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A COMPARISON OF THE HABITUATION OF THREE RESPONSES
IN THE LIZARD, ANOLIS CAROLINENSIS

BY

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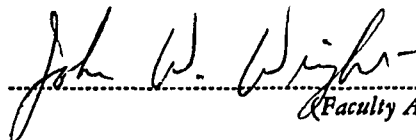

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A COMPARISON OF THE HABITUATION OF THREE RESPONSES
IN THE LIZARD, ANOLIS CAROLINENSIS

CHAPTER I

INTRODUCTION

Habituation is typically considered to be a decrease in responding with repeated stimulation and a simple and ubiquitous form of behavioral plasticity (Harris, 1943; Humphrey, 1933; Lorenz, 1965; Thompson & Spencer, 1966; Thorpe, 1963). The relatively permanent waning of a response has been used as a criterion for the inclusion of habituation as a form of learning and to distinguish it from effector fatigue and sensory adaptation (Denny & Ratner, 1970; Thorpe, 1963).

Habituation is of practical and theoretical importance for the following reasons: (a) it enters into the procedures used in other learning paradigms (Carlton & Vogel, 1967; Denny & Ratner, 1970; Lubow, 1973), (b) it offers a means of investigating neuronal mechanisms underlying changes in behavior (Thompson & Spencer, 1966), (c) it may be found in all species (Harris, 1943; Humphrey, 1933; Thorpe, 1963) and (d) it is important for survival by reducing responsiveness to biologically irrelevant stimuli (Humphrey, 1933; Lorenz, 1965, 1969; Thorpe, 1963). In addition, habituation has been used as (e) a paradigm for studying cognitive development and retention capabilities in human infants (Jeffrey & Cohen, 1971; Kessen, Haith & Salapatek, 1970), (f) a process in attention and perception (Sokolov, 1960, 1963b), (g) a means for studying arousal in the autonomic nervous system (Graham, 1973) and (h) a possible means for distinguishing between classically and instrumentally

conditionable responses (Kimmel, 1973a, 1973b).

There are numerous theories of habituation and recently there has been a proliferation of research dealing with habituation. Leibrecht (1972) compiled a list of 834 articles published between 1940 and 1970 that dealt with habitatory phenomena. A more recent survey (Leibrecht, 1973b) listed 850 references on habitatory phenomena, two-thirds of which were published since 1970.

A brief review of several theories of habituation is presented below, followed by a more detailed discussion of the "general process" theories of habituation as exemplified by Thompson and Spencer (1966) and Groves and Thompson (1970). The behavioral response habituation literature will then be reviewed. Following the review, an alternative approach to a general process theory is discussed as recently developed by Askew and Leibrecht (1973). From implications of this approach, a within-species comparative method used to study habituation is outlined. A description is then given of the species and responses studied. Next, a description of the general procedure and of each apparatus is given, followed by a detailed and separate account of each experiment. For each experiment, the methodology and obtained results are presented and are immediately followed by a discussion specific to that experiment. Next, a general discussion is given which integrates the experimental findings and offers several suggestions for future lines of research.

Theories of Habituation

Theories of habituation vary from broad conceptual and hypo-

thetical theories, to those dealing with specific brain structures and/or neural systems, to those dealing with chemical and/or synaptic modifications.

General-Conceptual Theories. Humphrey (1933) was the first to discuss habituation as a form of learning and as a possible adaptive mechanism which eliminates unnecessary activity by an organism. Humphrey also suggested that habituation was due to the interaction of inhibitory and excitatory processes.

Thorpe (1963) discussed habituation as a learning not to respond to stimuli that are without significance in the life of an organism. According to Thorpe, a response habituates relatively permanently as a result of an active build up of inhibition due to a failure to release the appropriate consummatory act.

Lorenz (1965, 1969) maintained that the function of habituation and its survival value is in eliminating an organism's response to a frequently recurring, biologically irrelevant stimulus without affecting the organism's response to other stimuli. Habituation prevents fatigue on the motor side of a response by occurring specifically to only a particular stimulus. Lorenz (1965) also asserted that very different physiological processes may account for the behavioral change labeled habituation.

Hinde (1970a, 1970b) discussed the complexity of habituation and stressed that habituation is not a unitary concept. According to Hinde (1970a), habituation may be the result of the interaction of processes that decrease responding and processes that increase responding. This interaction of multiple decremental and incremental processes may vary from one response to another. Hinde (1970a,

1970b) does not mention any physiological mechanisms or structures that might underly these processes.

Ratner (1970) presented an "elicitation and interference" theory of habituation which emphasizes the eliciting value of a stimulus and the effects of competing responses on the course of habituation. The elicitation of a response is followed by a refractory period, wherein response strength is reduced. During the refractory period, concurrent, more dominant, eliciting stimuli may elicit responses which intrude and compete with the originally elicited response. The build up in strength of these competing responses produces habituation. Stimuli and responses may be organized along a dimension of "orienting" (appetitive), "consummatory" and "postconsummatory" sequences of behavior (Denny & Ratner, 1970). Denny and Ratner suggest that habituation occurs more readily for orienting (appetitive) behaviors than for consummatory behaviors. Ratner (1970) suggested that the amount of retention is less for consummatory sequences of behavior than for orienting or postconsummatory sequences.

Hinde (1970b) also suggested that the rate of waning and the rate of recovery is characteristic of the response. However, contrary to Denny and Ratner (1970; Ratner, 1970), Hinde suggested that the early phases of a response sequence wane more slowly and recover more quickly than later ones. The literature appears to support Hinde (see review of literature below).

In general, a major feature of all the above theories is the consideration of the biological significance of habituation. How-

ever, this consideration has been rather superficial in that none of the theories have elaborated upon, in any detail, the possible selection pressures operating on a species that might favor the evolution of particular habitatory "processes and mechanisms."

Neural Systems Theories. There have been several theories to account for the habituation of the orienting reaction (OR). Pavlov (1927) suggested that with repeated stimulation of cortical neurons an inhibitory process is generated which raises the threshold of responding. This internal inhibition spreads to the whole of the cortex and then the subcortex and accounts for the elimination of an OR.

Sokolov (1960, 1963a, 1963b) offered a more extensive two-stage model of the habituation of the OR. With repeated stimulation, the cortex forms a "neuronal model" of the stimulus which is compared with incoming information. If there is a match between the neuronal model and the incoming information, the cortex transmits impulses to the reticular formation which in turn blocks non-specific inputs that would normally elicit an OR. This blocking results in habituation of an OR. If a mismatch occurs, an OR is elicited.

Konorski (1967), viewing habituation as a perceptual process, suggested that with repeated stimulation a model of the specific stimulus patterns is developed by the associative cortical neurons ("gnostic units"). Response waning occurs as a result of the activation of an inhibitory system (mediated by the "gnostic field") which suppresses the arousal system.

Hernández-Peón (1960) and Pribram (1967) have offered afferent neuronal inhibition theories of habituation. Hernández-Peón

maintains that habituation in specific sensory pathways is due to decreased responsiveness at the periphery as a result of inhibitory signals sent from the reticular formation. Input is actively filtered at the periphery. Pribram proposed that the limbic forebrain has an important role in habituation by controlling two forms of afferent inhibition (collateral and recurrent). Polysensory motor cortical systems enhance recurrent inhibition which lead to a reduction of differences within afferent channels and a decreased responsiveness. Increases in responsiveness are due to the suppression of collateral inhibition by the frontotemporal systems.

Other neural systems theories have proposed cholinergic inhibitory systems in the cortex (Carlton, 1968), corticofugal influence of the frontal cortex (Griffin, 1970), the limbic system (Buchwald & Humphrey, 1972; Douglas, 1972; Vinogradova, 1970) and the reticular formation (Groves & Lynch, 1972).

In general, the major feature of the neural systems theories is the emphasis on the probable role of various brain structures and systems in habituation.

Synaptic Modification Theories. Many theories have stressed the possible synaptic mechanisms underlying habituation. Synaptic processes occurring in neurons different from the habituating neuron (extrinsic mechanisms) and synaptic processes occurring within the habituating neuron itself or the neuron responsible for its action (intrinsic mechanisms) have been postulated to account for habituation.

The extrinsic mechanism of postsynaptic inhibition has been

proposed for a mammalian system (Wicklegren, 1967a, 1967b) and in invertebrates (Kandel & Spencer, 1968). The cumulative build-up of inhibition as a result of post-tetanic potentiation (Wall, 1970) and postsynaptic membrane desensitization due to repeated application of transmitter substance (Sharpless, 1964) have been advanced.

Intrinsic synaptic mechanisms have been proposed based on studies of the gill withdrawal response of Aplysia and the neuromuscular junction in crayfish. Low frequency depression is the mechanism proposed to account for habituation in Aplysia (Castellucci, Pinsker, Kupfermann & Kandel, 1970; Kupfermann, Castellucci, Pinsker & Kandel, 1970; Kupfermann, Pinsker, Castellucci & Kandel, 1971) and in crayfish (Bruner & Kehoe, 1970). Horn (1970) has suggested that habituation is due to "self-generated depression" within the response system. Self-generated depression includes after-hyperpolarization, conductance block and synaptic depression. Recently, synaptic depression and a depressive process originating in the polysynaptic neuron has been suggested to account for habituation in Aplysia (Stephens, 1973a, 1973b).

A General Process Theory of Habituation

A "general process" view of learning assumes that all behaviors can be equally associated with any arbitrary stimulus and that all behaviors obey common laws (see Seligman, 1970). Applying a general process view to habituation, the present dissertation will consider a general process theory of habituation as one that attempts to explain habituation in different species and responses in terms of a limited set of "mechanisms" and/or "processes" (e.g.,

neural, synaptic, structural, etc.). Thus, it is argued that all the theories reviewed above, except for Hinde (1970a) and Lorenz (1965), are process theories. Although some theories were developed for a particular taxa (e.g., Applewhite & Gardner, 1971; Krasne & Roberts, 1967) or for certain behaviors (e.g., Berlyne, 1960; Sokolov, 1960), nearly all theories imply a considerable generality of the "mechanisms" and/or "processes" underlying habituation.

The "dual-process" theory of Thompson and Spencer (1966) and Groves and Thompson (1970) will be examined next. The dual-process theory was chosen because it is the most detailed and widely cited theory of habituation and because it best exemplifies the general process approach and the assumptions underlying general process theories of habituation.

The Dual-Process Theory of Habituation. From the behavioral response habituation literature on intact organisms, Thompson and Spencer abstracted nine "parametric characteristics" which describe the most commonly observed properties of behavioral response to repeated stimulation (Thompson, Groves, Teyler & Roemer, 1973). These nine parametric characteristics which serve as an operational definition of habituation are: (1) a negative exponential decrease of responding, (2) spontaneous recovery, (3) successively more rapid habituation with repeated series of habituation and spontaneous recovery (potentiation of habituation), (4) a direct relationship between the frequency of stimulation and the rate and/or the amount of habituation, (5) an inverse relationship between the strength of a stimulus and the rate and/or amount of habituation,

(6) effects of habituation training proceed below zero or asymptotic response level ("below zero" effects), (7) stimulus generalization of the habituated response to other stimuli, (8) recovery of the habituated response with the presentation of another stimulus (dishabituation) and (9) habituation of dishabituation. It appeared that there was "...virtually complete agreement on the parametric characteristics of the phenomenon in such a wide variety of animals and responses (Thompson & Spencer, 1966, p. 19, italics mine)."

From their investigations and use of the hindlimb flexion reflex of the acute spinal cat as a "model" system, Thompson and Spencer suggested that the final behavioral response is due to the interaction of two hypothetical central nervous system processes that develop independently of each other. One process is decremental (habituation) and the other incremental (sensitization) in nature. Habituation and sensitization presumably occur in interneuron pathways in the spinal cord. The process of habituation may be due to the cumulative effect of a polysynaptic low-frequency depression, while dishabituation is a superimposed sensitization possibly resulting from facilitatory after-discharge. Furthermore, the process of low-frequency depression, after-discharge and membrane desensitization may interact in all instances of habituation.

Elaborating Thompson and Spencer's (1966) earlier treatment, Groves and Thompson (1970) tentatively made the distinction that habituation occurs in the "S-R pathway", supposedly the most direct route through the central nervous system from stimulus to response,

while sensitization occurs in the "state system", the regions, systems and pathways that determine the general responsiveness of the organism. Groves and Thompson suggested that distinct classes of spinal interneurons and synapses subserve the process of habituation ("Type H" interneurons and synapses) and sensitization ("Type S" interneurons and synapses). Groves and Thompson further suggested that similar classes of interneurons may exist in the brain to mediate habituation and sensitization in the intact organism. Recently, Thompson et al., (1973) simplified the assumptions of the effects of stimulus frequency and stimulus intensity and included another model system. Under limited conditions, the absolute number of stimuli presented, independent of stimulus frequency, may determine the rate and/or amount of habituation. Stimulus intensity, rather than having a weak effect, has no effect on relative habituation. The ventral root response to dorsal root stimulation in the isolated frog spinal cord was included as another model system.

Assumptions Underlying the Dual-Process Theory of Habituation.

Askew and Leibrecht (1973) have analyzed the general process theories of habituation, especially that of Thompson and Spencer, and have brought to light the assumptions underlying the dual-process theory. These assumptions as outlined by Askew and Leibrecht are as follows:

1. An objective survey of the behavioral response habituation literature yields a number of specific characteristics common to virtually all reported examples. Although there are some differences from one experimental situation to the next (as in recovery time), overall the similarities either far outweigh the differences, or are at least theoretically much more important (p. 9).

2. This relatively high degree of similarity in the specific characteristics of behavioral response habituation (for different responses and species) implies the operation of the same, common or identical neural processes and mechanisms (p. 9).

3. Based on the preceding assumption, it appears reasonable to attempt to formulate a general physiological (general process) theory which can account for habituation of virtually all responses and species in terms of a limited set of common neural processes and mechanisms (p. 10).

4. The empirical basis necessary to formulate and continually test and modify such a general process theory can and should be obtained by generalizing the physiological knowledge acquired in "model" experimental situations (p. 11).

5. Because of the great many similarities and relatively few significant differences among specific examples of behavioral response habituation, the functional and historical evolutionary considerations generally necessary to successfully account for diversity are not especially relevant to the formulation of a general theory of habituation (p. 11).

Only to the extent that the above assumptions are accurate can they be considered to characterize the dual-process theory. By focusing on similarities, Thompson and Spencer appear to have ignored the differences in behavioral response habituation. Differences in response habituation across species and responses would pose difficulties for a general process approach. The following review of the behavioral response habituation literature of intact organisms attempts to assess the extent of species and response diversity in habituation. The present dissertation argues that, contrary to the general process approach exemplified by Thompson and Spencer, Groves and Thompson and other theorists previously mentioned, there are differences across (and within) species and responses and that the course of habituation may be related to the functional significance or nature of the response or response system. Since the present

dissertation is concerned with the investigation of various responses within a single species, as discussed more fully below, the review of the literature was organized by phylum. Finer taxonomic classifications were used where justified.

