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ML Agarwal
Department of Entomology
Dr Rajendra Prasad Central
Agricultural University,
Pusa, Samastipur, Bihar, India

Vyshnavi Sunil
Department of Entomology
Dr Rajendra Prasad Central
Agricultural University,
Pusa, Samastipur, Bihar, India

Corresponding Author:
ML Agarwal
Department of Entomology
Dr Rajendra Prasad Central
Agricultural University,
Pusa, Samastipur, Bihar, India

Basic behavioural patterns in insects and applications of behavioural manipulation in insect pest management

ML Agarwal and Vyshnavi Sunil

Abstract
Insects are a result of culmination of evolutionary development and vast majority of them occupy different ecological niches. The huge number and great diversity of insects have lead them to express diverse behavioural patterns. The study of animal behaviour is termed 'ETHOLOGY'. Behaviour is the way in which organisms adjust to and interact with the environment. Most behavioural patterns of insects are generally determined and thus behaviour is 'stereotyped'. In insects, since the behavioural patterns are essentially the outcome of inherited properties and such patterns are innate. However, some learned patterns are also exhibited by insects. The movement of insects are highly dependent on rhythmic and light reactions. Chemicals like hormones, pheromones also play an important role in modifying behavioural patterns of insects. Insect behaviour has been manipulated and used in many pest management practices. It is also used in identifying species. Behavioural characters like sound and light production, host associations, nest constructions, pheromones, reproductive patterns have pertinent role in separation of closely related taxa or sibling species. The recent use of insect behaviour is the extraction of GFP (Green Flouroscent Protein) which is used for tagging and learning the expression of certain genes. Thus it is necessary to understand the basic behavioural patterns in insects for the behavioural manipulation and their use in successful and eco-friendly management of insect pests.

Keywords: Behaviour, insect, pest management, innate, stimuli

Introduction

Insects are highly specialized animals and represent the culmination of evolutionary development (Agarwal, 2009) [1]. They exist in almost all types of habitats. They exhibit great diversity and constancy and the vast number of over one million insect species named so far. Many behavioural specializations and other characteristics have made them the dominion of evolutionary sequences. Responses shown by insects are directly or indirectly results of genes, e.g. the flight of any insect depends on presence or absence of wings, and whether it has wings or not depends largely on its genes.

Most of the management strategies against insect pests involve some sort of change to their behaviour (Gould, 1991; Forster and Harris, 1997) [2, 3], whether it is through chemical (i.e. volatiles and non volatile compounds, feeding deterrents), visual or auditory signals. The concept of manipulating pest behavior for insect control has been known for centuries through the practice of trap cropping (Hokkanen, 1991) [4].

Concept of ethology

Study of animal behaviour is termed ethology (*Gr*. Ethos - character or habit or custom; Logos – study. In simple words behaviour has been defined as what animals do or movement of animals, e.g. movement of wings during flight. In some behavioural activities no movement occurs, e.g. production of sound by vibration of a membrane in cicada; death-feigning.The behaviour is also the way in which an organism adjusts to and interacts with its environment.Another efficient property of living beings is their ability to respond to stimuli and is termed as 'irritability'.

Types of insect behaviour

1. Innate: 'Stereotyped' behaviour consists of more or less fixed response or a series of genetically determined responses. Thus, behaviour is stimulus bound and outcome of inherited properties of the nervous system. Also termed inborn, inherent or instinctive behavior.

The imprints of such patterns are genetically programmed into the nervous system and difficult to alter such patterns, also transmit from parents to offspring.

Innate behaviour is always:

- Heritable — encoded in DNA and passed from generation to generation
- Intrinsic — present in animals raised in isolation from others
- Stereotypic — performed in the same way each time by each individual
- Inflexible — not modified by development or experience
- Consummate — fully developed or expressed at first performance

Since innate behaviour is encoded in DNA, it is subject to genetic change through mutation, recombination, and natural selection.

2. Learned: The behaviour is variable and modifiable through experiences. Obviously, such patterns are not inherited. The learning includes a change in the functioning of the nervous system.

Simple innate behavior-Reflexes

The simplest impulse conduction known as 'reflex action' occurs in CNS. It is rapid, automatic, unlearned, involuntary response to a stimulus. The pathway of reflex action called 'reflex arc'.

Two types 'phasic or 'tonic'.

