

INSTRUMENTAL CONDITIONING OF LEG POSITION
IN THE HONEY BEE: AN AUTOMATED
PARADIGM USING WORKBENCH PC
SOFTWARE

By

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PREFACE

The purpose of the present paper is to extend the Forman paradigm to instrumental conditioning of leg position in the honey bee and establish an automated method developed in our laboratory for measuring this type of learning. This technique allows subjects to be restrained in a manner identical to that long since standardized in the olfactory conditioning of honey bees and permits physiological measurement. Two paradigms were examined using this technique: punishment and escape, each including yoked and delayed conditioning controls. Analysis of variance between control and experimental groups indicates that learning is being measured by the new paradigm and that it is an effective means of conducting detailed analyses of instrumental and operant learning in invertebrates.

I would like to express my sincere appreciation to the members of my committee, Dr. Charles Abramson, Dr. James Price, and Dr. Bill Scott, whose guidance, assistance, and encouragement were invaluable to the development and completion of this study. I am especially indebted to Dr. Abramson for chairing the committee and providing continued support and constructive guidance throughout this project.

Finally, I owe a very special expression of gratitude to my parents, James & Kati Maines and Jimmy & Lana Stone, and to my grandmother, Dorine Stone, for their unconditional support and encouragement. And to my wife Julie, who means more to me than words can say.

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CHAPTER I

INTRODUCTION

Background

Honey bees have become popular for comparative and physiological research because of their economic importance, relatively simple physiology, and ability to perform well in experimental measures of learning. The technique used in many of these experiments is the classical conditioning of the proboscis extension reflex in harnessed foragers (Menzel & Muller, 1996). The reflex is studied by confining bees in small metal harnesses. One or more presentations of an odor and sucrose feeding increases the probability of proboscis extension to the odor. The development of this Pavlovian conditioning procedure has made possible a variety of sophisticated experiments on honey bee learning (Menzel & Muller, 1996). In comparison to work with classical conditioning protocols, the number of honey bee experiments devoted to the comparative and physiological basis of instrumental conditioning is remarkably small (Abramson, 1994).

The most popular instrumental conditioning technique used with honey bees is training free-flying foragers to shuttle back and forth from the hive to the laboratory where they take sucrose solution from targets distinguished by color, odor, and/or position (Abramson, 1994; Kartsev, 1996). The free-flying technique is limited, however, in several important respects. Perhaps most importantly, it precludes the use of many types

of experimental designs because of the lack of experimental control inherent in the paradigm. Employing physiological and biochemical techniques, such as measuring neuronal activity directly or investigating the effects of different chemicals on learning, can be difficult if not impossible because of problems in getting the animal to return to the laboratory if learning has in fact been affected. Additionally, the experiment can only be conducted in favorable climatic and ecological conditions (Abramson, 1994), and the experimenter cannot control whether the foraging bee is rewarded on every trial, nor other important training variables such as intertrial interval and stimulus duration. It is also difficult to present an unrewarded trial. If a foraging bee does not receive a reward on each visit to the experimental station it will not return in a timely manner. There is an interpretive problem as well: although the free-flying procedure is instrumental in character (i.e., the animal must land on the rewarded target and consume the sucrose), it is possible that, like in some maze and runway situations, the controlling variable is the classical conditioning of an approach response to the target (Mackintosh, 1974).

The problems of controlling training variables in the free-flying situation have been addressed by modifying the experimental situation so that 1) the animal must wait for a brief period of time before landing on a target (Grossmann, 1973), 2) the animal is trained to fly into a tunnel at the end of which is a target(s) (Sigurdson, 1981), and 3) the animal is presented with training stimuli while feeding on a target (Abramson, 1986). Even here, however, these situations do not control all of the relevant training variables, remain under the influence of climatic and ecological conditions, and make physiological and biochemical manipulations difficult. Shuttle box situations are available for the study of honey bee behavior that control all the relevant training variables and permit physiological

and biochemical manipulations, but the range of behavior so far studied has been limited to escape and Sidman avoidance (Abramson, 1986; Bermant, McNeil, & Ashby, 1973).

The comparative analysis of instrumental conditioning in honey bees will be greatly advanced if a technique is available that is fully automated, useful with a wide range of experimental designs, and amenable to physiological and biochemical manipulations. The present study reports on a modification of the Forman (1984) leg lift paradigm meeting these criteria.

Efficacy of Leg Lift Conditioning as a Measure of Learning

Horrige's (1962) leg position learning experiment in headless roaches (Figure 1) demonstrated that a learned behavior could be traced back to a single ganglion in the insect leg, thus supporting the applicability of the simple systems approach in studying the underlying physiology of learning. Horrige's methodology has been criticized since its publication for a number of reasons. An anecdotal report rather than a quantitative analysis of behavior was given; animals' heads were removed, which added support to the simple systems approach but complicated the analysis of learning per se; number of shocks delivered to the leg after extension beyond criterion were counted, even though the animal could make any of several different movements to avoid shock; and shock itself was undoubtedly partially responsible for the retraction of the leg (Church & Lerner, 1979).

Thompson, Patterson, and Teyler (1972) discuss in their article, however, that the leg-lift paradigm may not generalize to other species because specific neuronal pathways which exist in one species do not necessarily exist in another. While this is a valid concern in terms of the simple systems approach, Forman (1984) demonstrated that locusts could