A Functional Classification of Responses

In order to facilitate comparisons in behavioral response habituation between responses and within phyla, it was necessary to develop a classification of responses or response systems. A functional classification of responses was developed from extensive reading of the habituation literature and other general readings in comparative psychology (e.g., Denny & Ratner, 1970; Harler & Hamilton, 1966) and ethology (e.g., Eibl-Eibesfeldt, 1970; Hinde, 1970a; Thorpe, 1963; Tinbergen, 1951).

This classification is outlined in Table 1 on the following page. It is not meant to be an exhaustive classification. The behaviors listed are not necessarily mutually exclusive. Some responses may be part of several different behaviors. For instance, orienting responses may be found during exploratory, defensive, feeding and reproductive behaviors. This points to the importance of the context within which a particular response is occurring and habituating. Defensive responses primarily concern reactions to a predator or a potentially threatening stimulus. Most of the behavioral response habituation literature deals with defensive and feeding (reaction to a prey) behaviors.

TABLE 1

A FUNCTIONAL CLASSIFICATION OF RESPONSES

-
-
1. ORIENTING BEHAVIORS (towards stimulation)
 - A. Body movements
 - B. Other responses - heart-rate, GSR

 2. EXPLORATORY BEHAVIORS (towards stimulation)
 - A. Orienting responses (e.g., visual)
 - B. Locomotion
 - C. Investigatory - manipulation (contact), visual, other (sniffing, rearing, etc.)

 3. DEFENSIVE BEHAVIORS (avoidance of stimulation)
 - A. Orienting responses
 - B. Freezing Responses - startle reaction, tonic immobility
 - C. Escape responses - fleeing, withdrawal reflex
 - D. Fighting and/or frightening predator
 - E. Other responses - heart-rate, GSR

 4. FEEDING BEHAVIORS (towards stimulation)
 - A. Orienting responses
 - B. Hunting responses - approach, following, chase
 - C. Prey capture - strike
 - D. Eating
 - E. Drinking

 5. REPRODUCTIVE BEHAVIORS (towards stimulation)
 - A. Courtship responses (i.e., displays)
 - B. Copulation
 - C. Care of young - nest building; licking, retrieval and defense of young
 - D. Intraspecific fighting

 6. GENERAL MAINTENANCE
 - A. Care of body surface - grooming, headshake, sandbathing
 - B. Responses to pain
 - C. Responses to temperature changes
 - D. Postural responses
-

A Review of the Behavioral Response Habituation Literature

Phylum: Protozoa

A contraction response elicited by tactile stimulation or mechanical shock habituated rapidly (3-9 trials) and recovered within minutes in Spirostomum (Applewhite, 1968, 1971; Applewhite & Morowitz, 1966). Habituation to a mechanical shock dishabituated with the presentation of tactile or electrical stimulation (Applewhite, 1968, 1971). The contraction response did not habituate to an electric shock, but did habituate to a mechanical shock within 10 minutes and completely recovered in 45 minutes, with some recovery after 5 minutes of rest (Osborn, Blair, Thomas & Eisenstein, 1973). Habituation of the contraction response in Vorticella proceeds rapidly to mechanical and electric shock (Patterson, 1973). Displacement via rotation elicited a contraction response in Stentor which habituated rapidly (Wood, 1970b). Recovery was nearly complete in 6 hours with evidence of potentiation of habituation. The contraction response did not dishabituate with the presentation of a more intense stimulus or electric shock. Habituation to a mechanical shock was not influenced by responding to either an electric shock (Wood, 1970b) or photic stimulation (Wood, 1973). As in Spirostomum (Osborn et al., 1973), contraction elicited by electric shock did not wane in Stentor (Wood, 1970a).

The above cited studies and those reviewed by Harris (1943) indicate that when the contraction response decrements, it does so rapidly. Habituation to one stimulus seems to be independent of habituation to a different stimulus.

Phylum: Coelenterata

The contraction response of Hydra, elicited by mechanical agitation (i.e., rotation), took hours to wane (Rushforth, 1965; Rushforth, Burnett & Maynard, 1963; Rushforth, Krohn & Brown, 1964). After animals habituated to mechanical agitation, they reacted fully to a light exposure. Contractions did not wane with light presentations. Harris (1943) mentions the studies of Goldsmith (1927) and Wagner (1905) that found no habituation in Hydra to mechanical stimulation if complete extension of the body was allowed between contractions. Harris also cites the studies of Jennings (1905), Kinoshita (1911) and Pieron (1908) of the contraction response in Actinozoa (sea-anemones). With short inter-trial intervals (e.g., 60 sec), rapid habituation occurred to mechanical shock and touch. The duration of contraction became shorter with successive stimulation (Kinoshita). Kinoshita also found differences between species in the amount of time to extend the body after the presentation of the initial stimulus. All the species, however, reached a similar level of habituation within the same number of trials.

Phylum: Platyhelminthes

The contraction response of the flatworm Stenostomum wanes rapidly to touch (6-7 trials) and electric shock (12-14 trials) (Applewhite, 1971). Habituation to touch and electric shock were independent of each other. Waning of the raising of the body, elicited by slow rotation, occurred within 12 trials in planaria and completely recovered within 30 seconds (Walter, 1908 in Harris,

1943). Planaria, Dugesia dorotocephala, took 20 days (25 trials per day) to habituate to light presentation and were slow to recover (Westerman, 1963). The swimming response of the Trematoda rapidly decremented and recovered with the repeated presentation of a shadow but did not wane with tactile stimulation (Miller & Mahaffy, 1930 cited in Harris, 1943).

Phylum: Annelida

Class: Polychaeta. The withdrawal response of the "errant" polychaete Nereis pelagica (Clark, 1960a, 1960b; S. Evans, 1969b) and Nereis diversicolor (Clark, 1960b; S. Evans, 1969a, 1969b) habituates at different rates to mechanical, photic and tactile stimulation. The withdrawal response of N. pelagica (Clark, 1960a) decremented with mechanical shock, a sudden decrease in light intensity and a moving shadow within 20 trials, while habituation to a sudden increase in light intensity took 60 trials. Minimal recovery of waning to a decrease in light intensity occurred after 45 minutes of rest, while complete recovery of the withdrawal response to a moving shadow occurred in 40 minutes. Complete recovery of habituation to a sudden increase in light intensity occurred after 17 hours of rest, with some retention of habituation after 1 hour and 5-1/2 hours. Habituation to mechanical shock was independent of habituation to a moving shadow, while habituation to a moving shadow and a sudden decrease in light intensity interacted in a complex way. N. diversicolor (an estuarine species) waned slower to a moving shadow and faster to a decrease in light intensity than N. pelagica (Clark, 1960b). There were no interactive effects in

habituation to a moving shadow and a sudden decrease in light intensity in N. diversicolor as there was in N. pelagica (Clark, 1960b).

Habituation of the withdrawal response in nereids may function as a means of dealing with the conflicting needs of an animal to escape possible predators and to continue normal activities (S. Evans, 1969b; Nicol, 1950). A moving shadow may signal the approach of a predator, a possible food source or an innocuous stimulus. Rapid recovery of the withdrawal response would have survival value.

The waning of the withdrawal response to a sudden increase in light intensity differentiated N. pelagica, N. diversicolor and Platynereis dumerilii from each other (S. Evans, 1969b). N. diversicolor habituated the slowest, P. dumerilii the fastest and N. pelagica was intermediate. Anterior tactile stimulation elicited withdrawal in N. pelagica during the first few trials, but thereafter, more frequently attacked the stimulus object. N. diversicolor and P. dumerilii habituated the slowest to tactile stimulation than to any other stimulus. These differences in responding to tactile stimulation may be related to the feeding habits of the worms (S. Evans, 1969b). N. pelagica is carnivorous, and it might be advantageous for the withdrawal response to be relatively unresponsive to anterior tactile stimulation if such stimulation signals a possible food source. The other two species are herbivorous and react to anterior tactile stimulation as a signal for a possible predator (S. Evans, 1969b). Both N. diversicolor and P. dumerilii habituated more slowly to a simultaneous presentation of a

mechanical shock and a sudden decrease in light intensity than did N. pelagica.

The withdrawal response of a sedentary polychaete, the sabel-lid worm Branchiomma vesiculosum, wanes rapidly to a sudden decrease in light intensity, more slowly to a moving shadow and not at all to tactile stimulation (Nicol, 1950), unless stimulus intensity is controlled (Krasne, 1965). In the latter case, habituation to tactile stimulation occurred within 24 trials, with 80% recovery after 24 hours of rest (Krasne, 1965). Habituation of the withdrawal response to a moving shadow was independent of habituation to a decrease in light intensity (Nicol, 1950) unlike N. pelagica (Clark, 1960a). Mercierella enigmatica habituated rapidly to a moving shadow, more slowly to mechanical shock and slowest to a combination of the two (Rullier, 1948 in Jacobsen, 1963). Hydroides dianthus habituates to repeated shadows (Hargitt, 1906 and Yerkes, 1906 in Harris, 1943) with little or no decrement to tactile stimulation (Yerkes). The amount of time the scaleworm Hesperonoë adventor took to traverse an alley increased within days, with some retention of habituation across days (Dyal & Hetherington, 1968).

The rate of habituation of the withdrawal response in polychaetes (except perhaps N. pelagica) may be related to the likelihood that the stimulus indicates the presence or approach of a possible predator (e.g., Clark, 1960b; Nicol, 1950). Tactile stimulation might indicate contact between predator and prey (S. Evans, 1969b). It seems reasonable that habituation of the withdrawal response to such stimulation should proceed slowly.

Class: Oligochaeta. The waning of contraction in the earthworm, Lumbricus terrestris, occurs independently to mechanical, thermal and electrical stimulation (Kuenzer, 1958). The frequency of contraction to light onset does not seem to habituate although the latency of responding increases with repeated stimulation (Ratner & Gardner, 1968; Ratner & Stein, 1965). The contraction response consists of a withdrawal and a posterior hooking component that wane at different rates to the same vibratory stimulus (Gardner, 1968). The withdrawal component rapidly habituated to criterion, while the hooking component waned slowly. Retention of habituation of both components was evident after 4 days of rest, with less retention of the hooking than the withdrawal component. The differences in habituation and retention of the two components may be related to the function of each. Hooking (a flattening of the posterior body segments) serves to attach an earthworm to the sides of its burrow, making it difficult to remove, while the anterior serves to escape into a burrow or search for and gather food. L. terrestris is nocturnal and light may elicit a more vital defensive reaction than vibration (Ratner, 1970) and account for the difficulty in obtaining habituation.

Class: Hirudinea. The movement response of the leech, Macrobdella decora, waned within 35 trials to light onset and water current caused by rotation (Ratner, 1972). There was retention of habituation to light onset after 24 hours of rest.

Phylum: Mollusca

The limited number of investigations of habituation in intact

specimens of Mollusca hinder direct comparisons within species. Yet, there seem to be certain consistencies with other studies that warrant mentioning.

The withdrawal response of the freshwater snail, Limnaea stagnalis, habituated at somewhat different rates to mechanical and photic stimulation (Cook, 1971). Response to vibration and mechanical shock waned faster than response to a change in light intensity or a shadow. Habituation to photic stimulation was independent of habituation to mechanical stimulation. Recovery occurred in 5 minutes. The gill withdrawal response of Aplysia wanes rapidly to tactile and photic stimulation (Lukowiak & Jacklet, 1972; Pinsker, Hening, Carew & Kandel, 1973; Pinsker et al., 1970) with 80% recovery occurring in 10-20 minutes and complete recovery in 2 hours (Pinsker et al., 1970). With repeated daily testing, retention was evident after 21 days of rest (Carew, Pinsker & Kandel, 1972).

The components of the prey catching response in the cuttlefish, Sepia officinalis, wane at different rates (Messinger, 1973). The orientation component waned the slowest, while striking at the prey waned the fastest (cf. studies under Arthropoda). Recovery was a complex phenomenon, depending on at least two processes. Retention was greater and recovery was less after 1 hour than after 22 minutes of rest. Retention was still evident after 2 days. Mouthing of inedible objects by octopus waned within 20 trials, with some retention after 24 hours (Wells & Wells, 1957; Wells & Young, 1968). At the same time, touching (investigation) of the objects did not habituate (Wells & Wells, 1957).

Phylum: Arthropoda

Again, because of the limited number of studies of habituation in Arthropoda valid comparisons are more difficult to make. Nevertheless, certain important observations can be made. The various components of the prey catching behaviors of spiders wane and recover at different rates. The initial orientation towards a prey (or stimulus signaling the presence of a prey) habituates last (Drees, 1952; Peckham & Peckham, 1887 in Thorpe, 1963; Precht & Freytag, 1958; Szlep, 1964) and recovers first (Precht & Freytag, 1958) or may not wane with high levels of food deprivation (Gardner, 1966). Recovery of prey catching behaviors was complete in 24 hours with some retention across days (Szlep, 1964). The orientation response of the waterbug Notonecta glauca to a prey stimulus is more resistant to habituation than is approach and capture (Wolda, 1961). Recovery was complete in 24 hours with some evidence of retention.

The frequency of head movements (orientation) and attacks of mantids towards a prey waned within 80 20-sec trials (Maldonado, 1972). The decrement in head movements was smaller than the decrease in attacks. Both responses dishabituated with the presentation of another stimulus. Both responses retained habituation after 8 days. The strike response of mantids towards model flies waned in 2-3 minutes and completely recovered in 30 minutes, while the strike response towards live flies waned in 4-5 hours (Rilling, Mittelstaedt & Roeder, 1959). The difference in the rate of waning of the strike response of mantids in the above studies may have been due to the differences in procedure, apparatus and/or species.

The deimatic ("frightening") response of mantids shown towards live bird predators wanes within 30 3-minute presentations and across days (Balderrama & Maldonado, 1971). Recovery was complete after 2 or 6 days. More recovery and less retention was evident after 6 days than after 2 days. Habituation was slower, recovery greater and retention less to the natural bird predator of mantids than to other birds. The abdominal rotation response in pupae of Tenebrio molitor habituates to electrical and tactile stimulation (Askew & Kurtz, 1974; Hollis, 1963). Waning occurred more rapidly to electrical than tactile stimulation (Askew & Kurtz, 1974). There was 50 % retention to tactile stimulation after 15 minutes, with complete recovery after 2 hours (Askew & Kurtz, 1974).

The courtship behavior of male Mormoniella vitripennis towards nonreceptive females wanes within 20 presentations, with some retention and complete recovery in 24 hours (Barrass, 1961). Orientation towards and chasing after the female did not seem to wane. Courtship behavior of Lycosid spiders towards nonreceptive females also wanes rapidly (Rovner, 1968).

The shadow reflex of the barnacle, Balanus improvisus, wanes within 30-60 trials and rapidly recovers with approximately 25 % retention after 10 minutes rest (Lagerspetz & Kivivuori, 1970). The crayfish escape response decreases rapidly to light presentations (Chow & Leiman, 1972) and to pinching of the abdomen (Krasne & Woodsmall, 1969). There was 60 % recovery after 8 hours (Krasne & Woodsmall, 1969). Waning of an escape response in a fiddler crab occurred rapidly and dishabituated easily (Walker, 1972).