1. Phasic -rapid, of short duration and involves rapid movement of body or its parts, e.g. proboscis extension, sudden flight to a threat
2. Tonic - slow, long-lived, e.g. maintenance of body posture/ position in space, balance, etc.

Orientation behaviours

Coordinated movements (walking, flying, swimming, etc.) that occur in response to an external stimulus. They are adaptive for survival

- Kinesis - speed of movement (Orthokinesis) or frequency of turning (Klinokinesis) is directly proportional to the intensity of a stimulus. It is non-directed orientation in which the animal exhibits a "random walk".
- Taxis - movement is directly toward (positive) or away from (negative) a stimulus, *i.e.* Phototaxis = light; Geotaxis = gravity; Thigmotaxis = contact with other objects.
- Dorsal light reaction - (Telotaxis) in which movement occurs at a constant 90° angle to a light source. By keeping the light source directly overhead, a flying or swimming insect can insure that it travels parallel to the ground (or water surface).
- Light compass reaction - (Menotaxis) in which insects (e.g. honey bees) fly away from the nest site at a fixed angle (x°) to the sun and return at the supplementary angle (180-x°).

Other reflexes

- 'Chain reflex' or 'cyclic reflex'- Series of reflexes in a definite sequence, e.g. walking of an insect.
- Righting reflex - When an insect is placed on its back and help to restore normal body position.
- Reflex bleeding - Reported in many Orthoptera, Coleoptera, Lepidoptera and other groups, in which small drops of fluid or blood are released from various points of their body, due to an increase in hydrostatic pressure. Most meloids (blister beetles) exhibit similar reflexes. This behaviour is of protective value and help in escaping.

Complex Innate Behaviour

Fixed action patterns (FAPs)

These patterns are determined by genes and exhibited automatically without having seen or learnt from conspecifics. These are performed by an animal even raised in isolated conditions

These patterns are

- Inherited and similar in individuals of a species.
- Cannot be influenced by external stimuli.
- Conservative in evolution of a species.
- Elicited by specific stimuli, called 'releasers' or 'sign stimuli'

Motivation

State of 'internal readiness' or 'motivation' due to extrinsic or intrinsic factors. The intrinsic factors may be neural or hormonal.

Appetitive behavior

When an insect is in a state of readiness (motivated) it may engage in activities that increase the possibility of exposure to a releasing stimulus. Such a pattern is called 'appetitive behaviour'. Chirping by a cricket is regarded as an appetitive behaviour because it increases the chances of finding a mate and satisfying the sex drive.

Learned behavior

Learning brings about certain adaptive changes in the behaviour of an animal as a result of experiences. However, it is more pronounced in higher and complex animals. Thorpe (1963) proposed "learning is the process which manifests itself by adaptive changes in individual behaviour as a result of experiences" [5]. Learning also involves storage of information (memory).Though most actions of insects are FAPs, in many cases they also exhibit learning ability. Insects with less number of neurons (about 100000) in the brain are poor learners; but some of their behavioural patterns are highly complex. Alloway (1972) identifies conditioning, Instrumental learning, shock avoidance learning and olfactory conditioning as four examples of learned behavior experimentally demonstrated among insects: however, other behaviourists claim that insects also display habituation, latent learning, imprinting and insight learning [6].

Learned behaviors will always be

- Nonheritable-acquired only through observation or experience
- Extrinsic - absent in animals raised in isolation
- Permutable - pattern or sequence may change over time
- Adaptable - capable of modification to suit changing conditions
- Progressive -subject to improvement or refinement through practice

Habituation

It is the simplest form of learning and observed throughout the life of an animal. In habituation a repeated stimulus is given to an animal, the intensity of response gradually decreases and may disappear ultimately. By showing no response to old and unimportant stimuli animals save energy and their reactions to new stimuli increases. Wigglesworth (1941) demonstrated that in human louse, *Pediculus humanus* repeated contact stimuli, not followed by any injury are no longer responded [7].

Classical Conditioning

The concept was developed by Russian Physiologist Pavlov (1927) after conducting experiments on dog and therefore, also called as Pavlovian conditioning [8]. In this type of learning when two different stimuli are repeated simultaneously for a number of times, animal develops the ability to respond to one of the stimulus to which it does not customarily elicit the response. Thus two stimuli are involved, one- the unconditioned stimulus (UCS), which elicits the unconditioned response (UCR), without any prior training. The other, conditioned stimulus (CS), must not elicit a response similar to UCR prior to conditioning. The conditioning procedure involves pairing of CS and UCS in a close succession (CS briefly preceding the UCS), and after conditioning the animal gradually elicits the response called conditional response CR (similar to UCR) also to CS

- Takeda (1961) used various olfactory stimuli (CS), which were initially unable to produce proboscis extension response (PER) in *Apis mellifera*, but after repeated pairing with the presentation of sugar syrup (UCS), the olfactory stimulus (odour of coumarin) also elicited proboscis extension. The workers performed the best at the age of 14-16 days old [9].