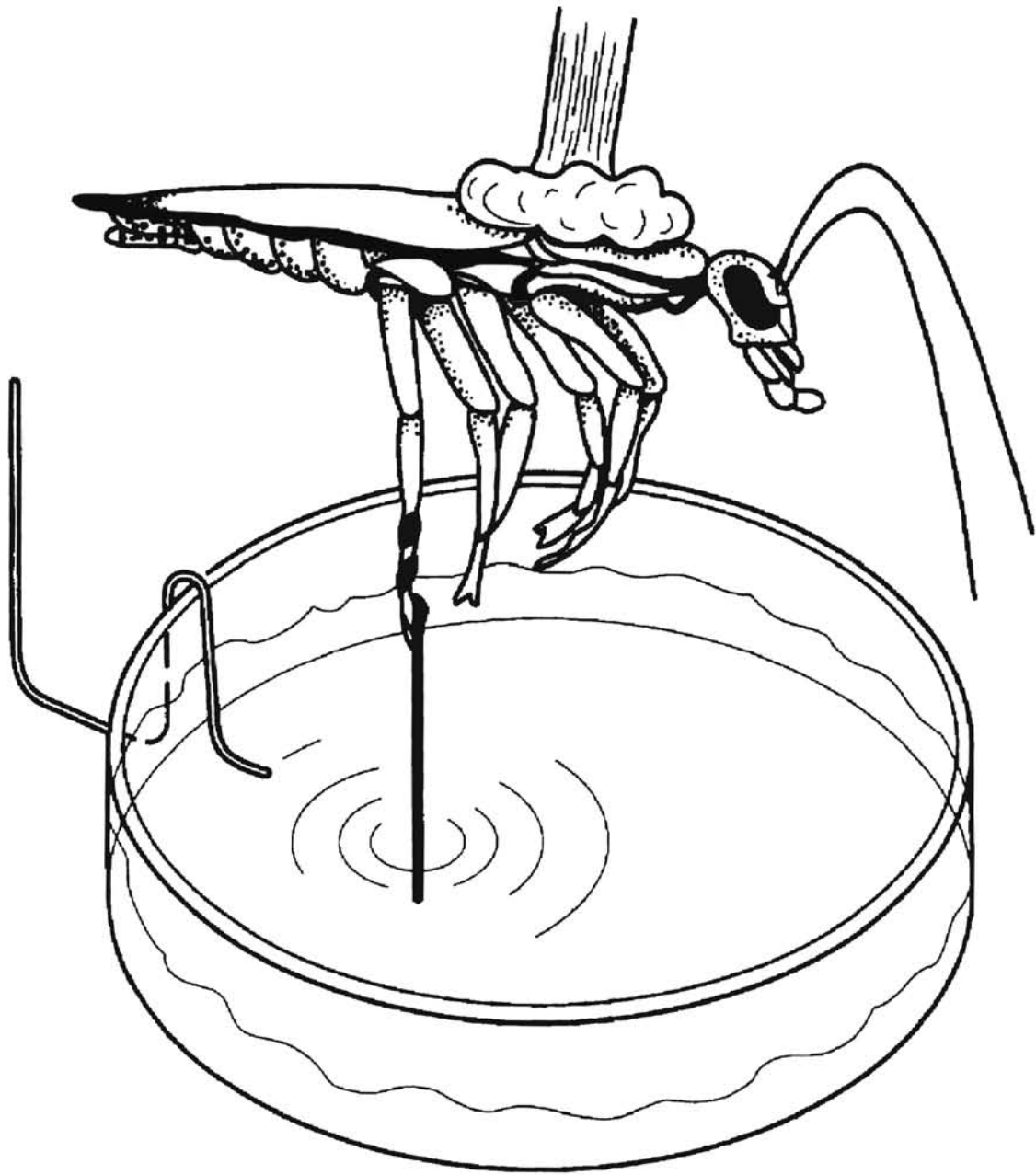


Figure 1. A Horridge leg lift paradigm for the cockroach. The animal must keep its leg contracted, or the wand attached to the leg contacts the water, closing the shock circuit and delivering an electric shock to the leg. From *A Primer of Invertebrate Learning: The Behavioral Perspective* by C. I. Abramson, 1994, p. 91. Copyright 1994 by the American Psychological Association. Reprinted with permission of the author.

be trained in an operant conditioning leg lift paradigm, thereby showing that the leg-lift paradigm can be a valuable tool to demonstrate learning in insects regardless of whether the neuronal pathway of that learning is traceable. Forman was able to identify three distinct behavioral strategies used between animals to avoid aversive stimulation: repeated rapid flexion-extension movement, maintained leg extension beyond criterion, and rapid leg extension beyond criterion followed by gradual return contraction. This finding further complicated the single-ganglion explanation: Forman had allowed his locusts only one type of leg movement, and yet managed to discover three behavioral strategies of leg-lift in place; Horridge's headless roaches could make any number of leg movements to avoid shock, and explained this learning in terms of one ganglion. It has yet to be fully investigated whether Horridge was indeed measuring learning.

The apparatus diagrammed in Figure 2 is a modification of Forman's (1984) technique developed to measure leg position learning in the locust. This technique is a significant advantage over Horridge's (1962) original leg position learning paradigm because the aversive stimulus is natural, learning can be identified in individual animals, the instrumental response is arbitrary, and reliance on the yoked control design to demonstrate learning is unnecessary (Abramson, 1994; Abramson & Feinman, 1987; Church & Lerner, 1976; Forman, 1984; Hoyle, 1980; Willner, 1978). Heat was selected as the aversive stimulus because it is a stimulus insects naturally experience (Forman 1984) and does not evoke a reflexive response (i.e., the required change in behavior can be either an extension or a retraction of the leg).

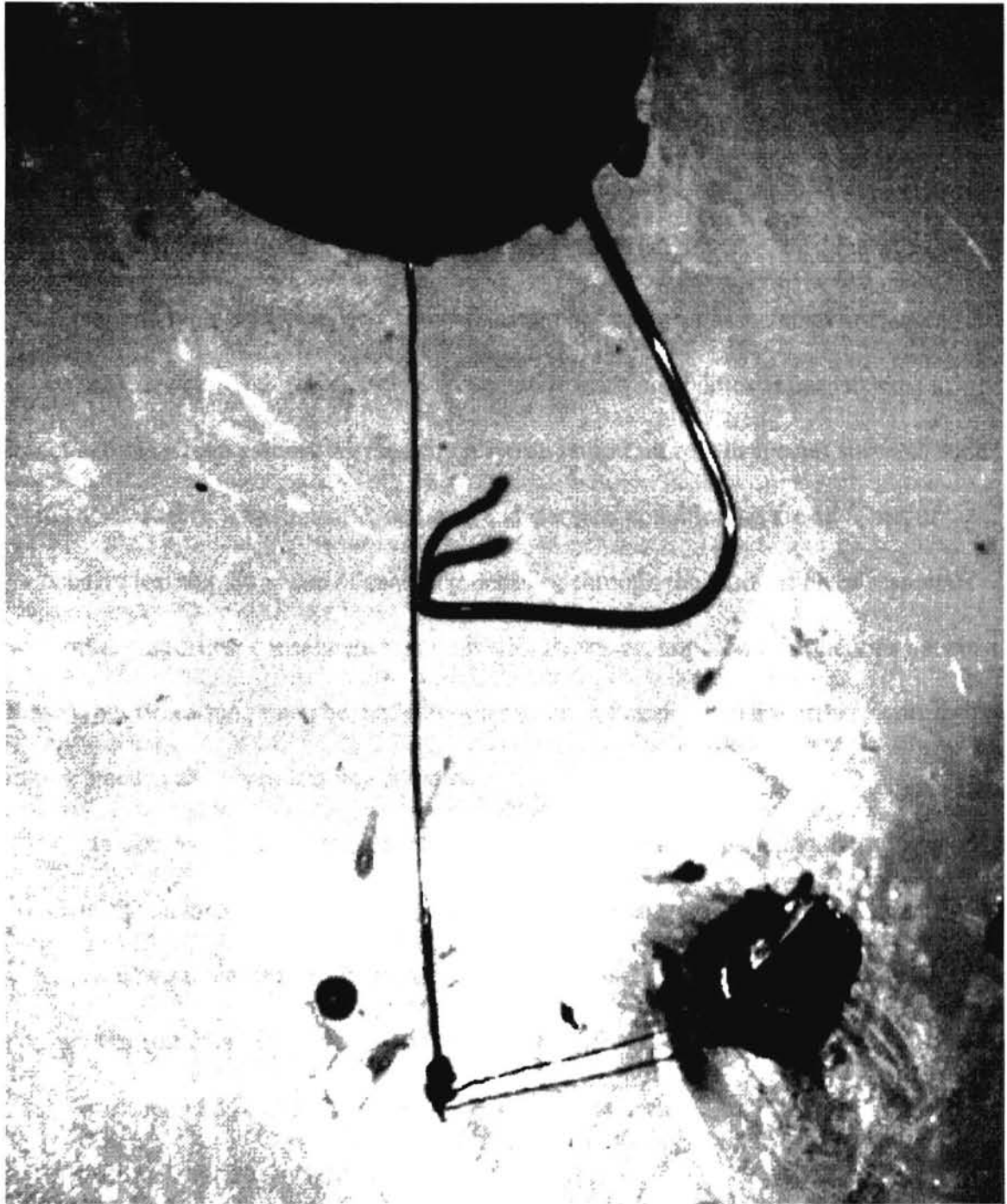


Figure 2. A modification of Forman's (1984) leg lift paradigm. A wand attached to the animal's leg is shown connected to the digital switch. The animal retracts its leg a predetermined distance thereby closing the switch and registering a response.

Distinguishing Instrumental Conditioning from Operant and Classical Conditioning

Forms of learning can be broadly grouped into the categories of associative and nonassociative learning. Examples of nonassociative learning can be found in all animal groups, and mechanisms involved in this type of learning are currently thought to compose the behavioral building blocks necessary to form more complex associative learning processes (Hawkins & Kandel, 1984). Associative learning abilities appear to exist in insect species where associative capacity plays an important role in species survival, such as in social insects. Instrumental, operant, and classical conditioning are all forms of associative learning by virtue of changing behavior through the association of responses with other responses, consequences, or stimuli. However, important distinctions between these types of learning must be made in order to operationally define whether “learning” is taking place in any given learning situation.

In classical conditioning, an originally neutral stimulus is paired with a stimulus which elicits an innate response (e.g., an air puff presented to the eye of a crab elicits eye withdrawal) such that the originally neutral stimulus takes on the eliciting properties of the non-neutral stimulus. Put more simply, Abramson (1994) defines classical conditioning as “a family of methods for the acquisition of associations between two or more stimuli or between stimuli and responses” (p. 123).

Instrumental and operant conditioning are often interchangeably defined as learning in which behavior is controlled by its consequences, and thus differ from classical conditioning in several respects. Learning in classical conditioning is dictated by the contingencies of the paradigm, while in instrumental and operant conditioning, an action

produces reinforcement. Therefore, it follows that the type of response which must be learned in classical conditioning is necessarily related to the unconditioned response, unlike the arbitrary response which may be selected by the experimenter to demonstrate instrumental or operant learning. The experimenter has much more control over training variables in classical conditioning procedures, such as when an unconditioned stimulus is applied, but relies upon a more simplistic measure of occurrence of conditioned response as a measure of learning. Instrumental and operant conditioning procedures can better measure more intricate forms of learning (detailed below) and may use a discriminative stimulus (or S_d) to indicate the temporal relationship between a response and a reinforcer.