One outstanding characteristic of the above studies is that an

orientation response during various behavior sequences is the last response to habituate. This suggests the possibility of independence of underlying mechanisms, processes etc., and that the rate of habituation may be characteristic of the response (cf. Hinde, 1970b; Ratner, 1970). There is also some suggestion from the above and the review to follow that defensive behaviors may be more likely to recover and show minimal retention (with one or two exceptions), while responses toward a prey may recover and show longer retention.

Phylum: Chordata Subphylum: Vertebrata

Class: Osteichthyes. The "tail-flip" escape response of the goldfish, Carassius auratus, elicited by pressure waves produced by tapping the side of an aquarium, wanes within 40 trials (10 trials/day), while an orienting response to the same stimulus wanes more slowly (Rodgers, Melzack & Segal, 1963). The tail-flip response habituated slower to simultaneous presentations of a tap and a visual stimulus (more indicative of a predator) than to either stimulus alone. A fear response (i.e., freezing and descending) of C. auratus to an intense stimulus waned within 30 trials and dishabituated with light onset (Olson & May, 1973). The fleeing ("jerk") response of the guppy, Lebistes reticulatus, to repeated presentation of a shadow decrements within 40 trials and completely recovers after 2 days, but with 60 % recovery in 2 hours (Russell, 1967). A freezing response waned slower. As in goldfish, orienting responses continued after the waning of the fleeing response. The tail-flip (Rodgers et al., 1963) and fear response

(Olson & May, 1973) of goldfish and the fleeing response of the guppy (Russell, 1967) dishabituated with the presentation of a novel stimulus.

The predatory response (biting) of C. auratus and the paradise fish, Macropodus opercularis, towards live brine shrimp habituated within 10 minutes and across 6 days (Peeke & Peeke, 1972). Recovery was incomplete after 5 and 10 days of rest, with C. auratus recovering more than M. opercularis. No dishabituation occurred with the presentation of a novel stimulus.

From the above, it seems that some of the defensive behaviors of fish habituate and recover quickly, while feeding responses wane rapidly but recover slowly. Again, an orientation response is the slowest to habituate.

The habituation of intraspecific aggression has been most extensively studied in teleost fish. The response components of the threat display of the Siamese fighting fish, Betta splendens, wane at different rates (Clayton & Hinde, 1968; Figler, 1972; Peeke & Peeke, 1972; Shapiro & Shuckman, 1971). The same response component may wane at different rates to different eliciting stimuli (Figler, 1972; Shapiro & Shuckman, 1971) and recover at different rates (Figler, 1972). Different responses (e.g., biting, gill cover extension) habituate and recover at different rates (Clayton & Hinde, 1968; Peeke & Peeke, 1970).

Bites of the three-spined stickleback, Gasterosteus aculeatus, directed at conspecifics exposed for short periods of time wane across days (Peeke, Wyers & Herz, 1969) and within longer sessions (Peeke & Veno, 1973). Bites habituate faster than "charges" made

at a stimulus, while orientation responses were more resistant to waning (Peeke, 1969).

The aggressive display and biting of the convict cichlid, Cichlasoma nigrofasciatum, towards a conspecific wane at different rates (Gallagher, Herz & Peeke, 1972; Peeke, Herz & Gallagher, 1971). The display recovered slowly after many days of testing, while bites showed minimal or no recovery (Peeke et al., 1971).

The aggressive display of M. opercularis shown towards a conspecific or mirror image waned within and across days and was slow to recover (Brown & Noakes, 1974).

Habituation is considered to be a means of reducing aggression between territorial conspecifics (Peeke & Peeke, 1973; Peeke & Veno, 1973), which allows for the continuation of other activities. Slow recovery and long lasting retention (e.g., Clayton & Hinde, 1968; Brown & Noakes, 1974; Peeke et al., 1971) and the stimulus specificity of habituation (Peeke & Veno, 1973) support the above contention. The differential rates of waning of the components of a response to the same stimulus, of one response to different stimuli and of different responses to the same stimulus and the differential recovery rates suggest the possibility of different control systems underlying habituation of aggression in the above studies.

Class: Amphibia. The wiping reflex elicited by tactile stimulation repeatedly applied to the skin of a frog increases rather than wanes (Franzisket, 1963), unless stimulation is applied to the exact same spot (Kimble & Ray, 1965). The the latter case, decreased responding occurs slowly across days. Recovery of a wiping reflex in a toad may reach 56 % in 1 hour and proceed more slowly

thereafter (Kuczka, 1956 in Hinde, 1970a). A frog or a toad's orientation (turning the body) towards a prey habituates rapidly with 60 % recovery after 10 minutes of rest (Ewert, 1967 in Goodman & Weinberger, 1973; Ewert & Ingle, 1971) and dishabituates easily (Ewert & Ingle, 1971). Striking at a prey dummy waned within 5 minutes (Ingle, 1973). The response components of the orienting reflex of the mud puppy, Necturus maculosus, wane at different rates (Goodman & Weinberger, 1973).

Class: Reptilia. Of all the vertebrate Classes reviewed, habituation has been least investigated in Reptilia. The few systematic studies available are of turtles, particularly the red-eared turtle, Pseudemys scripta.

The visual alarm reaction (head withdrawal) of P. scripta to an enlarging shadow (an approaching predator) required days to habituate to criterion (Hayes & Saiff, 1967; Ireland, Hayes & Ladden, 1969). Some retention was evident after 10 days. The optomotor response (moving the entire body) of P. scripta did not wane to a field of moving stripes (Hayes & Ireland, 1972), while head and eye nystagmus rapidly waned within 6 minutes with some recovery after 2 minutes of rest and complete recovery after 24 hours (Hayes, Hertzler & Hogberg, 1968). Head turning of the box turtle, Terrapene carolina, elicited by repeated body rotation did not habituate (Crampton & Schwam, 1962).

Class: Aves. The heart-rate response (an orienting reaction) of pigeons to an initial presentation of a light is a cardioacceleration (contrary to the human literature, see Graham & Clifton, 1966) that rapidly wanes within 10 trials and remains at a low

level, while a small acceleratory component is more persistent (Cohen & Macdonald, 1971). The exploratory behavior of chickens, as measured by activity in an open-field, decreases within 10 minutes but increases across days (Candland & Nagy, 1969) contrary to data on exploratory behavior in rodents (see below).

The fear responses of mallard ducks to a model of an aerial predator habituated within 40 trials (Melzack, Penick & Beckett, 1959), while orientation responses to the same stimulus failed to habituate after 2000 presentations (Melzack, 1961). Fear responses of the bobwhite quail, Colinus virginianus, habituated rapidly to a live predator, while orienting responses increased (Martin & Melvin, 1964). Freezing also rapidly habituated with brief daily spaced (Gardner & Melvin, 1971) or massed trials (Melvin & Cloar, 1969). With massed trials, retention of habituation was evident after 18 days of rest (Melvin & Cloar, 1969). Several different anti-predator responses of the ring dove, Streptopelia risoria, wane at different rates. (Vowles & Prewitt, 1971). Escape or fleeing responses required fewer trials to habituate than aggressive (pecking and wing-slapping) or defensive (wing-raising, leaning) reactions. Defensive reactions waned the slowest. An orientation response towards the stimulus was maintained. The habituation and recovery of the mobbing response of the chaffinch, Fringilla coelebs, towards a predator seems to involve multiple incremental and decremental processes with differing time courses (Hinde, 1954a, 1954b, 1960). The "chink" call habituated to zero within 30 minutes and rapidly recovered within 15-30 minutes with minimal recovery thereafter, suggesting some permanent long-term decrement (Hinde, 1954a).

There was evidence of short- and long-term incremental processes that interacted with short- and long-term decremental processes (Hinde, 1954a, 1954b, 1960).

The escape response of chickens, measured as the amount of activity elicited by the shadow of a predator, habituated within 10-12 trials and recovered in 2-3 hours (Hirsch, Lindley & Tolman, 1955).

The duration of tonic immobility of chickens slowly decreased across days with repeated testing but showed minimal or no decrement within a single session (Gilman, Marcuse & Moore, 1950; Ratner & Thompson, 1960). After waning, the duration of tonic immobility increased (dishabituated) with a change of experimenter, location or method of induction (Gilman et al., 1950). Other studies of tonic immobility (e.g., Gallup, Nash & Ellison, 1971; Gallup, Nash, Potter & Donegan, 1970) suggest that tonic immobility may be an innate fear reaction that has evolved as a response to a predator and which enhances survival through a reduction in movement.

The duration of fixating on a mildly fear provoking stimulus (i.e., a mealworm) rapidly declined in young junglefowl chicks, while the number of bouts of fixating remained constant (Hogan, 1965). The pecking response of 2-day old herring gull chicks (a food eliciting and gathering response) towards different colored stripes of paper presented for 15 seconds every 15 seconds habituated within 12-22 trials, while an orienting response was maintained (Nyström, 1973). The pecking response dishabituated and completely recovered in 3 hours.

The aggressive response of territorial male white-crowned sparrows, Zonotrichia leucophrys, to the playback of conspecific songs slowly habituated (Petrinovich & Peeke, 1973). The number of flights and songs of territorial males gradually waned across 80 trials. Recovery was substantial after 70 minutes of rest, with some evidence of retention.

The sexual performance level of male Japanese quail, as measured by the number of cloacal contacts, declined rapidly within 10 minutes and was not significantly affected by the introduction of a new female (Schein & Carter, 1972), which is unlike the findings for mammals (e.g., Wilson, Muehn & Beach, 1963).

The habituation of post-rotational nystagmus (head turning elicited by rotating the body) in pigeons was slow to recover and was retained for weeks (Fearing, 1940, 1941).

The minimal or no habituation of an orienting response to a predator or prey agrees with previously mentioned studies in mollusks, arthropods and fish. It is not clear at this time whether the long-term retention of habituation of responses to a predator in some instances (i.e., Balderrama & Maldonado, 1971; Hinde, 1954a, 1954b; Melvin & Clear, 1969) is due to the length of testing, the constancy of the experimental situation or the use of the specific predator of the species.

Class: Mammalia. Order: Carnivora. The habituation of nystagmus elicited by repeated body rotation wanes rapidly in cats (Brown, 1965; Collins, 1964, 1969; Crampton & Schwam, 1962) with some retention after 2 weeks (Brown, 1965).

Exploratory behavior of cats, measured by activity in an open-

field, decreased within a 10 minute session, but remained constant across days (Candland & Nagy, 1969).

The earlier components of the prey catching behavior of cats wanes more slowly and recovers more quickly than later ones (Leyhausen, 1965 in Hinde, 1970b).

Order: Rodentia. An orienting reaction of rats to a "distress cry" (Zeiner & Peeke, 1969) or a tone (File, 1973b; File & Russell, 1972; Leaton, 1974) presented during drinking rapidly habituated, and was retained for many days. Habituation to a tone was independent of habituation to a light (File & Russell, 1972; Leaton, 1974). Orienting reactions of mice to tones rapidly habituated (Scourse & Hinde, 1973).

Exploratory behaviors have been extensively studied in rodents, particularly in rats and mice (cf. review by Archer, 1973). Locomotor exploratory behavior in a novel environment habituates rapidly within brief sessions and across days, in rats (Hine & Paolino, 1972; Montgomery, 1951, 1953a, 1953b; Pare, 1964; Thompson, 1953; Welker, 1959; Williams, Zerof & Carr, 1962; Zimbardo & Montgomery, 1957), in mice (Blizard, 1971; Brookshire & Rieser, 1967; Candland & Nagy, 1969; Goodrick, 1973; Hughes, 1969), in gerbils (Bols & Wong, 1973; Glickman & Hartz, 1964; Oldham & Morlock, 1970; Thompson & Lippman, 1972; Wilz & Boulton, 1971) with evidence of long-term retention (Denny & Leckart, 1965; O'Brien & Corman, 1970) and of age related changes (Bronstein, 1972, 1973; Feigley, Parsons, Hamilton & Spear, 1972; Furchtgott, Wechkin & Dees, 1961; Parsons, Fagan & Spear, 1973; Valle, 1971), while other responses change differently at the same time. Within a session, sniffing (orienting) decreases

(Berlyne & Slater, 1957; Bindra & Spinner, 1958; Furchtgott et al., 1961; Huges, 1969; Woods, 1962) while grooming increases (Bindra & Spinner, 1958; Bolles, 1960; Doyle & Yule, 1958; Horvath, Kirby & Smith, 1971; Valle, 1971; Woods, 1962). With 10 minutes or more exposure to a novel environment, heart-rate decreases within a session and fully recovers across days (Candland & Nagy, 1969; Candland, Pack & Matthews, 1967), while with briefer sessions heart-rate may increase within and across days (Hine & Paolino, 1972). With repeated handling, heart-rate decreases within 30-60 minutes and fully recovers across days (Black, Fowler & Kimbrell, 1964; Blizard & Weltz, 1971). Exploratory behaviors enable an animal to become "familiar" with its environment and to spend less time recognizing or identifying a familiar situation and to continue other activities (Berlyne, 1960). If this is so, it makes sense then that certain exploratory behaviors would wane rapidly and be retained for long periods.

The acoustic startle reflex (a defensive behavior) of rats may habituate rapidly (Hoffman & Fleshler, 1963; Moyer, 1963), moderately fast (Davis, 1970a, 1970b, 1972; Prosser & Hunter, 1936; Wilson & Groves, 1973) or slowly (Hoffman, Marsh & Stein, 1969) depending upon the intertrial interval. There is some evidence for long-term retention (1-3 weeks) of habituation (Davis, 1972; Korn & Moyer, 1966; Moyer, 1963). Heart-rate during acoustic startle waned within a session and completely recovered between days (Korn & Moyer, 1966). Contrary to acoustic startle, an air-puff-elicited startle reflex in rats did not habituate (Galvani, 1970). The waning of acoustic startle in guinea pigs (Dodge & Louttit, 1926) may

have been the result of replacement of gross body movements by a pinna reflex (Burnham, 1939). As in rats (e.g., File, 1973b), an orienting reaction to a sound rapidly habituated in guinea pigs and did not recover after 4 days of rest (Miller & Murray, 1966). The duration of tonic immobility in guinea pigs waned slowly (Baynard, 1957). The optokinetic response of guinea pigs did not habituate (Hayes & Ireland, 1969; Ireland & Hayes, 1973). The sexual behavior of male guinea pigs waned within 10-20 minutes (Grunt & Young, 1952; Young & Grunt, 1951) and increased with the introduction of a new female (Grunt & Young, 1952).

The retrieval response of young mice, licking of the young and nestbuilding decrement at different rates (Noirot, 1964, 1965), with retrieval of young waning the slowest (Noirot, 1965; Zippelius & Schleidt, 1956 in Thorpe, 1963).

The head-shake response of rats elicited by an air-puff directed into the ear wanes rapidly (Askew, 1970; Askew, Leibrecht & Ratner, 1969; Kramer & Wright, 1971) and completely recovers within 24 hours with some retention of habituation after 6 hours (Askew et al., 1969; Leibrecht & Askew, 1969). Head-shake response also dishabituates (Leibrecht, 1973). Head-shake response of the chinchilla, Chinchilla lanigera, did not completely recover after 4 days nor dishabituate (Leibrecht & Kemmerer, 1974). Several different responses waned at different rates (Leibrecht & Kemmerer, 1974).