Instrumental Learning (Fig.1)

- Learning by trial and error
- Involve modifications of fixed action patterns through the application of positive reinforcers (rewards) or negative reinforcers(punishment)
- The most common form of instrumental learning involves use of a maze

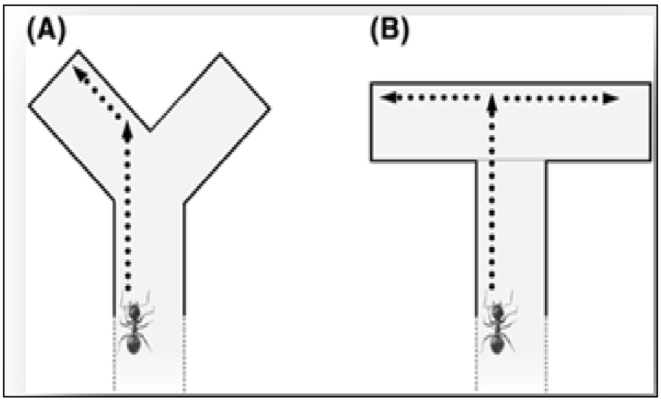

Fig 1: Instrumental learning as shown by an ant

Olfactory Conditioning

A form of habituation or latent learning. Exposure of some insects to repellent odour during a certain period of their development results in the loss of response to that odour by adults. Thrope (1939) demonstrated that adults of *Drosophila melanogaster* are normally repelled by odour of pepper mint oil but however if their larvae are reared in pepper mint scented diet, adults show a strong positive response to oil [10].

Shock Avoidance Conditioning

Horridge (1962) conducted an experiment in which headless cockroaches and locusts were learned to keep one leg raised to terminate a series of electric shocks [11].

- Pairs of decapitated insects were suspended over a container of electrified saline solution.
- In one insect (test insect) a shock was received, whenever its legs fell below a predetermined level.
- For another insect (control) same number and intensity of shocks were given to the corresponding leg in a random fashion.
- In the second phase of experimentation, two insects were separated and shocked independently, whenever their legs fell below a predetermined level.
- It was observed that test insect received significantly fewer shocks than control insect.

Latent Learning

Occurs without apparent reward or punishment. The animals learn a lot about their surroundings during the course of their daily activities. Bees and wasps learn the location of their nests through landmarks recognized and remembered from a previous orientation flight. Tinbergan and Kruyt (1938) discussed learning in digger wasp, *Philanthus Triangulum* [12]. They kept a few pine cones in a circle surrounding the nest as physical cues. The wasp learns to associate its nest with these n distinctive land marks by making an orientation flight or survey over nest entrance. The pine cones were displaced while the wasp was away for hunting and on return with prey she flew over the circle of pine cones even though it have been moved during her absence and expects to find her nest in the centre of ring of cones.

Insight Learning

Highest and most complex form of learning and similar to the term intelligence. Insight learning is drawing of past experience to solve a problem. Baerends (1941) conducted experiments on *Ammophila campestris* which make a number of nests [13]. The nests are constructed at different times thereby having young ones of different stages and capable of consuming variable number of caterpillars in a day according to their growth stage. The female used to inspect all nests and their contents in the morning and their contents in the morning. He replaced these nets by artificial ones, manipulated their contents and observed that during subsequent visits the pattern of wasps activity remain unaltered and she provided the number of caterpillars to the growing larvae as per the observations made in the morning

The use of a tool to perform certain task is usually considered as an example of insight learning and there are at least two examples of tool using among insects.

1. *Ammophila* females use small pebble held in mandibles to smooth the ground over their nests.
2. Ant, *Oecophylla smaragdina* holds one of its own larvae in its mandibles and uses silk the larva produced to tie leaves together as a nest.