The distinction between instrumental and operant conditioning is seldom made in contemporary usage. However, important differences exist between the two which may be easily made in terms of methodology and procedure. Both types of conditioning are defined primarily by the contingencies which are reinforced during the course of learning. Due to the literature's present lack of clear-cut evidence of operant learning in the honey bee (Abramson, 1994), the present study focuses on instrumental learning known to exist in the honey bee. Abramson (1994) enumerates several factors which distinguish instrumental from operant conditioning:

- 1) Instrumental paradigms typically incorporate discrete-trials, repeated measures procedures, and thus can involve measurements of rate, latency, or amplitude. Operant paradigms allow uninterrupted response, thus the term *free-operant*, in which the subject determines the intertrial interval, and emphasize the rate at which responses are made.

2) Operant paradigms traditionally employ fewer subjects and study them over a longer period of time than do instrumental paradigms, due to the nature of the design as described in (1) above.

3) Instrumental paradigms typically use species-typical behavior and its modification as a measure of learning, whereas operant paradigms tend to minimize species-typical behavior. Instrumental conditioning is demonstrated by modifying existing behavior in paradigms such as cockroach movement in a light/dark choice chamber (Szymanski, 1912; see Figure 3) and housefly locomotion following exposure to pesticide (Miller, Bruner, & Fukuto, 1971; see Figure 4). Operant paradigms, in contrast, emphasize the development of non-species typical behavior to demonstrate learning (Abramson & Feinman, 1990; see Figure 5).

4) Instrumental paradigms typically involve movement of the body from one location to another, whereas operant paradigms involve movement of an appendage. This distinction is due to the nature of measurement as described in (3) above.

A further conceptual distinction which is often useful is that in instrumental conditioning, an organism learns to make a general response which has specific results (such as pushing a button to call an elevator) and in operant conditioning an organism learns how to use a more specific response to achieve specific results (such as learning to push a stubborn button hard in order to call an elevator). Put more precisely, a technique is measuring an operant if some property of the response can be trained, such as its frequency, amplitude, or latency.

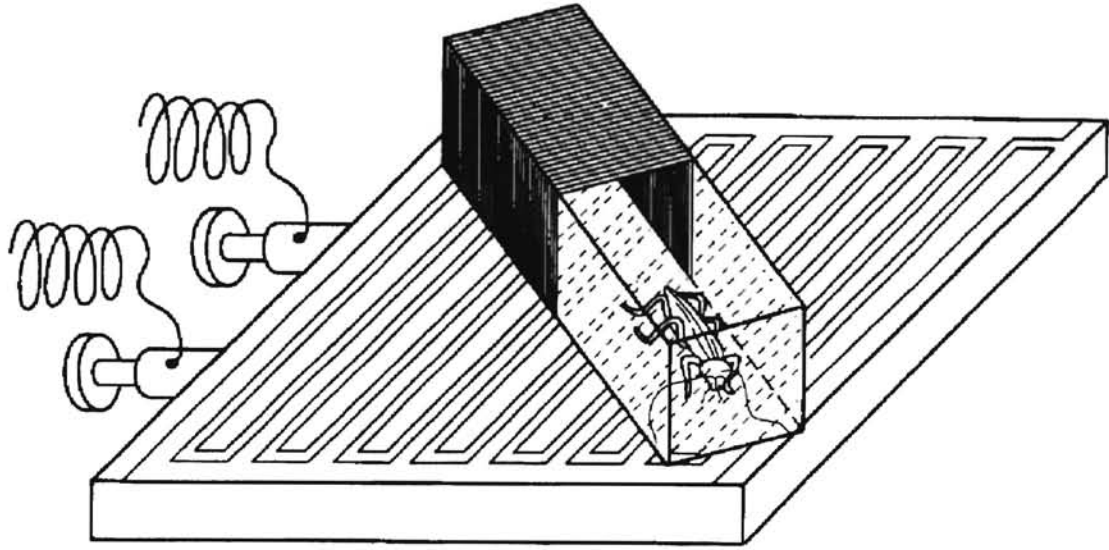


Figure 3. A choice chamber for the roach. The animal's preference for darker environments can be instrumentally altered by providing shock when the animal moves from the light to the dark side of the choice chamber. From *A Primer of Invertebrate Learning: The Behavioral Perspective* by C. I. Abramson, 1994, p. 77. Copyright 1994 by the American Psychological Association. Reprinted with permission of the author.

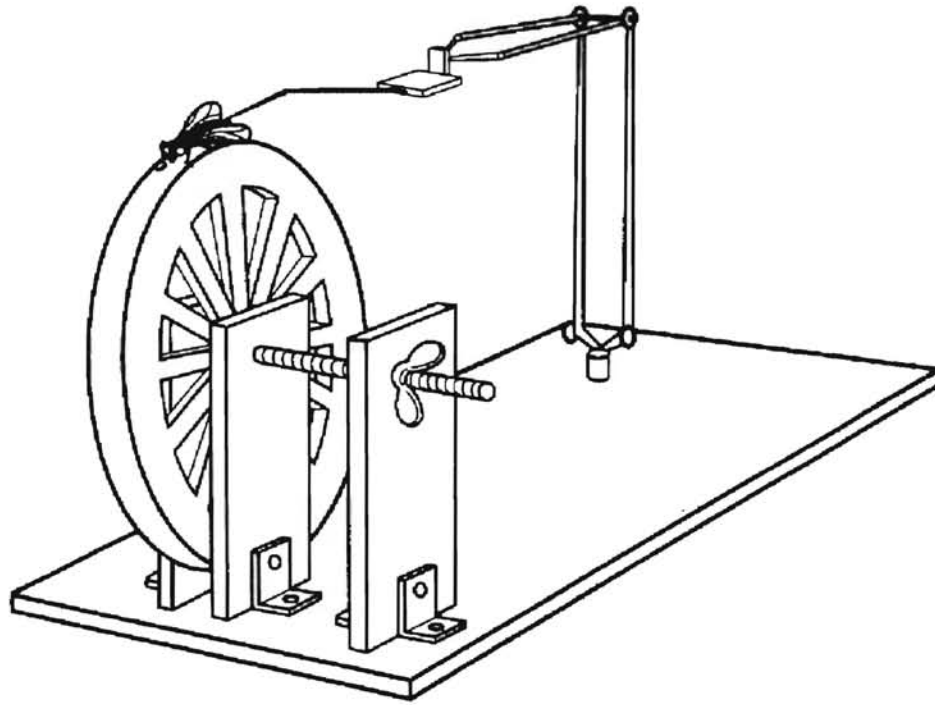


Figure 4. A running wheel for the fly. Environmental effects can be assessed through changes in learning behavior by comparing controls with treated subjects. From *A Primer of Invertebrate Learning: The Behavioral Perspective* by C. I. Abramson, 1994, p. 59. Copyright 1994 by the American Psychological Association. Reprinted with permission of the author.