In rodents, orienting and exploratory behaviors appear to wane rapidly with long-term retention of habituation. Habituation of acoustic startle shows long-term retention, while an air-puff

startle shows no habituation. Head-shake response may fully recover within 24 hours in rats but not in chinchilla. Decreases in heart-rate fully recover in 24 hours, while retrieval of young by parents shows minimal habituation.

Order: Primates. The heart-rate component of the orienting reaction of monkeys wanes rapidly (Weisbard & Graham, 1971).

Locomotor exploratory behavior of monkeys wanes within 20 minutes and fully recovers in 24 hours (French, 1959; French & Harlow, 1955) unlike rodents.

The contacting or touching of novel objects by monkeys wanes within 6-10 minutes and across days (Carr & Brown, 1959; Welker, 1956a, 1956b) unless contact is very brief (Menzel, Davenport & Rogers, 1961), while manipulation of mechanical puzzles declined very slowly within a single session (Harlow, 1950). Recovery of manipulation was complete in 24 hours (Harlow, 1950; Harlow, Blazek & McClearn, 1956), while the number of attempts at the puzzles remained constant (Harlow, 1950).

The opportunity to visually explore objects did not wane in monkeys tested for hours or days (Butler, 1953, 1964; Butler & Alexander, 1955; Butler & Harlow, 1954; Gammon, Singer & Michels, 1972; Symmes, 1959), unless more responses are allowed which then produces a decrement in 25 minutes and which fully recovers within 24 hours (Rabedeau & Miles, 1959).

Fear responses of monkeys and chimpanzees to live snakes waned rapidly within and across days (Green, 1965; Haslerud, 1938; Joslin, Fletcher & Emlen, 1964; Murray & King, 1973; Schiller, 1952; Wolin, Ordy & Dillman, 1963).

The exploration (contact) of a novel object declined rapidly in marsupials (Russell & Pearce, 1971), prosimians (Ehrlich, 1970; Jolly, 1964) and other Classes (Glickman & Sroges, 1966).

Most of the habituation studies of humans stem from Sokolov's (1960) theory and deal with autonomic nervous system responses related to the orienting reaction (OR) (cf. Graham, 1973). An OR to a novel stimulus is composed of behavioral changes (e.g., eye movements, head movements, body movements, etc.) that focus attention towards the stimulation, and physiological changes (e.g., galvanic skin response, heart-rate, respiration, vasoconstriction, vasodilation) that sensitize the organism to incoming information and prepare it for action (Sokolov, 1960, 1963a, 1963b). As a mechanism for paying attention to a novel stimulus, an OR would be of survival value (Lynn, 1966). A generalized OR to a novel stimulus rapidly habituates and is replaced by a more localized OR in the cortical area of the sensory modality being stimulated. With repeated stimulation, an OR can be replaced with an adaptive response that reduces stimulation and is resistant to habituation. With more intense stimulation, a defensive response (e.g., fleeing, freezing, fighting) would be elicited which protects the organism and is slow to habituate (Sokolov, 1960, 1963a, 1963b). If the presentation of a novel stimulus has no consequences for an organism, the OR rapidly habituates. If the stimulus has consequences an OR will be replaced by an adaptive or defensive reaction depending upon the circumstances.

The galvanic skin response is the measure most frequently used, along with heart-rate changes, in studies of OR habituation (Graham

& Clifton, 1966). In general, representative findings indicate that the OR habituates rapidly (Bishop & Kimmel, 1969; Germana, 1968; Greene & Kimmel, 1966; Lovibond, 1969; Kimmel & Goldstein, 1967; Koepke & Pribram, 1966; Zimny & Schwabe, 1966), dishabituates (Zimny, Pawlick & Sauer, 1969; Zimny & Schwabe, 1966) and shows long-term retention of habituation (Bishop & Kimmel, 1969; Kimmel & Goldstein, 1967).

Critique of the Dual-Process Theory of Habituation. As mentioned earlier, species and response diversity in habituation would be contrary to a general process approach. A systematic relationship between the course of habituation and the functional significance or nature of the response or response system would also be contrary to the general process approach exemplified by Thompson and Spencer (1966) and Groves and Thompson (1970). After reviewing the behavioral response habituation literature, it is evident that there are important species and response differences (and similarities) in habituation and that the course of habituation may be related to the functional significance or nature of the response system. This species and response diversity and similarity in habituation and the relationship between the course of habituation and the nature of the response are summarized next.

Orienting reactions to innocuous stimuli habituate rapidly in birds (Cohen & MacDonald, 1971) and habituate rapidly and recover slowly in rodents (File, 1973a, 1973b; Miller & Murray, 1966) and primates (Bishop & Kimmel, 1969; Kimmel & Goldstein, 1967; Weisbard & Graham, 1971). In contrast, orienting reactions wane slowly during responses elicited by a possible predator (Melzack, 1961;

Rodgers et al., 1963; Russell, 1967; Vowles & Prewitt, 1971), prey or food source (Drees, 1952; Messinger, 1973; Nyström, 1973; Precht & Freytag, 1958; Szlep, 1964; Wells & Wells, 1957; Wolda, 1961), a mate (Barrass, 1961) or conspecific (Peeke, 1969). Locomotor exploratory behaviors wane rapidly and recover slowly in rodents (Blizard, 1971; Bols & Wong, 1973; Brookshire & Rieser, 1967; Montgomery, 1951, 1953a, 1953b; O'Brien & Corman, 1970; Pare, 1964; Welker, 1959; Zimbardo & Montgomery, 1957), while recovery is complete within 24 hours in cats and fowl (Candland & Nagy, 1969) and monkeys (French, 1959; French & Harlow, 1955). Some investigatory responses wane rapidly and recover slowly in monkeys (Carr & Brown, 1959; Welker, 1956a, 1956b) and other primates (Ehrlich, 1970; Glickman & Sroges, 1966; Jolly, 1964; Russell & Pearce, 1971), while other investigatory responses in monkeys wane slowly or not at all (Butler, 1953; Butler & Alexander, 1955; Butler & Harlow, 1954; Harlow, 1950).

Escape responses (e.g., fleeing, withdrawal, contraction) wane rapidly in some species (Applewhite, 1969, 1971; Clark, 1960a; Hirsch et al., 1955; Krasne, 1965; Krasne & Woodsmall, 1969; Melzack et al., 1959; Pinsker et al., 1973; Rodgers et al., 1963; Russell, 1967), but not in others (Hayes & Saiff, 1967; Ireland et al., 1969; Ratner & Gardner, 1968; Rushforth, 1965; Rushforth et al., 1963). Some freezing responses (e.g., freezing, startle) wane rapidly (Gardner & Melvin, 1971; Hoffman & Fleshler, 1963; Moyer, 1963) and are retained over long periods (Davis, 1972; Korn & Moyer, 1966; Melvin & Clear, 1969), while other freezing responses wane slowly or not at all (Baynard, 1957; Galvani, 1970; Gilman et

al., 1950; Ratner & Thompson, 1960). Striking at a prey or food source decrements rapidly (Ingle, 1973; Maldonado, 1972; Messinger, 1973; Nyström, 1973; Peeke & Peeke, 1972; Rilling et al., 1959; Wolda, 1961) with evidence of long-term retention (Maldonado, 1972; Messinger, 1973; Peeke & Peeke, 1972; Szlep, 1964; Wells & Wells, 1957), while the orienting component of feeding behaviors wanes the slowest (Drees, 1952; Hogan, 1965; Maldonado, 1972; Messinger, 1973; Nyström, 1973; Precht & Freytag, 1958; Szlep, 1964; Wells & Wells, 1957; Wolda, 1961). Some reproductive behaviors wane slowly (Noirot, 1963, 1965), while others wane rapidly (Grunt & Young, 1952; Schein & Carter, 1972; Young & Grunt, 1951). Some general maintenance behaviors decrement slowly (Franzisket, 1963; Kimble & Ray, 1965), while others wane rapidly (Askew et al., 1969; Brown, 1965; Collins, 1964, 1969; Crampton & Schwam, 1962). Recovery of general maintenance behaviors occurs rapidly in some instances (Askew et al., 1969) and slowly in others (Brown, 1965; Fearing, 1940, 1941; Leibrecht & Kemmerer, 1974).

In various species, habituation of a response to one stimulus is unaffected by habituation of the same response to another stimulus (Applewhite, 1971; Clark, 1960a, 1960b; Cook, 1971; Nicol, 1950; Wood, 1973), although this is not always the case (Clark, 1960a). Components of a response or response sequence may undergo different changes during habituation (Clayton & Hinde, 1968; Davis, 1948; Davis & Van Liere, 1949; Figler, 1972; Gardner, 1968; Peeke & Peeke, 1970). The habituation of exploratory behavior (Bronstein, 1972, 1973; Feigley et al., 1972; Furchtgott et al.,

1961; Parsons et al., 1973; Valle, 1971; Welker, 1956b, 1956c) and defensive behaviors (Askew & Kurtz, 1974; Ratner & Thompson, 1960) may change with age. Waning of reactions directed at a predator may be retained for days (Balderrama & Maldonado, 1971; Hindé, 1954a, 1954b, 1960). While various defensive (Gardner, 1968; Gilman et al., 1950; Hollis, 1963; Olson & May, 1973; Rodgers et al., 1963; Rushforth et al., 1963; Russell, 1967; Walker, 1972), feeding (Ewert & Ingle, 1971; Maldonado, 1972; Nyström, 1973) and reproductive (Beach & Jordan, 1956; Grunt & Young, 1952; Wilson et al., 1963) behaviors dishabituate easily, other defensive (Wood, 1970b), feeding (Peeke & Peeke, 1972), reproductive (Schein & Carter, 1972), orienting (Zimny & Schwabe, 1966) and general maintenance (Collins, 1967; Leibrecht, 1973; Leibrecht & Kemmerer, 1974) behaviors show minimal or no dishabituation. Other differences could be listed which were not mentioned in the present review. These include differences in potentiation of habituation, below-zero effects, effects of intertrial interval, strength and duration of the stimulus and the shape of habituation curves. However, it should be evident by now that the behavioral response habituation literature is replete with differences, as well as, similarities.

The habituation of a limited number of responses has been investigated within and across species. Differences in experimental situations, species and the number of responses studied suggest a certain amount of caution in making any generalizations concerning the relationship between the course of habituation and the functional significance or nature of the response. However, there are

certain observations that can be made. It appears that an orienting response to a nonsignificant stimulus rapidly habituates and is retained for days. Certain exploratory behaviors (i.e., locomotion, contact) wane rapidly and recover slowly in some Orders but not others. Defensive responses in species possessing a single "multifunctional" response seem to habituate slower and recover more quickly to stimuli that signal the presence of a predator. There is some suggestion that habituation is slower to tactile stimulation than to other stimuli in those same species. In those species with a larger behavioral repertoire, defensive responses seem to habituate moderately fast and fully recover in 24 hours, with a few noted exceptions. Prey catching responses appear to rapidly habituate, with habituation retained for more than 24 hours. The orienting component of defensive and prey catching behaviors seem to habituate last and recover first in contrast to orienting responses to nonsignificant stimuli. It appears that orienting responses during courtship and conspecific aggression wane the slowest, although the evidence is not as strong.

Citing evidence from studies of intact organisms, Hinde (1970b) questioned both the generality of the nine parametric characteristics of habituation given by Thompson and Spencer (1966) and the implication of the similarity of the underlying mechanisms of habituation.

The question arises, however, whether the characteristics listed by Thompson & Spencer are detailed enough either to establish similarities between phenomena at different levels of analysis, or to be much guide to the nature of the mechanisms. Similarities in direction of change are not in themselves sufficient to imply similarities in mechanisms, though they are the more likely to

do so the more detailed the similarities (Hinde, 1970b, p. 35). This problem of the similarity in behavior and physiological mechanisms seems to have been recognized by the dual process theorists (Thompson et al., 1973), but it has not altered their approach or assumptions.

To briefly summarize, Thompson and Spencer (a) abstracted from the behavioral response habituation literature certain similarities that may characterize response habituation in a wide variety of species and responses, (b) demonstrated that similar characteristics (as those abstracted from the literature) may also occur at the neuronal level and suggested, therefore, that (c) similar mechanisms may underly habituation across various species and responses. It is here argued that Thompson and Spencer's review, although well done, is limited in that neither the diversity in response habituation nor the influence of the response system on the course of habituation have been adequately represented. The diversity in response habituation and the possible influence of the response system have been documented in Chapter I. What appears to be a needed addition is an approach that deals with diversity (and similarity) in habituation. Such a possible alternative approach, outlined next, attempts to deal with similarities and differences by viewing habituation within an evolutionary context.

An Alternative Approach

A species' behavioral repertoire has an evolutionary history (Hinde & Tinbergen, 1958; Lorenz, 1950; Mayr, 1958, 1963; Simpson, 1958a, 1958b; Thorpe, 1963; Tinbergen, 1951). In the same sense,

response habituation may be considered to have evolved (Hinde, 1970a; Lorenz, 1965, 1969; Petrinovich, 1973; Thorpe, 1963; Wyers, Peeke & Herz, 1973). Applying this consideration to habituation, Askew and Leibrecht (1973) suggest that "Responses habituate because selection pressures favoring the development of habitulatory mechanisms and processes have acted to modify the mechanisms and processes underlying the responses themselves (p. 16)." Perhaps, those responses, and their underlying system(s), were selected which enhanced survival through reduced responding, possibly to biologically irrelevant stimuli (Lorenz, 1965; Thorpe, 1963).

According to Askew and Leibrecht, the behavioral similarities (i.e., Thompson & Spencer, 1966) in the habituation of the same or similar response across species implies the operation of similar selection pressures acting on those species. The physiological mechanisms, structures or processes underlying the habituation of those responses may or may not be similar in ways other than function. Askew and Leibrecht suggest that the system(s) underlying the response are more likely to be the same if the species are closely related and the response is homologous. If the response developed in a parallel fashion (similar selection pressures), the system(s) underlying the response would probably be similar. If the response was acquired in unrelated species through convergent evolution, the system(s) underlying the response would most likely be similar in function, although they need not be. The similarities in the habituation of various responses within the same species may also imply the operation of similar selection pressures acting upon those responses. The system(s) underlying the habituation of

those responses may or may not be similar in ways other than function. Likewise, differences in the habituation of responses across and within species may imply the operation of different selection pressures acting on those species and responses. The systems underlying habituation in those species and responses may or may not be different. It should be pointed out, however, that while similarities in habituation may be the result of different processes, mechanisms, structures, etc., differences in habituation may be due to very similar mechanisms, processes, structures, etc. At present, the extent of any differences in the systems underlying habituation across various species and responses is little known.

The adequacy of Askew and Leibrecht's approach may, of course, be questioned. The important point, however, is that it attempts from a different perspective to interpret and assimilate similarity and diversity in habituation. In addition, the emphasis of the general process theories on the similarities in habituation has not encouraged systematic comparative investigations of habituation as evidenced by the scarcity of such studies (e.g., Clark, 1960b; S. Evans, 1969a, 1969b), while Askew and Leibrecht encourage comparative studies as a necessity. The within-species comparative method employed in the present dissertation and outlined below was derived from Askew and Leibrecht's orientation.