Behavioural Manipulation for Pest Management

Insect's compound eye typically contains three types of photoreceptor cells with the spectral sensitivity peaking in the UV, blue and green wavelength regions. Light traps are used for forecasting pest outbreaks, population monitoring, mass trapping and mating suppression. Yellow pan traps are used for conducting surveys for pest outbreaks and yellow sticky plates are used for pest control of diurnal insects such as aphids and whiteflies. Lamps that give off yellow illumination have been used effectively to control nocturnal moths and thus reduce the damage to fruit, vegetables, and flowers.

Phonotaxis in Insect Pest Management

The ultrasonic pest repellent is used to keep insects away from your home, bedroom, basement, office, restaurant, kitchen, hotel room, or any other indoor space. It is used against mosquitoes, flies, rats, roaches, crickets, and other bugs and rodents.

Chemotaxis in Insect Pest Management

Pheromones

The use of behavior modifying chemicals has found world wide application particularly with insect pheromones as a tool of great importance in insect management strategies. Insect pheromones or synthetic attractants (sex, alarming, oviposition-deterring or epideictic, aggregation, and trail pheromones are essential components of monitoring and management of target pest insects. Karlson and Lüscher (1959) proposed the term 'pheromone' to represent chemical(s) used for communication between individuals of a given species [14]. Sex pheromones are among the most powerful of all chemical attractants. Ever since Butenandt *et al*. (1959) first discovered them in adult silkworms, *Bombyx mori*, these chemicals have aroused great interest because of their potential as efficient pest management agents [15]. Some of these new chemical weapons are much safer for the environment and more species specific than most of the conventional insecticides.

The specificity of pheromones and incredible ability of an insect to detect its minute quantities, have offered much potential to use these chemicals as a management tool. Once the structure of the behavioural chemical is determined it can be produced synthetically and then efficient systems are devised to utilize them for a range of management purposes. Besides this, consumer demand for pesticide-free produce is increasing steadily, pushing pheromone use forward. The availability of synthetic pheromone 'gossyplure' formulated to disrupt mating of pink bollworm, *Pectinophora gossypiella* has fostered alternative management strategies and efforts have been made to control this pest by using this synthetic commercial formulation in many countries.

Detection and monitoring

Pheromones are species-specific and every species has an exclusive sex pheromone. These can be exploited to determine the pest population size, temporal distribution of pest, detection of outbreaks, and establishment of emergence time of adults. Traps containing the appropriate sex pheromone are placed in the fields or orchards and reliable information concerning the size of the pest population can be acquired.

Mass trapping

The fundamental assumption of this approach is that use of traps in the field ensures that a large number of individuals will be trapped, thus significantly hindering fertilization and the production of a new generation of pests. At high pest population density, pheromone can be used for mass trapping of sexually active adults (usually males) to reduce population density and lower a pest's reproductive potential. It is used for direct insect population suppression.

Mating disruption

A variety of approaches employ pheromones to manipulate or disrupt the natural mating behaviours of insects, such that population levels are reduced and crop damage diminished. The technique involves blocking of communication channel between individuals of both sexes by flooding the environment with sex pheromones. This techmique has the benefit of only affecting male of that insect species, while leaving other non target organisms unaffected. Many commercial pheromones are available and their use is considered as a 'biorational' approach to insect control.

Attract and kill

Attract and kill' or 'lure and kill' strategies fall into two groups: (i) those that employ some form of 'target device', e.g. a trap, and (ii) those that rely on attracting the pests onto a natural surface, e.g. host tree foliage. In first strategy insecticides are placed inside centrally located containers or other sources that are baited with sex or aggregation pheromones. The insect is attracted to the dispenser loaded with the pheromone and comes into contact with the insecticide. The efficiency of chemical pest control is increased, and also environmental pollution is minimized.

Inhibition of oviposition

Anti-oviposition' or 'oviposition deterring' pheromones have been reported in some Lepidoptera and Diptera. Such pheromones act as epideictic pheromones with respect to their effects of reducing intraspecific competition.

Alarm pheromone. Many aphid species release a linear sequiterpenoid, (*E*)-β-farnesene (EBF), which acts as alarm pheromone upon the approach or attack of a predator or parasitoid (Bowers *et al*., 1972) [16]. This volatile chemical is released through the cornicles as part of a defence secretion and can be detected on the antennae of neighboring aphids.