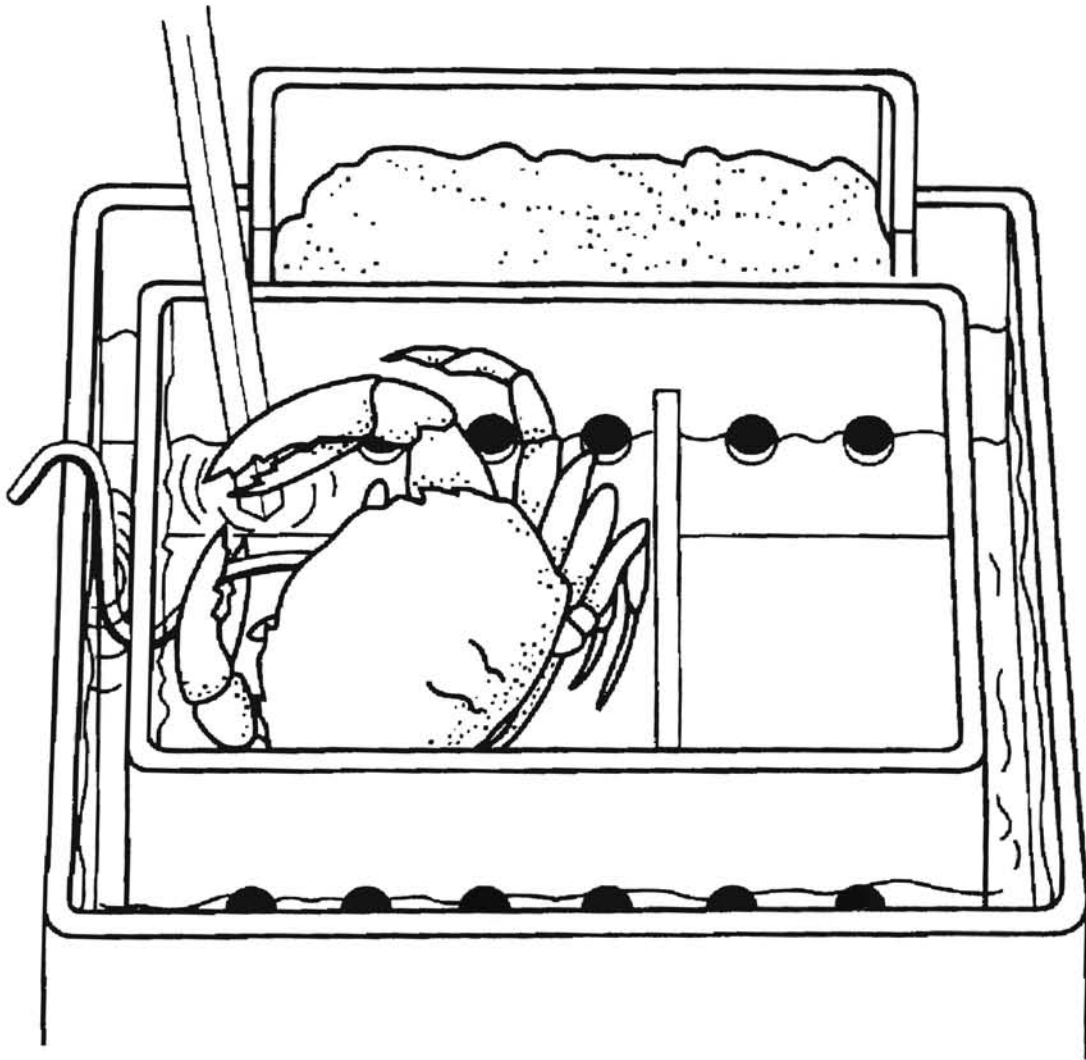


Figure 5. A lever-press situation for the crab. Animals can be trained to press a lever to gain a reward, an example of training non-species typical behavior in an operant paradigm. From *A Primer of Invertebrate Learning: The Behavioral Perspective* by C. I. Abramson, 1994, p. 69. Copyright 1994 by the American Psychological Association. Reprinted with permission of the author.

Characterizing Punishment and Escape

Punishment and escape are two distinct procedures which were used in the course of the present study to examine leg-lift behavior in the honey bee. Escape was chosen because of its relevance in demonstrating the efficacy of the automated paradigm in a discrete trials situation; punishment was chosen because of its comparability to Forman's (1984) study, while requiring an instrumental rather than an operant response. Thus, two separate experiments were conducted which demonstrate instrumental leg-lift conditioning in the honey bee under two different learning procedures and the effectiveness of the automated procedure here used to measure learning.

Escape training is a form of reward training which has yet to be fully investigated in invertebrates (Abramson, 1994). Escape in the present context may be defined as removing the presence of an aversive stimulus by exhibiting a specific response. This form of aversive conditioning allows the experimenter to control the motivational level of the organism in a much more quantifiable way than does appetitive conditioning. While rewards must often be roughly operationally defined (i.e., an operational definition of hunger may be a span of 24 hours without food), the presentation of aversive stimuli can be more fully controlled (i.e., 100 volts was presented to the leg of the animal). This improved control extends to the manipulation of the intertrial interval and the amount of reduction of the aversive stimulus as well. Experiment 1 below describes an automated escape paradigm for the honey bee using heat as an aversive stimulus.

Punishment is defined as the presentation of an aversive stimulus contingent upon a specific response. As outlined above, aversive stimuli can afford the experimenter more

control than reward. Due to its universally motivational properties, electric shock has frequently been used as an aversive stimulus in punishment experiments. In some instances, however, shock may interfere with the trained response and in any case makes electrophysiological measurement difficult. Controversy surrounds the use of shock as a stimulus in contemporary research because it is an artifice of the laboratory: it may introduce effects which can be shown inside the laboratory which do not necessarily exist in nature. Thus, care must be taken to select an aversive stimulus which has relevance to training situations which may occur outside the laboratory but which are still effective in training.

Purpose and Scope

The purpose of this study is twofold: to demonstrate that instrumental leg lift can be conditioned in honey bees, and to verify the usefulness of the automated Workbench PC paradigm and apparatus. The methodology employed in this paper involves a modification of the Forman (1984) leg lift paradigm developed for roaches. This 1984 experiment was defined as an operant technique because of the requirement that the animal maintain its leg position within a certain range in order to avoid aversive stimulation. While the present study has in common with Forman's (1984) study that both are training a behavior based on its consequences, the experiments in the present study are instrumental in character because they require leg movement only past an arbitrarily set criterion (approximately 4 mm). Because leg movement is restricted to one axis and in order to maximize generalization to other organisms and techniques, learning is operationally defined as a difference in response over trials between the master group and

its controls (as discussed in Experiments 1 and 2). The second objective, verifying the usefulness of the Workbench PC program, will be demonstrated as well.

CHAPTER II

AN AUTOMATED INSTRUMENTAL LEG-LIFT APPARATUS

Advantages of the Automated Technique

The science of psychology has historically had difficulty keeping up with emerging technology. Several problems contribute to this. Experimentalists in the past have designed their own measurement apparatus, which lacked flexibility; demand for extensive development of most psychological instruments is practically nonexistent, as current research topics vary according to current funding considerations; and the publish-or-perish climate common at large universities often demands that a researcher spend his or her time writing rather than reading. Although fifth-generation research tools are now becoming available, first- and second-generation research tools such as Skinner boxes and snap lead hardware are often the norm in many laboratories. Chute and Westall (1996) define fifth-generation research tools as follows:

“Fifth-generation research tools will comprise software and hardware that overcome many of the problems of the previous generation of effort. These tools will have flexible, comprehensive graphical programming environments so that students and inexperienced users will be able to easily construct clinical, experimental, or teaching protocols. They will be platform independent. For the first time, experimental replication and collaboration

should be readily possible ... for the first time, our technology will be transportable and shareable" (p. 313).

The advantages of automation are many: experimenter bias and error can more easily be avoided, the experimenter can be more efficient, and training variables can be controlled much more precisely, to name just a few. Although psychological research tools have trended toward automation over time, the ease and effectiveness achieved has varied greatly. Workbench PC software, developed by Strawberry Tree, Incorporated, San Francisco, CA is a commercially available software package designed for data acquisition, automation, and process control and is an example of this newly emerging fifth-generation research technology (Workbench PC is designed for IBM compatible PCs; WorkbenchMac is available for Macintosh). Using Workbench, relatively advanced programs can be written in little time by persons unfamiliar with traditional line-by-line programming through a graphical programming interface which allows direct access to and full control of analog and digital input and output. Workbench programs written by researchers are fully automated and can be distributed, sold, or published (e.g., McGregor, 1996).

Description of the Apparatus

Software

Strawberry Tree Incorporated's Workbench PC version 2.0.5 was used as the development system for the custom instrumental leg-lift conditioning program, NSTRMNTL.WBB. Controls programmed from within the WorkBench environment

allowed the experimenter to control the interval and duration of all relevant training variables via a programmable on-screen user interface (Figure 6), as well as record data from subjects in detail by logging to disk. WorkBench PC data acquisition and control software is programmed by connecting functions, or icons, on screen; the NSTRMNTL program worksheet is shown in Figure 7. This process control software is used to program the contingencies of the experiment and to record data. Workbench was run from within MS-DOS 5.0.