Implications for Comparative Research

Although implications of the above approach may apply equally as well to comparative physiological investigations of habituation,

the present dissertation is concerned with the development of a comparative behavioral methodology not previously employed in studies of habituation.

Comparative Behavioral Investigations. There are two approaches comparative investigations could take: interspecific and intraspecific.

Interspecific. Comparisons between species has been the method typically used in comparative psychology (Beach, 1950; Bitterman, 1960, 1965a; Hodos & Campbell, 1969; Waters, 1960). To illustrate, various species have been compared on serial reversal and probability learning (Bitterman, 1965a, 1965b), learning set performance (Doty, Jones & Doty, 1967; Harlow, 1959; Jolly, 1964), active avoidance (Boice, 1970; Pearl, 1963), illness-induced aversion (Wilcoxon, Dragoin & Kral, 1971) and exploratory behavior (Glickman & Sroges, 1966) among others. The few interspecies comparisons of behavioral response habituation have been of the withdrawal response in polychaetes (Clark, 1960b; S. Evans, 1969b) and feeding behaviors (Peeke & Peeke, 1972; Rilling et al., 1959).

Comparisons between species may take two forms: "phylogenetic and/or analysis of adaptation" method (Hodos & Campbell, 1969). An understanding of the historical evolutionary development of habituation would require the study of related groups (phylogenetic method). An understanding of habituation as an adaptation to specific problems of survival would require the study of habituation of analogous behaviors in divergent groups (analysis of adaptation). The problems of (1) determining relatedness between species, (2) prior knowledge of whether the responses are homologous or non-

homologous, primitive or specializations, (3) the nonexistence of living representatives of truly ancestral forms and (4) the comparability of various responses across species (e.g., sensory-motor equipment, motivation) make conclusions and investigations about the evolution of habituation somewhat difficult. It seems reasonable to formulate at this time an approach that could lead to productive comparative research and could avoid some of the problems just mentioned. The within-species comparative method, outlined next, offers such an approach.

Intraspecific. Investigating similarities and differences in habituation of various responses within a single species is a comparative method that has not been systematically utilized in studies of behavioral habituation. A within-species comparative approach has been used to a limited extent in studies of the classical conditioning of taste aversion (Garcia & Koelling, 1966; Garcia, McGowan & Green, 1972), effects of rewarding and punishing the same behaviors (Bolles & Seelbach, 1964) and avoidance learning (Shettleworth, 1972). The only within-species comparative behavioral studies of habituation have been those investigating the characteristics of habituation of a single response elicited by various stimuli. Studies that best illustrate this single response approach are those of the habituation of defensive behaviors of invertebrates (Appelwhite, 1969, 1971; Askew & Kurtz, 1974; Clark, 1960a, 1960b; S. Evans, 1969a, 1969b; Nicol, 1950; Wood, 1970b, 1973) and aggressive behavior in fish (Figler, 1972; Shapiro & Shuckman, 1971). The species, responses and characteristics of habituation studied in this dissertation are

described next.

Species Studied

Because of the paucity of information of behavior in reptiles and of habituation in particular, the lizard Anolis carolinensis (commonly referred to as the "American chameleon") was employed in the present dissertation. The few systematic studies of habituation in reptiles have been only of turtles (see review, Chapter I) and thus studies of A. carolinensis will help fill the gap in our knowledge of behavior in reptiles. Some advantages of using A. carolinensis are: (1) the background information available on geographical distribution (Cochran & Goin, 1970), ecology and morphology (Collette, 1961), habitat (Schoener, 1968), social and courtship behavior (Crews, 1973; L. Evans, 1936a, 1936b; Greenberg & Noble, 1944; Noble & Bradley, 1933), effects of light and temperature on growth (Dessauer, 1955; Fox & Dessauer, 1957, 1958a; Michael, 1972) and reproduction (Fox & Dessauer, 1958b; Licht, 1967, 1969, 1971), preference for prey (Askew, Musumeci, Sloane & Stephan, 1970; Burghardt, 1964; Sexton, 1964; Sexton, Hoger & Ortleb, 1966; Schoener, 1968) and escape conditioning (Powell, 1967), (2) a relatively limited behavioral repertoire, (3) minimum maintenance needs and space requirements and (4) availability of related species for future comparative research.

Responses Studied

From pilot data, three responses were chosen for study.

1. Dewlap Extension. A dewlap extension refers to the distension of the "throat fan", a fold of skin located beneath the

throat of A. carolinensis and many other lizard species (Cochran & Goin, 1970; Smith, 1946; Stebbins, 1966). In A. carolinensis, dewlap extension is involved in social and courtship behavior (Crews, 1973; L. Evans, 1936a, 1936b; Greenberg & Noble, 1944; Noble & Bradley, 1933), conspecific fighting and territorial defense (L. Evans, 1936a, 1936b; Greenberg & Noble, 1944; Noble & Bradley, 1933). There have been no studies of dewlap extension given to a threatening stimulus (i.e., a possible predator), but A. carolinensis has been noted to flash its dewlap at humans (Gordon, 1956) and at a flying wasp (Meyerricks, 1960). Blue-jays, mockingbirds and cardinals have been noted to prey on A. carolinensis (Gordon, 1956). During pilot studies employing various live birds (e.g., canaries, parakeets, bishop birds, house sparrows) and other live animals (e.g., mice, gerbils, rats and conspecific Anoles), only house sparrows consistently elicited the dewlap response. Dewlap extension may be involved in reactions to predators.

In the context of the present experiments and until future research and field studies are performed, the dewlap response may be considered a defensive reaction which may function (in concert with an open mouth) to ward off a potentially threatening stimulus (i.e., a live bird). An Anole would typically push itself up on four legs, extend its dewlap and open its mouth. Such "threatening" behaviors are not uncommon in other animals (Eibl-Eibesfeldt, 1970). The distended dewlap and open mouth also occur during conspecific fighting and are usually accompanied by "bobbing" (rapid up-and-down head movements) in A. carolinensis

(Greenberg & Noble, 1944). Bobbing movements were never observed in any of the experiments, which suggests that although the components of the response (dewlap distension, open mouth) are similar to those found in intraspecific fighting, the two are functionally distinct. Since the dewlap response is involved in courtship behavior, intraspecific fighting and may be involved in defensive reactions, the dewlap response probably plays a primary role in species survival.

2. Optokinetic Response (OKR). The OKR refers to distinct head and eye movements of an organism when surrounded by a moving scene (typically a field of moving stripes), which serves to stabilize the image of a moving object on the retina (Gibson, 1966; Howard, 1973; Polyak, 1957; Smith & Bojar, 1938; Walls, 1942, 1962). The OKR has been studied in many different species from fruit flies (Mittelstaedt, 1964) and locust (Horridge, 1966b; Shephard, 1974) to crabs (Horridge, 1966a), turtles (Hayes et al., 1968), various reptiles and mammals (Tauber & Atkin, 1968), human infants (Tauber & Koffler, 1966) and adults (Brown, 1966). The OKR is probably important in visually guided behaviors such as locomotion (Tauber & Atkin, 1968), capture of prey and avoidance of fast moving predators. The behavior of Anoles given live house flies to eat is similar to those behaviors elicited in the OKR apparatus (personal observation). Anoles would follow a fly with rapid head movements, walk rapidly after it, jump at and capture the fly with their mouth. In addition to head movements elicited by rotation of the striped cylinder, animals in the present experiments would occasionally walk rapidly towards the stripes, follow

the stripes by walking alongside them and jump "at" the stripes. Whether these similarities in behavior are more apparent than real remains to be explored. For the moment, however, the OKR can be considered an orientation response involved in the capture of prey and other visually guided behaviors. Given the arboreal and insectivorous habits of A. carolinensis (Cochran & Goin, 1970; Collette, 1961; Schoener, 1968; Sexton, 1964; Sexton et al., 1966; Smith, 1946), the OKR probably plays an important role in species survival.

Habituation of OKRs has been studied in various species, but there have been relatively few such studies in reptiles. Those studies that are available are of turtles (Crampton & Schwam, 1962; Hayes et al., 1968; Hayes & Ireland, 1972).

3. Swimming Response. The swimming response refers to an animal actively moving while in water. Swimming has been used to study behavioral genetic differences between species of mice (Denenberg, Ross & Blumenfield, 1963; King, 1961; Winston, 1964) and rats (Griffiths, 1960; Wilcock, 1972) and the effects of irradiation (Casarett, 1973), drugs and old age (Kay & Birren, 1958) on rats. Swimming has not been investigated in lizards and, although not aquatic, A. carolinensis has been known to take to water and swim across ponds (Carr, cited in Smith, 1946). The swimming response of A. carolinensis consisted of an animal actively moving during the first part of a trial and then floating spread eagle for the remainder of the trial. Immersion in water is aversive for other species (King, 1961; Wilcock, 1972) and appeared to be

aversive for Anoles since animals would change color several times throughout the experiment and would turn motley.

Characteristics Studied

Since a different experimental procedure was employed in the present dissertation and since a species was used in which habituation had not been previously studied, three major characteristics of habituation were chosen for investigation as follows: (1) intertrial interval, (2) spontaneous recovery and (3) individual differences. Shorter intertrial intervals may result in faster or more pronounced habituation, while an habituated response will recover with rest (Thompson & Spencer, 1966). Individual differences are also considered a major characteristic of habituation (Denny & Ratner, 1970), but individual differences or consistency in habituation across various responses have not been systematically explored (Ratner, 1970). Neither general process theories nor Askew and Leibrecht's (1973) orientation deal specifically with individual differences in habituation even though such differences are theoretically important for both approaches as discussed in Experiment 3.

For each of the three characteristics mentioned above, a separate behavioral experiment was conducted. Each experiment will be found in Chapter III. In the following chapters, the methodology, procedures, results and discussions are presented.

CHAPTER II

GENERAL METHODOLOGY AND PROCEDURE

Subjects

Male and female Anolis carolinensis trapped in Louisiana and purchased from Charles P. Chase Co., Miami, Florida, 33166, were used as subjects for all experiments.

General Maintenance Conditions

Upon arrival, all animals were checked for good physical condition (absence of moles, dryness, kinky tail, activity), measured (snout-vent length), numbered in ink and assigned to a home cage such that within each experiment snout-vent length between groups did not differ. Groups of 20 animals were caged in screen covered wooden boxes, 29-1/2 x 12-3/4 x 17-1/2 in. Each home cage was supplied with branches, artificial leaves, a piece of clear plastic acetate and a plastic container to hold water. Animals were fed live Tenebrio molitor mealworms every 3-4 days. Water was sprinkled twice daily on the leaves, branches and plastic acetate. Water in the plastic containers was changed every 3-4 days. Six 25-watt light bulbs were suspended 21-1/2 in. above the home cages and were kept on a 12-hour light-dark cycle initiated at 0800 hours. Temperature was maintained between 25-27° C. All animals were kept in the laboratory at least two weeks prior to testing. Each animal was periodically checked and unhealthy specimens were replaced.

Apparatus

Experimental Enclosure. The experimental enclosure is depicted in Figure 1. The apparatus used for testing each response was placed within this wooden enclosure (inner dimensions: 15 x 15 x 21 in. high). The inside was painted flat white and the outside flat black. All sides were removable. A removable one-way mirror (7 x 9 in.) was attached to the front panel. The enclosure was equipped with a 15-watt light bulb and an exhaust fan, 4-1/2 x 4-1/2 in., which also provided a masking noise. A pulley system used for the dewlap and swimming apparatus was located on the outside top and side panels of the enclosure. The experimental enclosure rested on two wooden stands (12-1/2 x 18-3/4 x 30 in. high) placed 15 in. apart. The light from the enclosure and a discrimination light mounted on the recording stand provided the only illumination in the experimental room. The noise level within the enclosure that was associated with the operation of each apparatus was determined with a General Radio 1565-B sound level meter.

A Bodine Electric Co., 1/15 HP dc motor and a General Concord reversible variac speed control were used to operate the apparatus for each response. Only the speed of rotation varied.

Dewlap Extension. The dewlap extension apparatus is shown in Figure 2. A clear plastic bird container (5-1/2 in. high, 4-3/4 in. across) covered with a removable white plastic sleeve (7-1/4 in. high, 5 in. across) was placed within a transparent cylinder (5-1/4 in. high, 10 in. across), thereby forming a 2-1/2 in. wide

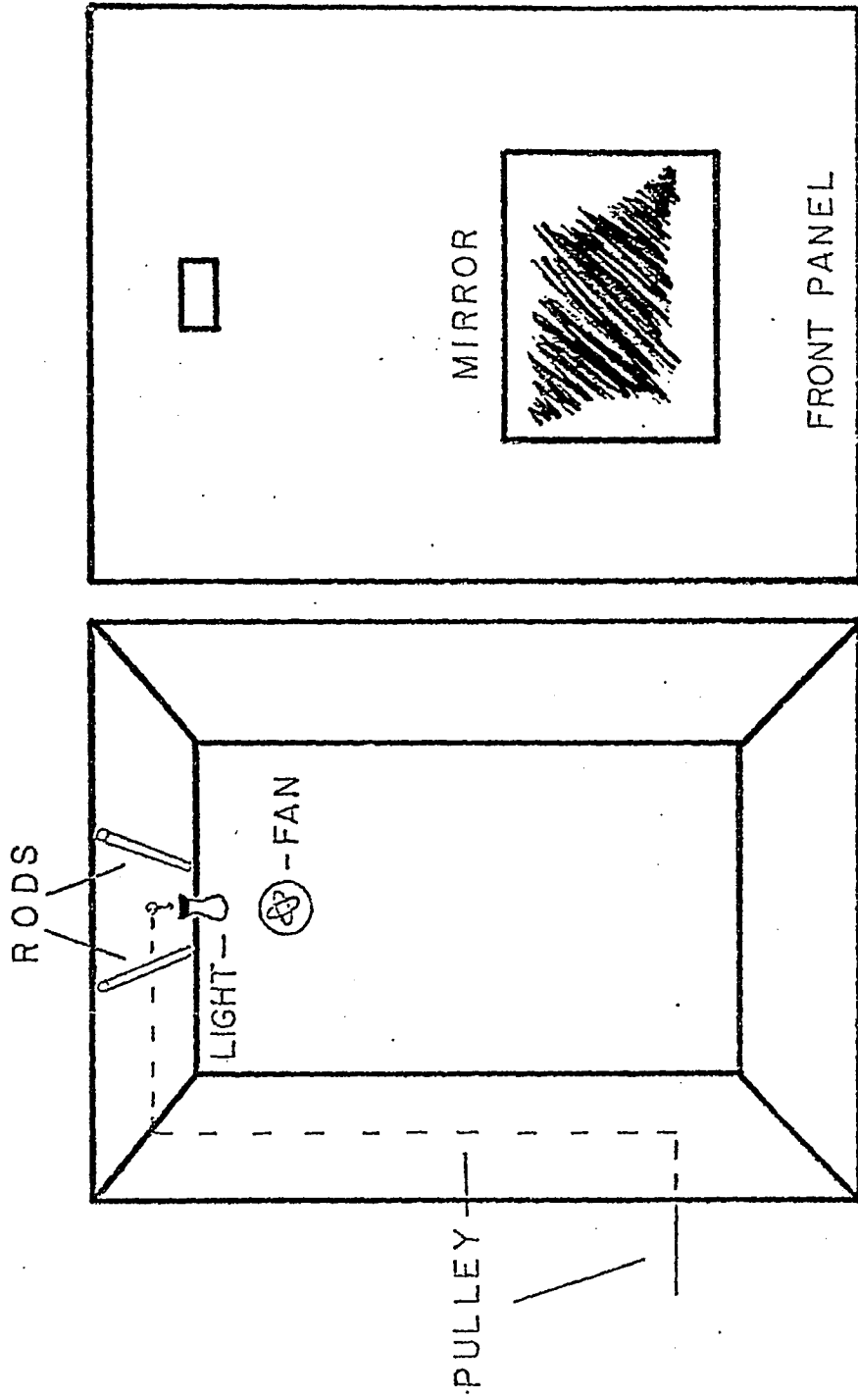


Fig. 1. Experimental enclosure.

