the olfactory attractant is effective. Figure 4 illustrates these events graphically.

Figure 5 shows what we have learned to date regarding the flow of information in the acoustic network from the receptors through the tympanic nerve, meso-metathoracic ganglia, prothoracic ganglion and brain to the motor nerves that control flight of the moth. As mentioned before, there are two networks that function in the moth to avoid bat predators. In the rapid reaction network the acoustic inputs from the A2 receptor cause the motor nerves to operate directly and provides for the quickest reaction possible to protect the moth. In the slow reaction network, acoustic information that arrives in the central nervous system is transmitted to the prothoracic ganglion and brain and receives some coding, such as the pulse marker neuron; a longer and slower route for the information to travel before a behavior can executed. This produces
Effects of Sensory Stimuli on Moth Behavior

Fig. 4. Schematic diagram of the effects of sensory stimuli on the behavior of the bollworm moth. The width of the arrows indicate the relative influence of sensory input to the central nervous system of a flying moth. The bars indicate blockage of behaviors elicited by specific stimuli. In event #1, all three inputs affect behavior. Event #2, the attractant behavior induced by ultraviolet light or sex pheromones are blocked if a repellent acoustic stimulus is received. In event #3, the olfactory stimulus of a sex pheromone is blocked when it is being release from a color trap that is repellent. In event #4, an olfactory stimulus (a sex pheromone) is attractive when no repellent acoustic or visual stimuli are present.

a precise turn behavior that puts the maximum distance between the moth and the sound source.

These "model" acoustic studies are establishing the boundaries and conditions that must be met in the neural circuits of the central nervous system of the moth for specific sensory stimuli to be functionally effective in controlling of their behavior. Normal or usual behaviors can be turned on and off when the proper sensory stimuli are presented according to specific conditions. To obtain maximum benefits from the use of non-insecticidal technologies to control insects, a full understanding of the levels of neural processing of sensory stimuli is needed. We also need to know the spheres and levels of dominance that specific sensory stimuli exert in controlling the behavior of pest insects.
Fig. 5. Schematic diagram of the tympanic neurones and associated circuitry to the motoneurones involved in evasive flight behavior. Two behaviorally-relevant systems appear to be present. The A2 acoustic cell has direct monosynaptic connections to the motoneurones within the meso-metathoracic ganglia, forming a rapid reaction network. On the other hand, the A and B cells appear to be additionally linked to interneurones and the brain reflecting their involvement in a slower and directed reaction network.

REFERENCES CITED

ACOUSTIC SIGNALS, ARMS RACES AND THE COSTS OF HONEST SIGNALLING

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ABSTRACT

Animal signals evolve as adaptations to social as well as physical environments. Where the interests of signalers and responders differ, a coevolutionary "arms race" cycle of signal adoption, exaggeration, and devaluation may result. Stable, reliable signals evolve when costs of signalling constrain the evolution of bluff and exaggeration. Acoustic signals are especially costly, compared to other signal types, and are therefore especially likely to evolve as reliable signals in such "social competition" situations. Costs of acoustic signals include physiological costs of growth and signal production, probes by conspecific rivals and discriminating members of the other sex, and attacks by natural enemies such as predators and parasites.

RESUMEN

Señales dadas por los animales se han desarrollado como adaptaciones al medio ambiental físico así como al social. Donde el interés del que señala y del que responde diferen, pudiera entonces resultar en un ciclo coevolucionario de "carrera hacia las armas" en la señal de adaptación, exageración, y devaluación. Señales estables y confi-