Hardware

A Strawberry Tree interface card and T-31 I/O terminal panel were connected to a 486-33 MHz PC-compatible machine. The digital/analog interface is necessary to input responses of the animal and to control the presentation of stimuli such as the heat lamp, which was used as an aversive stimulus in the current study.

Attaching the Animal's Leg to the Apparatus

Subjects were secured in individual restraining harnesses by a small strip of duct tape placed between the head and thorax and fastened to the sides of the harness. The harnesses were similar to those used in classical conditioning experiments with honey bees (see Smith, Abramson, & Tobin, 1991 for review), with the exception that the metal harnesses were constructed from .38 caliber shells to encourage standardization. Animals were placed in the tubes slightly off center to allow freer leg movement, described below. A second strip of tape was placed across the abdomen and fastened to the side of the harness to prevent excessive movement of the abdomen (See Figure 8). This ensured that

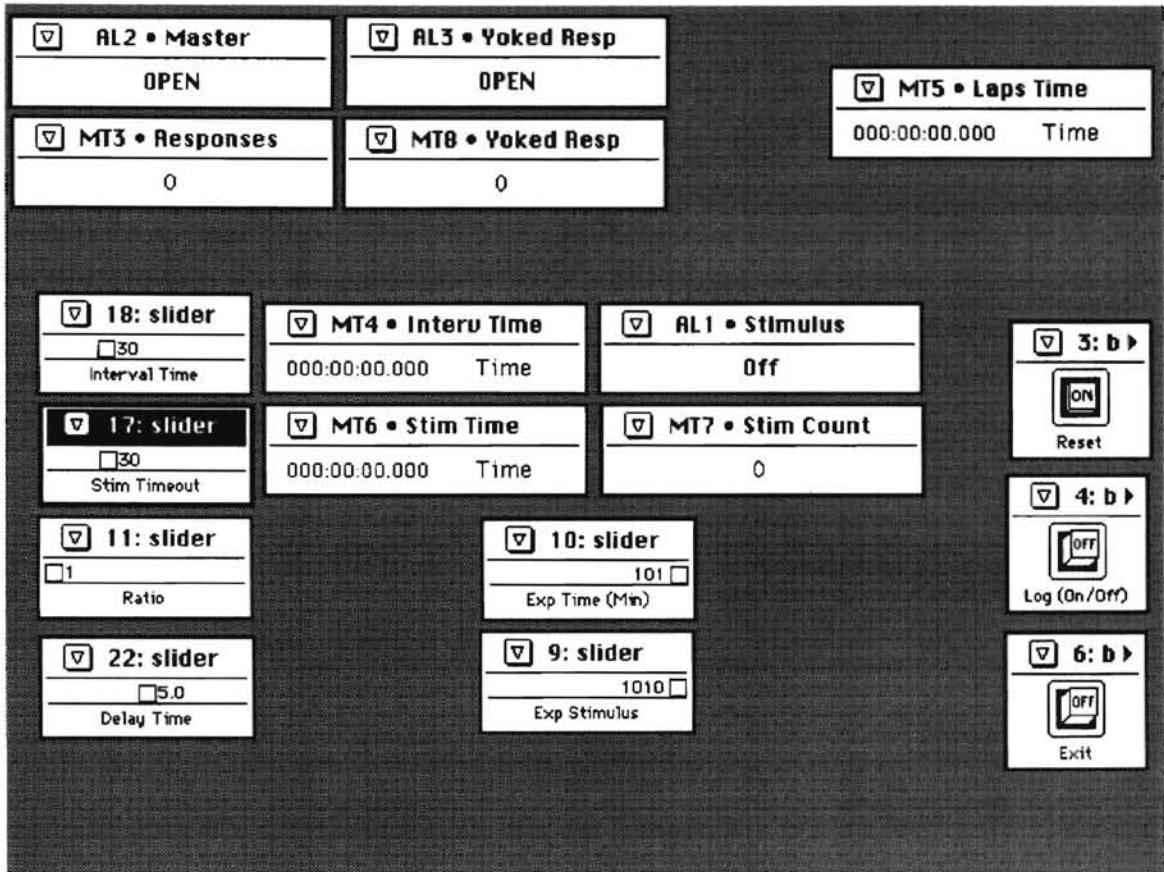


Figure 6. WorkBench PC's on-screen user interface allows control of all relevant training variables, and records data from subjects by logging to disk. Controls can be dragged and dropped by the user to create a fully customized interface.

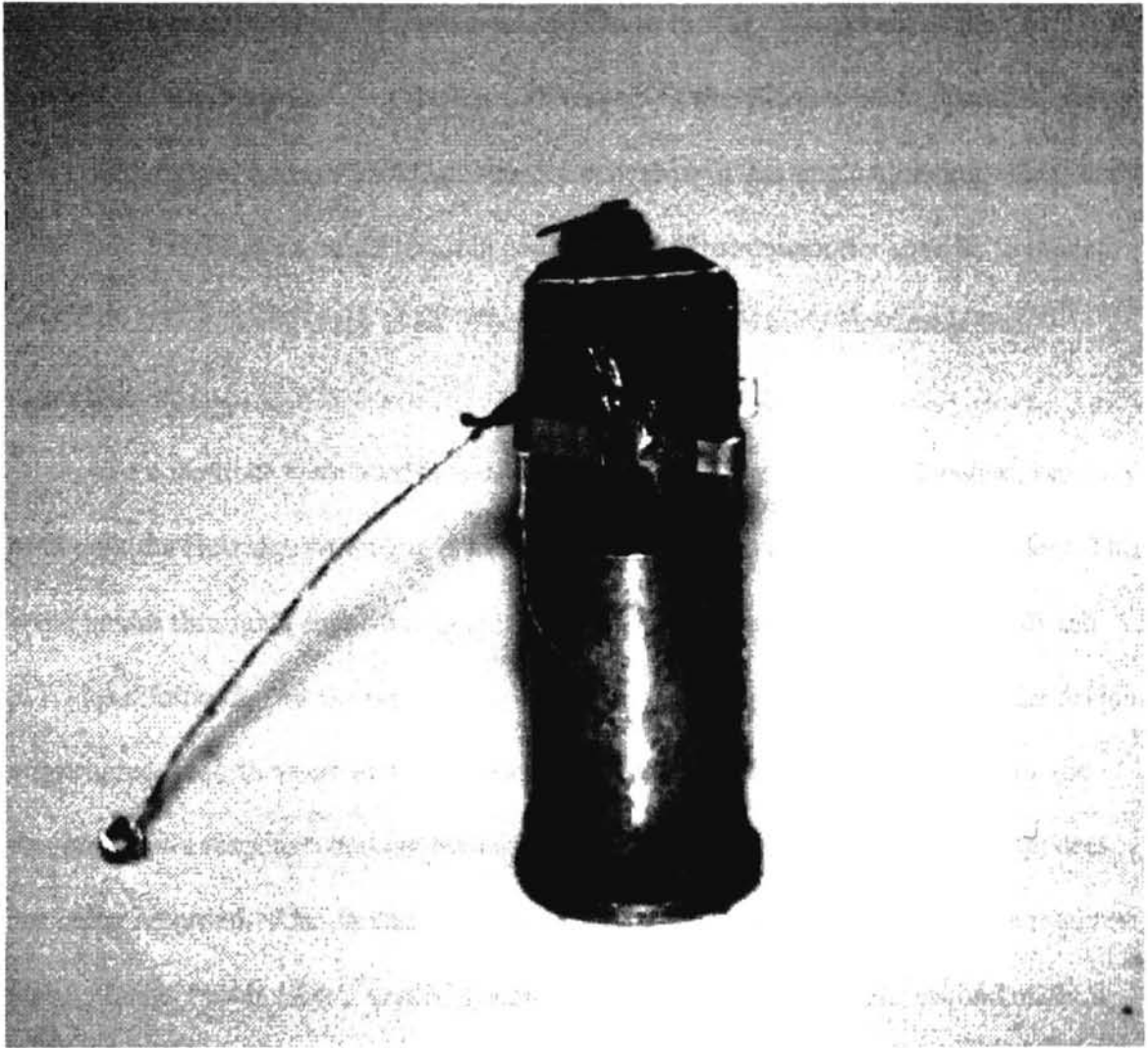


Figure 8. Animal in standard conditioning harness with tape securing the abdomen to prevent excess movement. A small wire is attached to the animal's leg with a loop at the other end for attachment to the digital switch.

any response was the result of movement specific to the leg. Movement of the abdomen changes the relative position of the leg with respect to the measurement apparatus, and thus could register a response which was not indicative of learning. Allowing excess body movement to take place could result in conditioning of movement not specific to the leg, or in no learning taking place at all. Therefore, the animal's body movement was restricted.