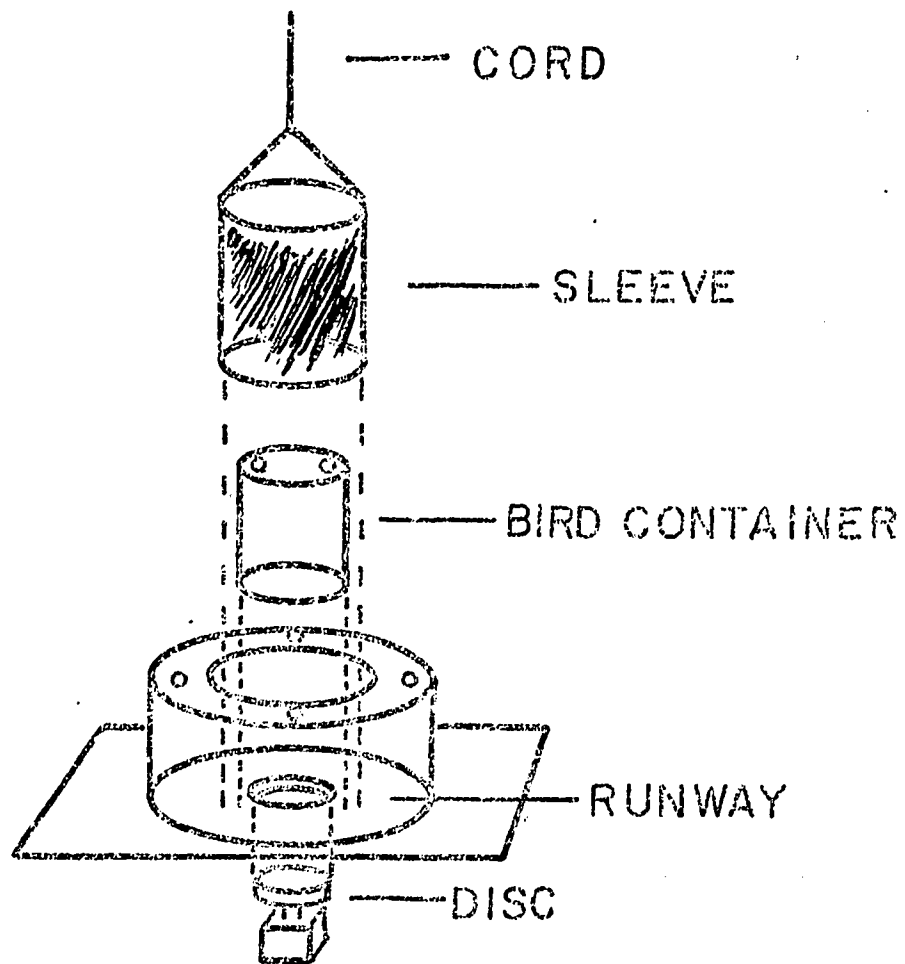


Fig. 2. Dewlap apparatus

x 5 in. high runway. A perforated plastic cover (10-3/4 in. across) with a 5 in. center hole prevented escape and permitted up and down movement of the white sleeve. The dewlap apparatus was mounted on a white wooden platform (17-1/2 x 17-3/4 x 3/4 in. high) and was placed within the enclosure, 3-1/2 in. from the bottom. To expose a stimulus bird, nylon cord tied to the white sleeve was attached via the pulley system to a revolving crossbar on the motor. When the motor turned (4.36 rpm), the white sleeve was raised and lowered exposing a live house sparrow, Passer domesticus. To keep the bird active, a circular wooden disc (3-1/2 in. across, 3/4 in. high) attached to a 10 rpm ac motor, was placed within the bird container. The disc revolved while the bird was exposed. Noise level ranged from 67-70 db.

Optokinetic Response (OKR). The OKR apparatus, motor and variac speed control are depicted in Figure 3. A transparent plastic cylinder (6 in. high, 12 in. across the top and 10-1/2 in. across the bottom) was mounted on an 8-3/4 in. shaft attached to the motor. Twelve stripes of 3/4 in. nonreflective black tape were placed at 2-1/2 in. intervals around the outside of the cylinder. A plastic container, 5-1/4 in. high and 6 in. across, was suspended from rods attached to the top of the enclosure and was centered within the striped cylinder, 1-1/2 in. from the bottom. Animals were placed inside the plastic container. A perforated plastic cover placed over the container prevented escape. The motor and striped cylinder were placed between the two wooden stands such that the striped cylinder extended 10 in. into the

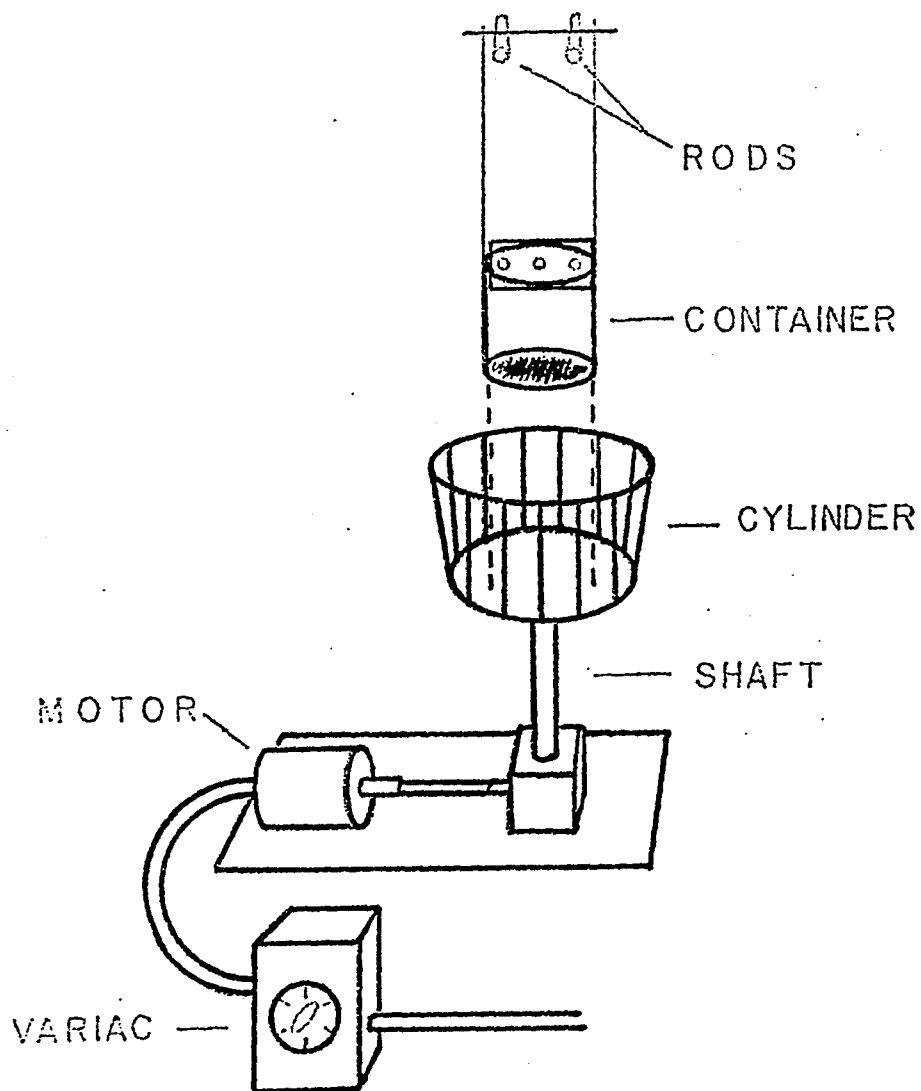


Fig. 3. Optokinetic apparatus.

enclosure. The striped cylinder rotated counterclockwise at 12 rpm. The noise level ranged from 64-66 db.

Swimming Response. Figure 4 illustrates the swimming apparatus. A white plastic bucket, 14 in. high and 11-1/2 in. across, was filled to a depth of 11 in. with 24 hour old tap water and rested on a stand (10-1/2 x 12 x 20-1/4 in. high) located between the two wooden enclosure stands. The bucket extended 4 in. into the enclosure. A perforated plastic platform (10-1/2 in. across, 1/8 in. thick) was attached 4-1/2 in. from the bottom of a steel rod (16-9/16 in. length, 1/8 in. diameter) and served as an elevator platform to lower and raise an animal into and out of the water. To facilitate immersion, six 1/2 oz weights were attached to the underside of the elevator platform. A clear plastic perforated cover (11-3/8 in. across, 1/8 in. thick) resting within the bucket and 1 in. from the top prevented escape. A hole in the center of the cover allowed movement of the rod and the attached elevator platform and a 7/8 in. opening with a sliding cover allowed entrance of an animal onto the elevator platform. Nylon cord tied to the rod was attached via the pulley system to a revolving crossbar on the motor. When the motor turned (4.36 rpm), the elevator platform was lowered or raised out of the water. White petroleum jelly was applied to the inside of the bucket above the water line to prevent animals climbing out of the water. A mirror, 12 x 12 in., attached to the inside rear panel facilitated observation. Noise level ranged from 65-68 db.

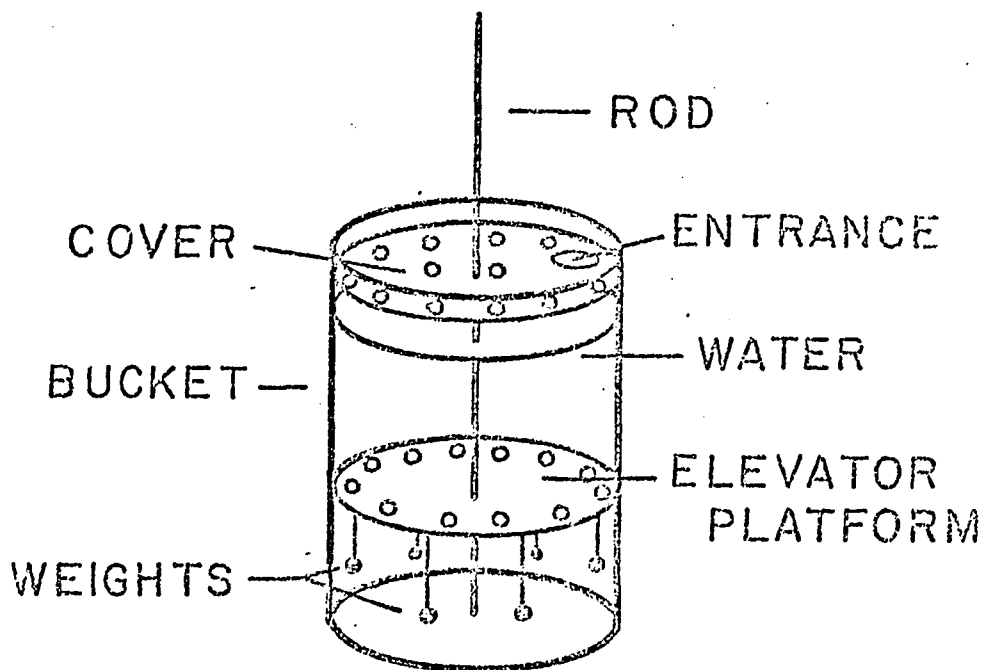


Fig. 4. Swimming apparatus.

Response Measures

As mentioned earlier, the dewlap response refers to the distension of the throat fan. The duration of the dewlap extension per trial was recorded. Occasionally, animals would open their mouth while the dewlap was extended and would direct the open mouth towards the bird. The duration of mouth-open was recorded on those occasions.

The optokinetic response (OKR), as defined here, refers to distinct head movements of an Anole when surrounded by a field of moving stripes. Recorded was the frequency per trial of head following in the direction of rotation of the moving stripes.

The swimming response refers to the amount of time an animal was actively moving while in water.

Reliability of the observations and measurements of the responses were determined by having each of three inexperienced judges and myself observe a different animal an average of 30 trials for each response. Three correlations, one for each judge and experimenter combination, were computed for each response and may be found in Appendix A. A Fisher's Z transformation was employed to compute a mean Pearson product-moment correlation coefficient for each response. The mean Pearson r_s for the dewlap, OKR and swimming responses were +.97, +.96 and +.98, respectively.

General Procedure

At the time of testing, an Anole was removed from its home cage, placed in a white plastic container, carried to the experimental room, placed in the experimental apparatus for 5 minutes

adaptation, tested, removed and returned to its home cage. A stop watch was used to determine all duration measurements. All stimulus presentations and intertrial intervals were programmed with electromechanical equipment, while response measures were recorded by hand. Observations were taken between 0900 and 1900 hours (EST and DST).

A control procedure was introduced in Experiment 1 to determine if the observed decrement was due to effector fatigue or sensory adaptation. Basically, the procedure involved the presentation of another stimulus that elicits the same response that was habituated or changing a feature of the original stimulus and presenting it again. Control procedures were not employed in the other experiments.

Treatment of Data

The habituation curves were analyzed in terms of several dependent variables commonly found in the habituation literature, namely: amount of habituation, percentage decrement, percentage of initial response, rate of habituation, amount of recovery and percentage recovery. The first four variables are defined in the Method section of Experiment 1, while the last two are defined in the Method section of Experiment 2.

CHAPTER III

RESULTS AND DISCUSSION

Experiment 1: Amount and Rate of Habituation:

Effects of Intertrial Interval

Method

Subjects. One hundred and eighty male and female A. carolinensis, divided into nine equal groups (20 per group) of comparable snout-vent length, were randomly assigned to one response and inter-trial interval (ITI) condition.

Procedure. A given animal was tested on one response for 40 trials, each trial of 30 sec duration, with either a 5, 30 or 120 sec ITI, and was then given five control trials with the same ITI and trial duration. The order of testing responses and ITIs was counterbalanced. A dewlap response was elicited from an Anole by presenting a live house sparrow. Control trials involved applying firm pressure with thumb and forefinger to the base of an Anole's tail while holding the Anole one inch above the apparatus platform. An OKR was elicited by rotating the striped cylinder counterclockwise. The control procedure consisted of reversing the direction of rotation of the striped cylinder. A swimming response was elicited by lowering an animal into a bucket of water. As a control for habituation, an animal was removed from the swimming apparatus, placed in a plastic container, comprised of a metal stem and cover, and was lowered by hand into a 10 gal aquarium filled to a depth of five inches with 24 hour old tap water.