Allelochemicals

Plant secondary compounds acting as allelochemicals are the key regulating factors of the coevolutionary processes and these relationships between plant chemicals and insects are seminal in understanding behaviour, ecology, distribution and speciation of insects. The potential application of allelochemicals comprise of development of new, safer and effective agrochemicals as pesticides and growth promoters. Being natural products allelochemicals are safer to use and easily biodegradable (Yazdani and Agarwal, 2005) [17]. Two types of allelochemicals are important for the pest management programmes, viz. 'allomones' and 'kairomones'. The allelochemicals not only affect organisms primarily through sensory modalities like olfaction and gustation, but also through tactile senses and via direct physiological pathways when ingested or absorbed. Allelochemical web links the various trophic levels and an understanding of interactions between trophic levels provides greater potential for the manipulations of their communication systems in pest management programmes. Host plant selection by phytophagous insects is a complex process involving the sequential effects of plant produced allelochemicals on insect behaviour through host finding, feeding, oviposition, and growth and development.

Deterrents

Chemical that inhibits behaviour such as feeding or oviposition, when applied to a site where such behavior normally occurs. In pest management, a deterrent is a resource that reduce or prevent the effects of pest behaviour like feeding. Chemicals that inhibit feeding of insects on a treated surface without necessarily killing or repelling them are called 'antifeedants'. These can result in cessation of feeding, either temporarily or permanently. Thus a different approach to crop protection is followed in which the elimination of the pest is not the prime objective rather the pest individuals are inhibited to feed upon the crop or commodity. They are also termed 'gustatory repellents' or 'feeding deterrents'.

Repellents

The strategy for using repellents is generally to stop a pest from finding a valued resource. Use of repellents to repel pest insects is the oldest and most widely used method. Repellents are 'chemicals that cause insects to move away from their sources'. The plant-derived volatile allomones such as 6-carbon aliphatic aldehydes and alcohols, the so-called 'green leaf volatiles' (GLV), have been suggested as both repellents and deterrents for tephritid flies. The GLV compounds are botanically ubiquitous, being the chief aroma contributors to the common green odour of leaves and immature unripe 'green' fruits (Visser, 1986) [18]. The release of GLVs is also indicative of plant tissue damage; as these are direct simple, cleavage products of fatty acid breakdown that damage to plant tissues caused by mechanical means and insect feeding and oviposition. The GLV have strong repellency against females of olive fruit fly, *Bactrocera oleae*.

Stimulants

Most known stimulants are involved in either feeding or oviposition, mainly the former. A number of secondary plant compounds that have no nutritional value to either plant or insect have been the subjects of considerable study. The plant as a chemical defence against herbivores may manufacture these substances but they unwittingly serve as token feeding stimulants to a select group of specially adapted species. Many appear to have no effects at all on insect herbivores, while others stimulate feeding and/or growth. Use of feeding stimulants (phagostimulants) allows the application of reduced dosages of insecticides assuaging some of the environmental and health concerns associated with traditional insect control tactics. Sugars are one of the best-documented groups of substances because of their feeding stimulant potential. Several other substances that may have feeding stimulant properties are amino acids, lipids, ascorbic acid, glucosinolates, and cucurbitacins. Besides, a variety of commercial feeding stimulants have been developed which elicit strong feeding responses. Many feeding stimulants are allelochemical-based and attract the pests. The addition of feeding stimulants to entomopathogens has in some cases increased the effectiveness of the control.