Two methods were tried to connect the animal to the interface. The first, typically used with the Horridge paradigm, is to connect a wire or "wand" to the animal's leg. This wand passes through a capacitive position transducer (Forman & Brumbley, 1980) and provides information on the angular displacement of the appendage. However, the device constructed to do this was so electronically noisy that drift was often registered by the equipment as a response, and decreasing the sensitivity resulted in many valid responses not being recorded. Also, it was discovered that the manual tuning of the device required when attaching each subject invited systematic experimenter error. The second method, which is the one used here, was to connect the wand directly to a digital switch. This method allows the experimenter to arbitrarily set the amount of travel necessary in order for the animal's leg to log a response, yet is much less error-prone. This approach has the virtue of requiring fewer components, being much easier to construct, and providing better accuracy in recording responses over long periods of time.

The physically constructed apparatus consisted very simply of the two conductors in a coaxial cable, together forming a digital switch. At one end of the cable, the center conductor was connected to a digital input on the T31 terminal panel and the shielding to the digital ground, thereby permitting a response to be registered whenever the two wires

at the other end of the coaxial cable came into contact with one another. The other end of the coaxial cable was anchored in a mound of clay which served to hold the cable in place. From the mound of clay, the center conductor of the coaxial cable extended approximately 4 in. The shielding was soldered to a 4 in piece of wire similar in gauge to the center conductor and bent into an S-shape, with the bottom curve of the S rotated 90 degrees toward the reader. This wire was extended from the mound of clay as well. This arrangement allowed the protruding center conductor to be moved an arbitrary amount before coming into contact with the other conductor, which triggered a response (See Figure 2).

The wand, which connected the animal's leg to the measurement apparatus, was attached to the leg after the bee was placed in the metal harnesses. One end of a single $2\frac{1}{2}$ in strand of 28-gauge wire was attached to the left hind tibia near the joint by crimping a loop, fashioned from the short section of wire, onto the leg and securing it with a small droplet of melted wax (see Figure 6) applied with a toothpick. A small loop or hook could be formed at this end of the wand and, using a pair of tweezers, the leg put through the loop. The loop was then crimped lightly and a small drop of wax applied to the crimp in order to keep the animal from shaking the wire loose. The other end of the wand was attached to the protruding center conductor of the coaxial cable, which formed the lever of the digital switch and which measured each response. Care must be exercised to avoid waxing either the joint, which prevents movement of the leg, or the wings. When done properly, the wire is firmly attached to the leg and can be easily removed for later use. The entire process is easily performed, with practice, in about 15 seconds.

The animal was placed so that when its leg was attached to the apparatus, the leg was at full extension with no tension being exerted on the leg by the center conductor. The S-shaped wire was then adjusted so that the animal had to move its leg a specific amount in order to bring the center conductor in contact with the other conductor, thereby closing the switch and registering a response. As long as the switch remained closed, only one response was recorded – the switch had to be opened again in order for another response to be logged. It was found that the bee could make responses ranging from a fraction of a millimeter (making it difficult to measure learning due to noise induced by small leg movements) up to 1 cm (making it difficult for the animal to respond at all). An intermediate range of 4 mm was chosen to minimize noise and maximize ability to respond, although this criterion could easily be adjusted by moving the second conductor wire.

CHAPTER III

EXPERIMENT 1

Punishment Training

Method

Subjects. Ninety-six bees worker bees divided into six groups of 16 animals each were collected in glass vials as they departed from the laboratory hive. Individual subjects were rendered unconscious by placing the glass vial containing the bee in an ice water bath. When the bee became inactive it was immediately removed from the vial and put into the restraining harness. Bees were secured in the harness by a strip of duct tape placed between the head and the thorax and fastened to the sides of the harness. After regaining consciousness, subjects were fed a 2.9 M sucrose solution from a syringe until satiated and trained a minimum of 30 minutes later.

Design and Procedure. Animals were attached to the apparatus as described in Chapter I and trained in a single 60 minute session in a punishment paradigm. Bees were randomly assigned to one of 6 groups containing 16 animals each. To control for calendar variables, animals from several groups were trained daily. In contrast to traditional studies of punishment in which the experimenter waits for the initial target response to occur before administering aversive stimulation, the target response was elicited by applying

heat. When the animal contracted its leg 4 mm, heat was terminated and thereafter, each extension of the leg beyond 4 mm was punished. Both a yoked control design and a delayed conditioning design were used to control for systematic effects of random error (Church, 1964) and for nonassociative effects (Abramson & Feinman, 1987).

In one group of bees, each movement of the leg beyond 4 mm was punished with heat. Heat could be terminated by the required 4mm movement in the master group. A control group was yoked to the master group in such a way that the yoked animals received the same heat presentations as their counterparts in the master group but independent of their own behavior. In the remaining groups, a delay was imposed between the contraction of the leg and termination of the heat; in groups 3, 4, 5, and 6 the delay was 0.5 s, 1 s, 2 s, and 5 s, respectively. An infrared heat lamp (GE Warm Up 250W) provided the aversive stimulation and maintained a temperature of approximately 49°C when placed 33 cm above the head of the animal.

Results

In Figure 7 the results are plotted in terms of the number of responses in each group as a function of ten 6-minute intervals. As the figure shows, substantial responding occurred in each group and the number of responses remained relatively stable over the course of the 60 minute session. This suggests that bees can easily emit the required 4 mm leg movement for long periods of time.

One-way repeated-measures analyses of variance ($\alpha = .05$) between the master group and each of the other groups were conducted. The Group main effect was determined to be of more relevance in determining whether learning took place than the

Group X Trial interaction because of the high variance in scores over time and evidence that some learning began to take place within the first block of trials, which could not be accounted for in the analysis of the interaction. Results are plotted in terms of the number of responses per trial in Figure 9. No significant differences were found between master and yoke groups, $F(1,30) = 1.74$, $p = .197$; master and .5 s delay, $F(1,30) = 1.54$, $p = .224$; master and 1 s delay, $F(1,30) = .48$, $p = .495$; or master and 2 s delay, $F(1,30) = .90$, $p = .350$. A significant difference in learning was found between the master and 5 s delay group, $F(1,30) = 4.70$, $p = .038$. Analysis of variance source tables for master versus yoked, 0.5 s, 1 s, 2 s, and 5 s can be found in Tables 1, 2, 3, 4, and 5, respectively. Independent samples t-tests were conducted between the master and 5 s delay group on trials 1 and 10 in order to confirm this finding. The test on trial 1, $t(30) = 1.666$, $p = .107$ confirmed that the two groups were initially the same, with the test on trial 10, $t(30) = 2.779$, $p = .009$, demonstrating that learning did take place in the master group as compared to the 5 s delay group.