Treatment of Data. The habituation curves were analyzed in terms of several dependent variables defined as follows: Amount of habituation (absolute decrement) refers to the difference in response level between the first and last trial of a session. Percentage decrement (relative decrement) is the amount of habituation divided by the first trial response level. If the last trial response level was equal to or greater than the first trial response level, the amount of habituation and the percentage decrement were considered zero. Percentage of initial response is the response level of each trial divided by the first trial response level. Because of the differences in response measures (i.e., frequency and duration), percentage of initial response was employed for comparisons across responses. Rate of habituation refers to the slope of the habituation curve.

Results

Figure 5 gives the mean response levels in 5-trial blocks (TB) for each response and ITI. As is obvious from Figure 5, each response curve decremented across trials. Except for the 30 sec ITI of the swimming response, control trials (TB-9) were significantly higher than the final response levels (TB-8) for each response and ITI as summarized in Table 2 below, all $F_s (1, 19) > 10.05$, $p < .01$, suggesting that the observed decrement was not due to either effector fatigue or sensory adaptation.

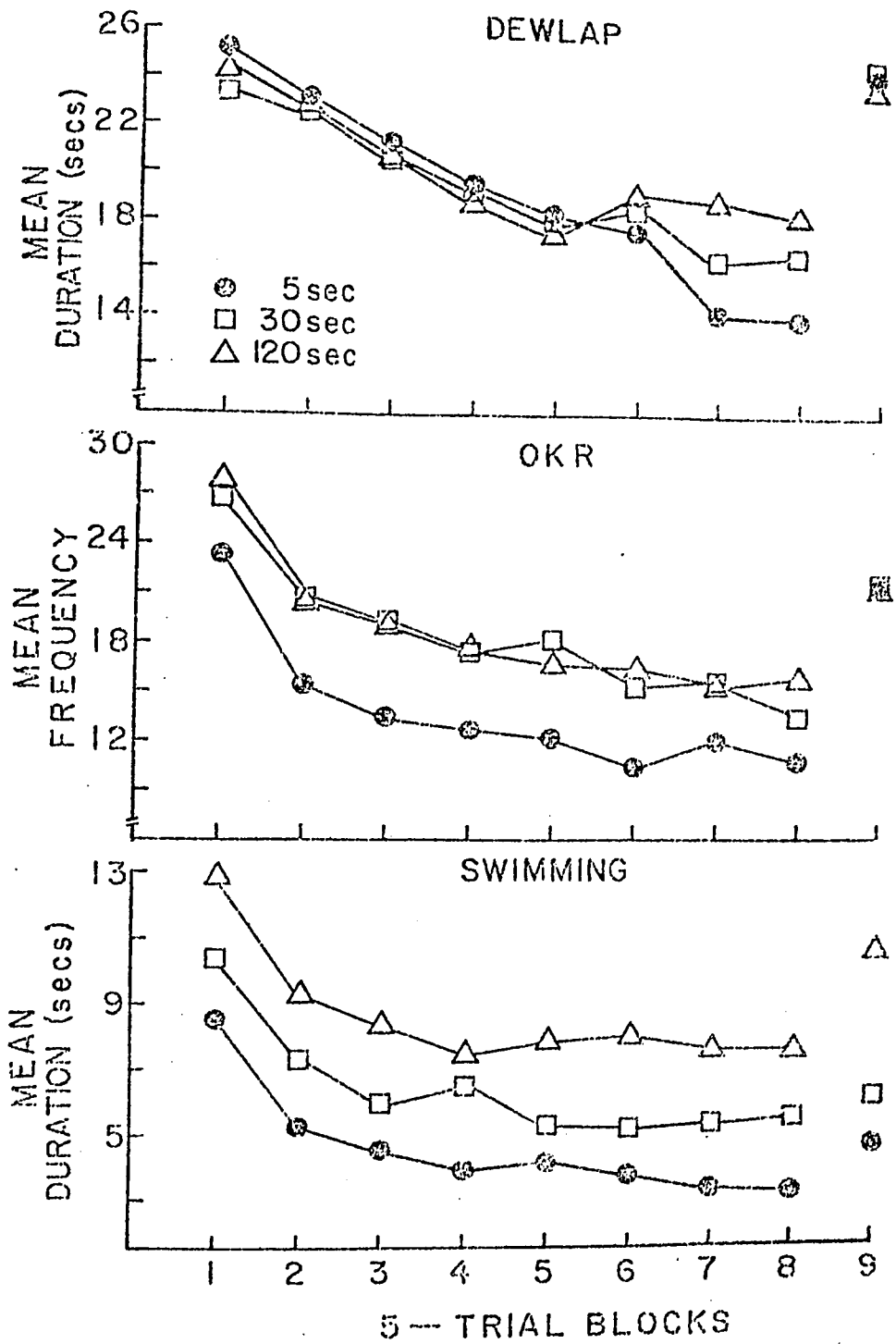


Fig. 5. Mean response levels for the dewlap, OKR and swimming responses as a function of intertrial interval

TABLE 2:

SUMMARY OF ONE-WAY WITHIN SUBJECTS ANALYSES OF VARIANCE OF CONTROL TRIALS FOR EACH RESPONSE AND INTERTRIAL INTERVAL

Source	df	DEWLAP					
		5 SEC ITI		30 SEC ITI		120 SEC ITI	
		<u>MS</u>	<u>F</u>	<u>MS</u>	<u>F</u>	<u>MS</u>	<u>F</u>
A (Subjects)	19						
B (Treatments)	1	1048.57	26.04*	611.52	13.98*	313.59	10.05*
Error	19	40.27		43.73		31.19	

OKR							
A (Subjects)	19						
B (Treatments)	1	1134.22	34.73*	606.84	25.01*	301.40	15.25*
Error	19	32.66		24.26		19.76	

SWIMMING							
A (Subjects)	19						
B (Treatments)	1	20.16	11.39*	3.48	3.05*	90.60	16.65*
Error	19	1.77		1.14		5.44	

* $p < .01$.

Because variances within each response were not homogeneous, a log transformation was applied to the data. This transformation did not, however, result in homogeneity of variances. Except for the dependent variables mentioned above, subsequent analyses of response levels were of untransformed data given the robustness of the F test when homogeneity of variance assumptions are violated (Boneau, 1960; Box, 1954; Lindquist, 1953), the use of equal sample sizes and the .01 significance level. Within each response, the response levels across 5-trial blocks were analyzed by means of two-

way analyses of variance with repeated measures (Winer, 1971, p. 525), the results of which are presented in Table 3 below.

TABLE 3
SUMMARY OF A REPEATED MEASURES ANALYSIS
OF VARIANCE WITHIN EACH RESPONSE

Source	df	DEWLAP	
		MS	F
A (ITI)	2	56.17	.10
Err (Bet)	57	585.92	
B (Trial Blocks)	7	464.77	22.58*
AB	14	31.73	1.54
Err (W)	399	20.59	

		OKR	
A (ITI)	2	1224.34	6.29*
Err (Bet)	57	194.58	
B (Trial Blocks)	7	991.89	58.65*
AB	14	10.48	.62
Err (W)	399	16.91	

		SWIMMING	
A (ITI)	2	660.88	27.70*
Err (Bet)	57	23.86	
B (Trial Blocks)	7	184.81	117.30*
AB	14	2.21	1.40
Err (W)	399	1.58	

* $p < .01$.

There was a significant effect on response level due to the ITI factor in the OKR, $F(2,57) = 6.29$, $p < .01$, and the swimming response, $F(2,57) = 27.70$, $p < .01$, but not in the dewlap response, $F(2,57) = .10$. While the Trial Blocks factor was significant in each response, there were no ITI x trial blocks interactions, thereby indicating

a pattern of a decreasing response level across trials for each ITI (see Figure 5) and further substantiating that habituation had occurred. Neuman-Keuls tests indicated that the 5 sec ITI response level was lower than both the 30 and 120 sec ITI in the OKR (both $p_s < .01$), while each ITI response level was different from each other in the swimming response (all $p_s < .01$), with the lowest response level in the 5 sec ITI condition and the highest in the 120 sec ITI condition.

Although Figure 5 is well representative of the total response curves for the OKR and swimming response, it obscures the initial increase in responding found for the dewlap response. This increase in responding for the dewlap response can be seen in Figure 6 which presents the mean response levels across trials for each ITI of the dewlap response. For each ITI there was an initial increment in responding above Trial 1 which persisted for approximately 20 trials. Eighty percent of the 60 animals tested on the dewlap response showed an increase from Trial 1 to Trial 2.

Amount of Habituation and Percentage Decrement. For each Anole, an amount of habituation, percentage decrement and percentage of initial response were determined as defined earlier and were employed in the below analyses. The means, standard deviations and one-way analyses of variance for the amount of habituation and percentage decrement within each response are given in Table 4 for each ITI. The variability in the dewlap response and OKR is immediately obvious. One-way analyses of variance on log transformations of the data yielded the results summarized in the second portion of Table 4.

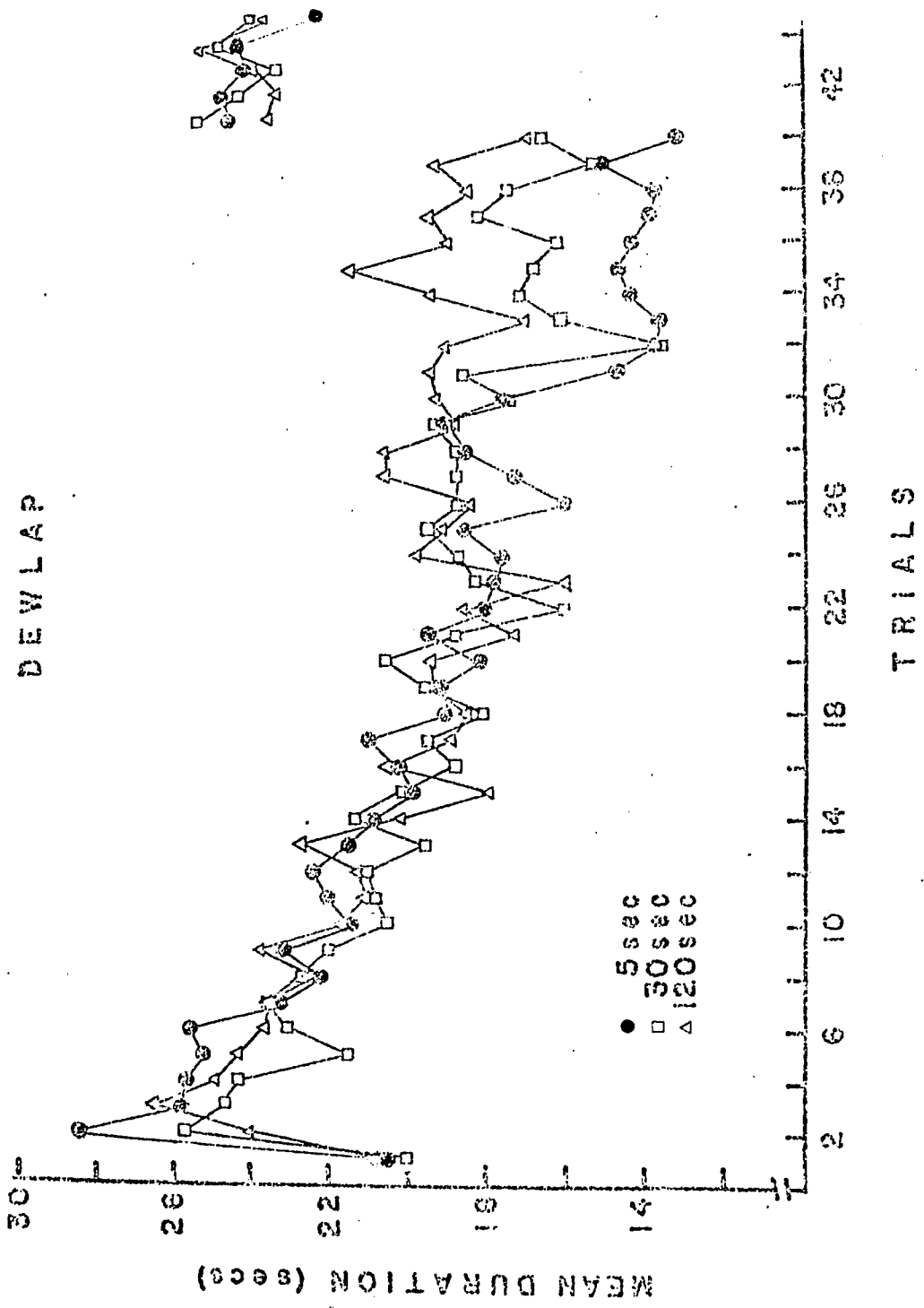


Fig. 6. Mean response levels of the dewlap response as a function of intertrial interval

TABLE 4

MEANS, STANDARD DEVIATIONS AND ONE-WAY ANALYSES
OF VARIANCE FOR THE AMOUNT OF HABITUATION AND
PERCENTAGE DECREMENT WITHIN EACH RESPONSE

Response	ITI	Amount Habituation		Percentage Decrement	
		<u>M</u>	<u>SD</u>	<u>M</u>	<u>SD</u>
Dewlap	5	10.20	10.33	45.49	44.45
	30	8.75	11.27	37.37	48.11
	120	7.65	10.62	34.33	45.67
OKR	5	19.80	9.09	64.23	25.50
	30	19.75	13.07	57.66	30.67
	120	18.20	10.19	57.32	27.30
Swimming	5	12.25	3.81	82.17	17.94
	30	9.75	3.59	61.40	19.47
	120	10.85	4.71	60.42	19.43

Response	Source ^a	<u>df</u>	<u>MS</u>	<u>F</u>	<u>MS</u>	<u>F</u>
Dewlap	Between	2	.178	.43	.009	.10
	Within	57	.415		.088	
OKR	Between	2	.021	.14	.071	1.34
	Within	57	.154		.053	
Swimming	Between	2	.065	1.86	.134	7.88*
	Within	57	.035		.017	

^aSource of variation and df are the same for both amount of habituation and percentage decrement.

* $p < .01$.

There were no differences in the amount of habituation as a function of ITI within any of the responses. It should be noted that there were no differences between ITIs within any response on the Trial 1 response level, all Fs (2, 57) < 2.12, while only in the

swimming response did ITIs differ on the Trial 40 response levels, $F(2, 57) = 8.03, p < .01$. This difference in the swimming response is reflected in the difference between ITIs in the percentage decrement, $F(2, 57) = 7.88, p < .01$.