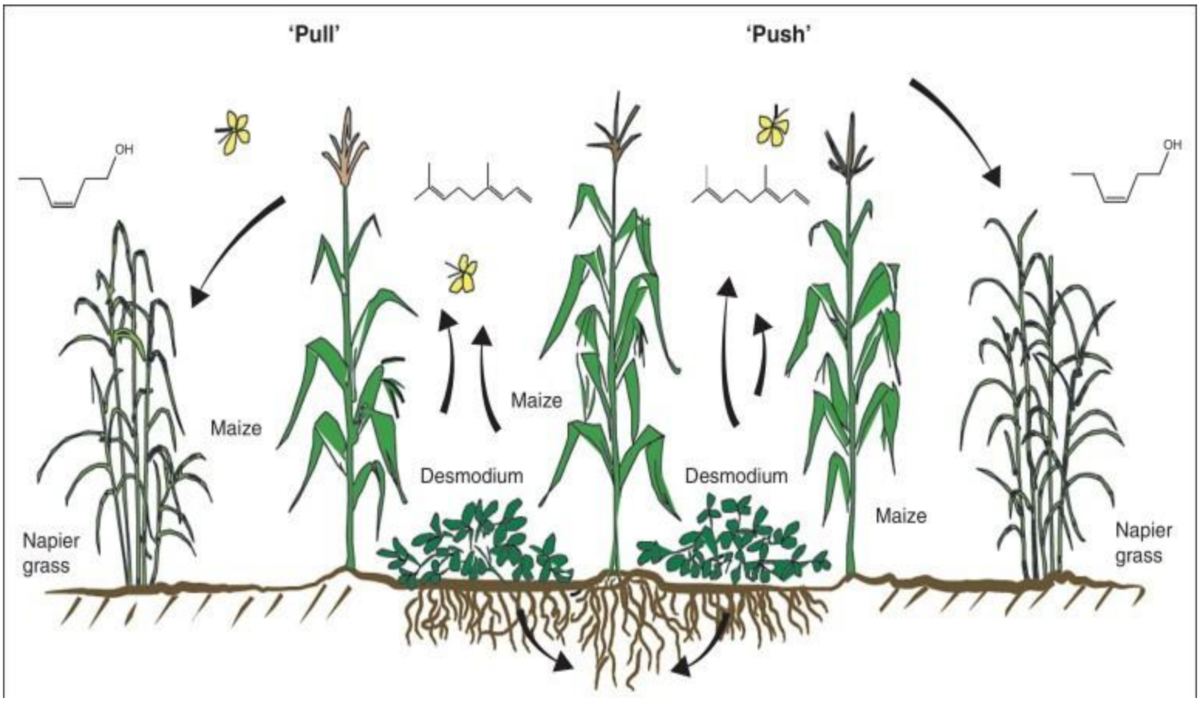

Fig 2: Push –Pull strategy in maize

Push-pull' or 'stimulo-deterrent diversionary strategy' (SDDS) (Fig.2)

- Involves 'pushing' pest insects away from the economic crop.
- 'Pulling' them onto a trap crop.
- Antifeedants, non-host volatiles, parasitoid attractants and compounds associated with plant defense can be used to achieve the 'push'.
- Sex pheromone and host volatiles can be used to 'pull' the insects onto the trap crop.

Khan *et al*. (2001) used 'push-pull' strategy for the control of stem borers in maize. Napier grass, *Pennisetum purpureum* was used as trap plants [19]. Two species of desmodium, *Desmodium uncinatum* and *D. intortum* were grown to repel ovipositing stem borers.

Green Flouroscent Protein

Use of the enhanced green fluorescent protein (EGFP) from the jellyfish, *Aequorea victoria*, is used as a genetic marker for the genetic transformation of mosquitoes. The EGFP gene of *Drosophila melanogaster* was inserted into the *Hermes* transposable element. Wild-type strain of the yellow fever mosquito were microinjected with this plasmid, together with a helper plasmid containing the *Hermes* transposase. Somatic EGFP expression was observed during early instars in one-half of all G_0 individuals. Two G_1 individuals arising from a G_0 female displayed high levels of EGFP gene expression during all stages of their development. EGFP was found to be transmitted in a Mendelian fashion to the G_2 and G_3 generations and molecular analysis confirmed the presence of the Hermes [actin5C:EGFP] gene in these insects. These results clearly demonstrated that EGFP can be used as an effective genetic marker in wild-type *A. aegypti* and most likely in other mosquito species as well.

Vibrations to Manipulate Insect Behaviour

Early attempts to use vibrations for manipulating insect behaviour goes back to the late 1970,s when Saxena and Kumar showed that airborne sounds of 200 Hz picked up by plants were able to interrupt the mating communication of a leafhopper and a planthopper, *Amrasca devastans* and *Nilaparvata lugens*. They suggested that music could be used for mating disruption, providing that steps for minimising noise pollution are taken (opportune frequencies, intensities, temporal activation, etc.).

Conclusions

Most of the insects show two kinds of behavioural patterns ie, innate and learned. Most behavioural patterns are innate, steriotyped and genetically programmed in their nervous system. Learned behavioural patterns are very less in insect because their learning capacity is very less as compared to other organisms due to very less number of neurons in their nervous system. By using different stimuli insect behaviour can be manipulated for the purpose of pest management. The recent development in the field of behavioural study is the extraction of green fluorescent protein which are incorporated into genes of insects to study the expression of various proteins. Such practices are eco-friendly and safe for human and animal health.

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