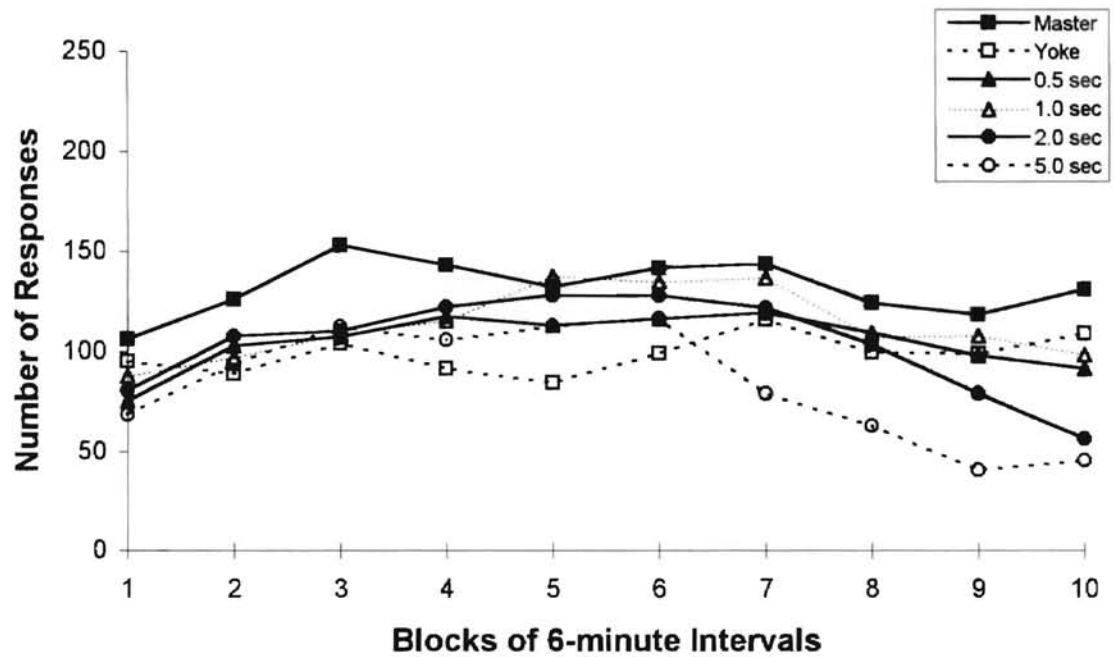


Figure 9. Mean number of responses per group over blocks of trials in Experiment 1. The graph indicates a decreased ability to learn with a longer delay duration.

Table 1
 Analysis of Variance Source Table
 Experiment 1 - Punishment

Master vs. Yoked Group

<u>Source</u>	<u>df</u>	<u>SS</u>	<u>MS</u>	<u>F</u>	<u>p</u>
<u>Between Subjects</u>					
Group	1	89612.58	89612.58	1.74	0.1970
Between Subjects Error	30	1544021.17	51467.37		
<u>Within Subjects</u>					
Trial	9	26503.97	2944.89	0.96	0.4695
Group X Trial	9	14644.64	1627.18	0.53	0.8499
Within Subjects Error	270	824054.89	3052.06		

Table 2
 Analysis of Variance Source Table
 Experiment 1 - Punishment

Master vs. 0.5 Second Delay Group

<u>Source</u>	<u>df</u>	<u>SS</u>	<u>MS</u>	<u>F</u>	<u>p</u>
<u>Between Subjects</u>					
Group	1	58725.70	58725.70	1.54	0.2237
Between Subjects Error	30	1141384.37	38046.15		
<u>Within Subjects</u>					
Trial	9	49022.72	5446.97	2.14	0.02
Group X Trial	9	6460.26	717.81	0.28	0.9794
Within Subjects Error	270	688770.32	2551.00		

Table 3
 Analysis of Variance Source Table
 Experiment 1 - Punishment

Master vs. 1 Second Delay Group

<u>Source</u>	<u>df</u>	<u>SS</u>	<u>MS</u>	<u>F</u>	<u>p</u>
<u>Between Subjects</u>					
		29070.31	29070.31	0.48	0.4951
Group	1	1828122.69	60937.42		
Between Subjects Error	30				
<u>Within Subjects</u>					
Trial	9	58106.08	6456.23	2.38	0.0130
Group X Trial	9	15830.43	1758.94	0.65	0.7539
Within Subjects Error	270	730968.69	2707.29		

Table 4
 Analysis of Variance Source Table
 Experiment 1 - Punishment

Master vs. 2 Second Delay Group

<u>Source</u>	<u>df</u>	<u>SS</u>	<u>MS</u>	<u>F</u>	<u>p</u>
<u>Between Subjects</u>					
Group	1	64071.20	64071.20	0.90	0.3495
Between Subjects Error	30	2127681.79	70922.73		
<u>Within Subjects</u>					
Trial	9	85202.49	9466.94	2.69	0.0052
Group X Trial	9	27984.30	3109.37	0.88	0.5411
Within Subjects Error	270	951056.21	3522.43		

Table 5
 Analysis of Variance Source Table
 Experiment 1 - Punishment

Master vs. 5 Second Delay Group

<u>Source</u>	<u>df</u>	<u>SS</u>	<u>MS</u>	<u>F</u>	<u>p</u>
<u>Between Subjects</u>					
Group	1	186100.28	186100.28	4.70	0.0383
Between Subjects Error	30	1189022.09	39634.07		
<u>Within Subjects</u>					
Trial	9	109296.03	12144.00	3.43	0.0005
Group X Trial	9	36246.38	4027.38	1.14	0.3367
Within Subjects Error	270	956476.09	3542.50		

CHAPTER IV

EXPERIMENT 2

Escape

Method

Subjects. Ninety-six bees worker bees were collected and harnessed as in Experiment 1. Subjects were randomly assigned to one of 6 groups containing 16 animals each.

Design and Procedure. Design was identical to the first experiment with the exception that a discrete trials escape procedure was used. Heat was presented every 30 seconds for 100 trials. Each trial began with the presentation of heat which could be escaped by contraction of the leg; it was not necessary for the bee to maintain its retracted leg position after escaping the heat. At the end of the 30 second period the heat was re-introduced. As in Experiment 1 a control (master) group was compared with a yoked group and delay groups of .5 s, 1 s, 2 s, and 5 s respectively

Results

Results are plotted by number of responses per block of trials (Figure 10.) One-way repeated-measures analyses of variance ($\alpha = .05$) were again conducted between

the master group and each of the other groups. The main effect for Group was again used as a measure of learning rather than the Group X Trial interaction. Statistical results were similar to those found in experiment 1: no significant differences were found between master and yoke groups, $F(1,30) = 1.02$, $p = .320$; master and .5 s delay, $F(1,30) = .72$, $p = .402$; master and 1 s delay, $F(1,30) = 1.40$, $p = .247$; or master and 2 s delay, $F(1,30) = 0.26$, $p = .613$. A significant difference in learning was found between the master and 5 s delay group, $F(1,30) = 13.3$, $p = .001$. Analysis of variance source tables for master versus yoked, 0.5 s, 1 s, 2 s, and 5 s can be found in Tables 6, 7, 8, 9, and 10, respectively. Independent samples t-tests were conducted between the master and 5 s delay group on trials 1 and 10 in order to confirm this finding. The test on trial 1, $t(30) = -0.572$, $p = .572$ confirmed that the two groups were initially the same, with the test on trial 10, $t(30) = -0.288$, $p = .003$, demonstrating that learning did take place in the master group as compared to the 5 s delay group.

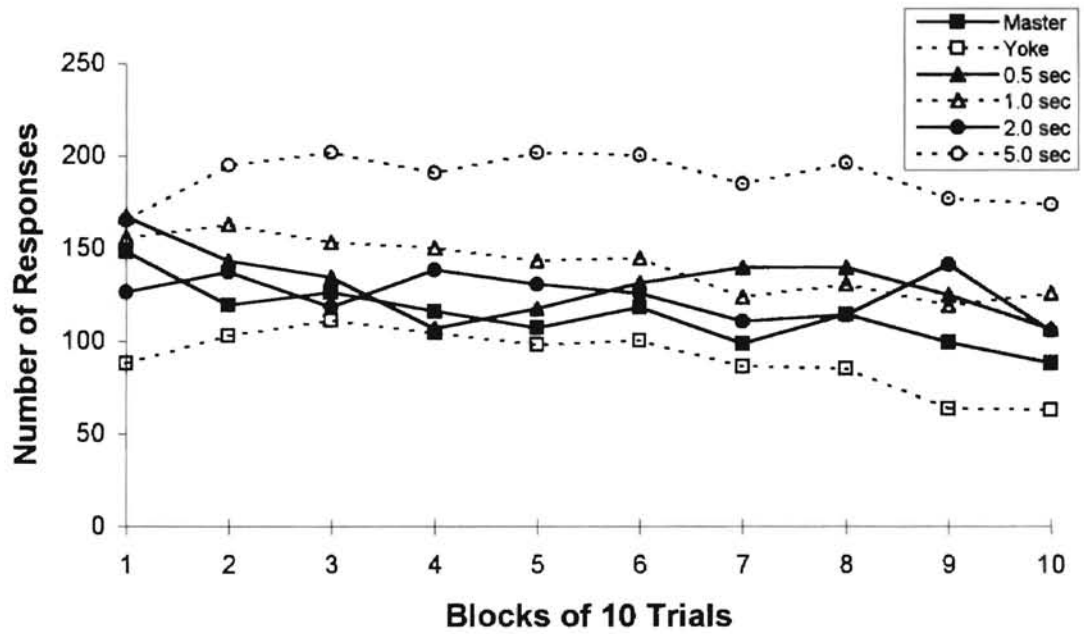


Figure 10. Mean number of responses per group over blocks of 10 trials in Experiment 2. Graph shows decreased ability to learn with increased delay, as measured by the difference from the control.

Table 6
 Analysis of Variance Source Table
 Experiment 2 - Escape

Master vs. Yoked Group

<u>Source</u>	<u>df</u>	<u>SS</u>	<u>MS</u>	<u>F</u>	<u>p</u>
<u>Between Subjects</u>					
Group	1	43477.81	43477.81	1.02	0.3198
Between Subjects Error	30	1274569.39	42485.65		
<u>Within Subjects</u>					
Trial	9	64139.49	7126.61	3.57	0.0003
Group X Trial	9	17404.50	1933.83	0.97	0.4653
Within Subjects Error	270	538372.61	1993.97		

Table 7
 Analysis of Variance Source Table
 Experiment 2 - Escape

Master vs. 0.5 Second Delay Group

<u>Source</u>	<u>df</u>	<u>SS</u>	<u>MS</u>	<u>F</u>	<u>p</u>
<u>Between Subjects</u>					
Group	1	24886.51	24886.51	0.72	0.4019
Between Subjects Error	30	1032438.28	34414.61		
<u>Within Subjects</u>					
Trial	9	77033.76	8559.31	3.20	0.0011
Group X Trial	9	12982.30	1442.48	0.54	0.8458
Within Subjects Error	270	723162.34	2678.38		

Table 8
 Analysis of Variance Source Table
 Experiment 2 - Escape

Master vs. 1 Second Delay Group

<u>Source</u>	<u>df</u>	<u>SS</u>	<u>MS</u>	<u>F</u>	<u>p</u>
<u>Between Subjects</u>					
Group	1	61023.63	61023.63	1.40	0.2466
Between Subjects Error	30	1310703.94	43690.13		
<u>Within Subjects</u>					
Trial	9	66189.84	7354.43	4.11	0.0001
Group X Trial	9	8471.34	941.26	0.53	0.8553
Within Subjects Error	270	483228.12	1789.73		

Table 9
 Analysis of Variance Source Table
 Experiment 2 - Escape

Master vs. 2 Second Delay Group

<u>Source</u>	<u>df</u>	<u>SS</u>	<u>MS</u>	<u>F</u>	<u>p</u>
<u>Between Subjects</u>					
Group	1	10488.20	10488.20	0.26	0.6129
Between Subjects Error	30	1204017.99	40133.93		
<u>Within Subjects</u>					
Trial	9	40437.01	4493.00	1.42	0.1802
Group X Trial	9	23537.80	2615.31	0.83	0.5934
Within Subjects Error	270	855698.39	3169.25		

Table 10
 Analysis of Variance Source Table
 Experiment 2 - Escape

Master vs. 5 Second Delay Group

<u>Source</u>	<u>df</u>	<u>SS</u>	<u>MS</u>	<u>F</u>	<u>p</u>
<u>Between Subjects</u>					
Group	1	450825.38	450825.38	13.30	0.0010
Between Subjects Error	30	1017082.54	33902.75		
<u>Within Subjects</u>					
Trial	9	33368.44	3707.60	1.40	0.1878
Group X Trial	9	32619.59	3624.40	1.37	0.2022
Within Subjects Error	270	714892.27	2647.75		

CHAPTER V

GENERAL DISCUSSION AND CONCLUSIONS

Discussion

General Discussion

In both the punishment and escape situations, the introduction of a .5 s, 1 s, or 2 s delay between response and removal of the aversive stimulus did not affect the number of responses. When the interval was increased to 5 s, however, there was a significant loss in leg position learning. These results are consistent with a similar experiment designed to punish eye elevation in crabs (Abramson & Feinman, 1987) and in a free-flying honey bee experiment in which subjects were punished for landing on a target (Abramson, 1986)

The inability of the present study to find significant differences in learning between master and yoked animals in either the punishment or escape paradigm was initially somewhat surprising. In review, however, the most obvious explanation is that, given the bees' high rate of response, leg position in yoked and short delay groups was being reinforced on a partial schedule of reinforcement. Of interest is that leg force generated during maximal reactivity in arthropods (such as in escape) can be 8 to 100 times greater than that used in normal movement, though only through a limited range of movement. Perhaps if the response requirement was increased from 4 mm, differences in experimental

and control performance would appear rather than be hidden by the experimental paradigm itself. Clearly, the difference in results between yoked and delay conditioning highlights the necessity of using multiple research designs in invertebrate research (e.g., Abramson, Aquino, Silva, & Price, in press; Abramson & Buckbee, 1995; Church & Lerner, 1976; Terry & Hirsch, 1997; Willner, 1978).

Conditioning of leg position in insects was one of the first paradigms to suggest that invertebrates can be used to investigate the neuronal basis of learning (Horridge, 1962). Leg position learning is a natural technique for the study of honey bee learning in much the same way as is the classical conditioning of proboscis extension because honey bees actively use their legs to gather and manipulate propolis (Winston, 1987). Although the original Horridge paradigm has a number of limitations (some mentioned by Horridge himself in the original experiments), which have here been addressed, its use as a tool for comparative analysis should not be underestimated. Leg position techniques are available for crabs (Dunn & Barnes, 1981a, 1981b; Hoyle, 1976), fruit flies (Booker & Quinn, 1981), locusts (Forman, 1984), roaches (Harris, 1976; Pritchatt, 1968), and spinal frog preparations (Farel & Buerger, 1972). The Horridge procedure can be used to train appendages other than the leg such as eye withdrawal in crabs (Abramson & Feinman, 1987), tentacle movement in snails (Christoffersen, Frederiksen, Johansen, Kristensen, & Simonsen, 1981), body orientation in fruit flies (Mariath, 1985), and claw movement in crayfish (Strafstrom & Gerstein, 1977).

In addition to its value as a tool in comparative investigations, the leg position paradigm developed for honey bees will stimulate new types of instrumental conditioning experiments. The instrumental conditioning apparatus described in this paper allows

automatic programming of events and data, thereby eliminating handling of subjects and experimenter-induced effects during a training session. Contingencies can be arranged to accommodate free operant or discrete trial procedures. A unique feature of the technique is that the bee is harnessed in the same apparatus used to study classical conditioning; this encourages standardization among experiments and experimenters, resulting in more reliable and replicable data. This arrangement allows for implementation of many new experimental designs in the analysis of honey bee behavior such as those used in transfer of training and conditioned suppression (Blackman, 1977; Rescorla & Solomon, 1967). In addition to the implementation of new experimental designs, existing biochemical and physiological methodologies developed for the analysis of classical conditioning of proboscis extension in the bee are easily extended to the study of instrumental conditioning and the interaction between instrumental and classical conditioning. These experiments would include investigating all parameters associated with instrumental conditioning (Bitterman & Schoel, 1970) and the influence of various types of drugs and chemicals on instrumental conditioning (e.g., Stone, Abramson, & Price, 1997). The methodology employed in the present paper literally opens the door to this type of experimentation because the instrumental conditioning situation described does not require that the honey bee be moved from one type of restraint to another in order to be tested in another paradigm.

Heat was used as an aversive stimulus in the studies reported here. The apparatus, however, can accommodate a wide range of stimuli. For example, electric shock can be added, and stimuli such as pheromones, repellents, attractants, and olfactory conditioned stimuli can be utilized easily by adding solenoid operated valves. For example, a bee that

has associated a floral odor with a sucrose feeding in a Pavlovian paradigm, should be expected to learn to manipulate leg position to obtain an odor previously associated with a feeding. Moreover, by adding a syringe pump, sucrose solutions can be used as a positive reinforcement (Hoyle, 1980). Additional outputs can be used to apply discriminative stimuli.

Final Conclusions

Honey bees are capable of leg position learning in an instrumental paradigm. The instrumental conditioning of leg position offers a new method for the study of instrumental conditioning in the honey bee. The technique used in the present study is fully automated, easy to use, accommodates a wide range of stimuli, and is readily adapted for physiological and biochemical investigations of the learning process.

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