Inspection of individual data revealed that some Anoles in each ITI of the dewlap did not habituate when amount of habituation and percentage decrement were employed as measures of habituation. It appeared that smaller Anoles were less likely to habituate. Thus the data for each response were further analyzed by dividing the animals in each ITI into two groups according to snout-vent length, one group of larger Anoles (> 59 mm) and the other of smaller Anoles (< 59 mm) according to the size differences found in the literature (see Discussion: Dewlap Response). The means, standard deviations and t values for snout-vent differences between larger and smaller Anoles within each response and ITI are given in Table 5. Each group of smaller Anoles differed in size from the

TABLE 5
SNOUT-VENT LENGTH OF LARGER AND SMALLER
ANOLES FOR EACH RESPONSE AND INTERTRIAL INTERVAL

ITI	Size	\bar{M}^a	\underline{SD}	\underline{t}^b	\bar{M}	\underline{SD}	\underline{t}	\bar{M}	\underline{SD}	\underline{t}
5	Larger	64.1	3.31	5.87*	64.5	2.95	7.48*	62.8	3.85	6.42*
	Smaller	52.9	2.85		52.2	2.78		53.8	2.20	
30	Larger	63.4	3.31	8.08*	63.2	3.79	7.57*	63.4	4.43	6.06*
	Smaller	52.6	2.63		52.5	2.37		53.8	2.35	
120	Larger	64.8	2.86	8.05*	63.0	3.53	7.41*	64.2	3.49	8.23*
	Smaller	53.0	3.65		53.3	2.16		52.7	2.71	

^a $n = 10.$ ^b $df = 18.$ * $p < .01.$

corresponding larger Anoles, all $t_s (18) > 5.86$, $p < .01$. Two-way analyses of variance with repeated measures (see Table 6 below) indicated that only for the dewlap response were there any differences between larger and smaller animals in the overall habituation curves.

TABLE 6

SUMMARY OF TWO-WAY ANALYSES OF VARIANCE ON RESPONSE LEVELS FOR DIFFERENT SIZE ANOLES WITHIN EACH RESPONSE AND ITI

Source	df ^a	DEWLAP					
		5 SEC ITI		30 SEC ITI		120 SEC ITI	
		MS	F	MS	F	MS	F
A (Size)	1	41.41	.07	4258.03	9.35*	4835.60	16.37*
Err (Bet)	18	596.92		455.63		295.37	
B (Trial Blocks)	7	314.24	14.03*	122.23	5.86*	91.77	5.29*
AB	7	2.85	.13	39.16	1.88	40.54	2.34
Err (W)	126	22.39		20.85		17.36	

OKR							
A (Size)	1	78.40	.53	14.28	.07	623.31	2.75
Err (Bet)	18	146.87		202.93		226.59	
B (Trial Blocks)	7	343.67	37.01*	332.92	17.09*	336.27	15.72*
AB	7	3.87	.42	30.42	1.56	26.75	1.25
Err (W)	126	9.29		19.48		21.39	

SWIMMING							
A (Size)	1	.36	.04	43.47	1.74	44.10	1.20
Err (Bet)	18	8.96		25.05		36.66	
B (Trial Blocks)	7	60.81	50.80*	62.18	40.95*	66.23	31.74*
AB	7	1.19	1.00	1.40	.92	.77	.37
Err (W)	126	1.19		1.52		2.09	

^a $n = 10$. * $p < .01$.

These differences are illustrated in Figure 7. As is evident from Table 6 and Figure 7, there were no differences between larger and

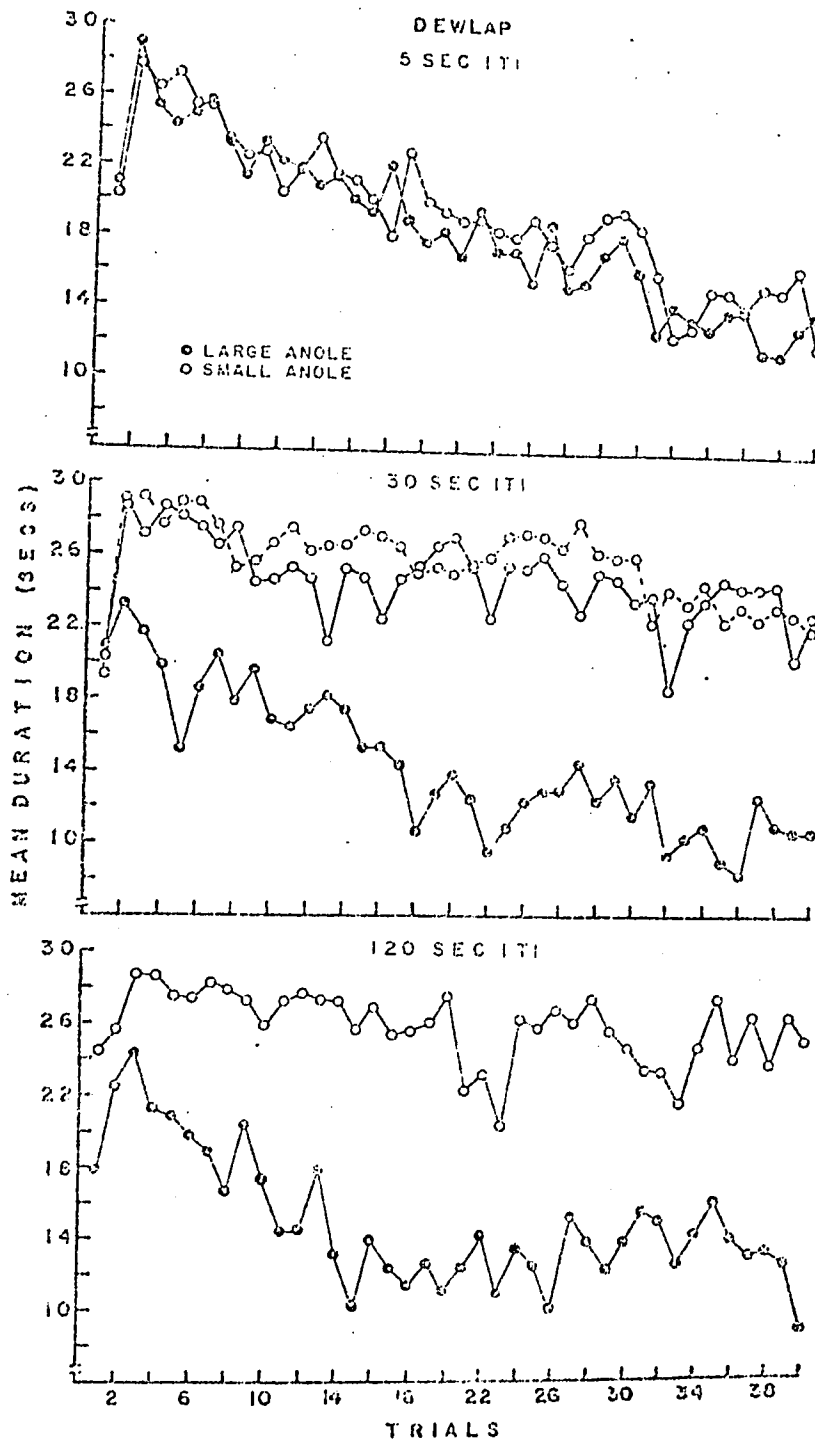


Fig. 7. Mean dewlap response levels of larger and smaller Angles as a function of intertrial interval.

smaller Anoles on the 5 sec ITI condition of the dewlap, while under the 30 and 120 sec ITI condition larger animals habituated but smaller ones did not. Another group of smaller Anoles (snout-vent length: $\bar{M} = 54.0$ mm, $\underline{SD} = 2.71$, $n = 10$) were tested with a 30 sec ITI, the results of which are also presented in the middle portion of Figure 7. The same results were obtained with this second group of smaller Anole, thus demonstrating that the difference between sizes is reliable and reproducible.

A two-way analysis of variance with repeated measures performed on the dewlap response data for larger animals again resulted in no differences in response level due to the ITI factor, $\underline{F}(2, 27) = .76$.

Because of these differences between larger and smaller Anoles on the dewlap response, comparisons across responses on the percentage of initial response were performed separately for larger and smaller animals.

Percentage Initial Response. Because of the variability of the data, an arc sin transformation was performed on the percentage of initial response prior to analysis. Three-way analyses of variance with repeated measures on one factor (Winer, 1971, p. 599) were employed for comparisons across the three responses. The results of these analyses for larger and smaller Anoles are summarized in Table 7. The Response (A) and Trial Blocks (C) factor were significant for larger animals while no interactions were significant, thereby indicating differences between responses and a decreasing pattern of responding.

TABLE 7

SUMMARY OF REPEATED MEASURES THREE-WAY ANALYSES OF VARIANCE
OF PERCENTAGE INITIAL RESPONSE FOR LARGER AND SMALLER ANOLE

Source	df	Larger Anole ^a		Smaller Anole ^a	
		MS	F	MS	F
A (Response)	2	.13	8.71*	.53	31.25*
B (ITI)	2	.008	.56	.015	.92
AB	4	.012	.82	.02	1.31
Err (Bet)	81	.015		.017	
C (Trial Blocks)	7	.017	3.09*	.01	1.46
AC	14	.001	.18	.001	.13
BC	14	.0002	.04	.001	.08
ABC	28	.0002	.04	.0003	.03
Err (W)	567	.005		.007	

^a $\underline{n} = 10.$ * $p < .01.$

The Response factor (A) was significant for the smaller Anole, while the Trial Blocks factor (C) was nonsignificant. The results of Neuman-Keuls tests for comparisons across responses under each ITI condition are given in Table 8 for larger and smaller Anole. For the larger animals, the dewlap response differed from the OKR and swimming response only under the 5 sec ITI condition. For smaller Anoles, the dewlap response and OKR were different from each other under each ITI, as were the dewlap and swimming responses. For both larger and smaller animals, there were no differences between the OKR and swimming response under any of the ITIs.

TABLE 8

NEUMAN-KEULS TESTS FOR COMPARISONS OF PERCENTAGE INITIAL RESPONSE UNDER EACH ITI CONDITION FOR LARGER AND SMALLER ANOLE

ITI	LARGER ANOLE ^a		
	Comparisons ^b		
	Dewlap-OKR	Dewlap-Swimming	OKR-Swimming
5	**	**	NS
30	NS	NS	NS
120	NS	NS	NS

	SMALLER ANOLE ^a		
5	**	**	NS
30	**	**	NS
120	*	*	NS

^a $\underline{n} = 10$. ^b $\underline{df} = 81$. * $\underline{p} < .05$. ** $\underline{p} < .01$. NS = nonsignificant.

Rate of Habituation. Rates (slopes) of habituation were determined through regression analyses and curve fitting procedures suggested by Lewis (1960). Orthogonal polynomials were used as first approximations to describe each curve. Each curve was fitted completely to the first degree (linear) and then fitted again to the first and second degree (quadratic) with the aid of the IMSL (International Mathematical and Statistical Libraries, Inc., Houston, Texas, 77036) program CALL RLFOTH and the BMD (Biomedical Computer Programs, University of California, Los Angeles, California, 90024) program BMD05R. The obtained \underline{F} values for each degree and curve fitted are found in Appendix B. Except for the 5 sec ITI of the dewlap, all habituation curves were curvilinear. A plot of

(log X, log Y) approached a straight line, therefore a log transformation of X (trials) and Y (mean response levels) was employed for the nonlinear curves and regression curves were obtained with a least-squares analysis. The regression equations and the standard errors of the slopes are presented in Table 9.

TABLE 9
REGRESSION EQUATIONS AND STANDARD ERRORS OF
THE SLOPES FOR EACH RESPONSE AND ITI

Response	ITI	Regression Equation ^a	S.E. of Slope
Dewlap	5	$Y = 25.70 - .3172X$.0194
	30 ^b	$Y = 28.31X^{-.2608}$.0274
	120 ^b	$Y = 24.43X^{-.1910}$.0302
OKR	5	$Y = 28.06X^{-.2661}$.0215
	30	$Y = 33.71X^{-.2274}$.0176
	120	$Y = 32.87X^{-.2114}$.0172
Swimming	5	$Y = 11.12X^{-.3404}$.0206
	30	$Y = 12.49X^{-.2528}$.0202
	120	$Y = 14.54X^{-.1947}$.0156

^aGeneral linear equation: $Y = a + bX$. General hyperbolic equation: $Y = aX^b$, where a = Y-intercept and b = slope.

^bRegression equations are for larger animals.

Since only larger Anoles habituated under the 30 and 120 sec ITI condition of the dewlap response, the regression equations found in Tables 9 and 10 (below) for those two ITIs were derived from

the data of larger Anoles. Although the regression equations in Table 9 describe each curve, no comparisons can be made between slopes because the curves are nonlinear functions. However, slopes of the linear component can be directly compared. The linear component gives an indication of the steepness of the curve. Table 10 lists the slopes and standard errors of the slopes of the linear component for each curve.

TABLE 10
SLOPES OF LINEAR COMPONENT AND STANDARD ERRORS
OF THE SLOPES FOR EACH RESPONSE AND ITI

Response	ITI	Slope	S.E. of Slope
Dewlap	5	-.3172	.0194
	30	-.2926	.0264
	120	-.2048	.0374
OKR	5	-.2741	.0427
	30	-.3128	.0325
	120	-.2871	.0369
Swimming	5	-.1206	.0213
	30	-.1157	.0213
	120	-.1134	.0208

Comparisons within each response of the slopes of the linear components yielded the t values listed in Table 11. There were no differences between slopes within either the OKR or swimming response, while slopes of the 5 and 120 sec ITI of the dewlap response were different from each other.

TABLE 11
OBTAINED t VALUES FOR DIFFERENCES BETWEEN SLOPES
OF LINEAR COMPONENTS WITHIN EACH RESPONSE

Comparisons ^{a,b}	Dewlap	OKR	Swimming
5 - 30 sec ITI	.75	-.72	.16
5 - 120 sec ITI	2.67*	-.22	.24
30 - 120 sec ITI	1.92	.50	.01

^aGroups treated as independent. ^bdf = 78. * $p < .01$, two-tailed.

For each curve, the correlation coefficients (\underline{r}) of the linear component and the proportion of variance in Y accounted for by the linear regression (\underline{r}^2) are listed in Table 12.

TABLE 12
CORRELATION COEFFICIENTS (\underline{r}) AND THE COEFFICIENTS OF
DETERMINATION (\underline{r}^2) FOR EACH RESPONSE AND ITI

ITI	DEWLAP		OKR		SWIMMING	
	\underline{r}	\underline{r}^2	\underline{r}	\underline{r}^2	\underline{r}	\underline{r}^2
5	-.9354	+.8749	-.7216	+.5207	-.6765	+.4577
30	-.3739	+.7637	-.8418	+.7085	-.6619	+.4381
120	-.6637	+.4405	-.7836	+.6140	-.6627	+.4392

Mouth Open. Since the frequency and duration of mouth open were so highly variable and since no transformations improved the situation, the data are presented as the percentage of animals

that opened their mouth at least once in a 5-trial block. Figure 8 indicates for each ITI and trial block the percentage of larger and smaller Anoles with a mouth open. There was essentially no difference between larger and smaller animals in the 5 sec ITI condition, while more smaller Anoles than larger Anoles responded with a mouth open in the 30 and 120 sec ITI. These results parallel those of the dewlap for larger and smaller Anoles (see Figure 7). That is, there were no differences between larger and smaller animals under the 5 sec ITI, while the duration of dewlap distension did not wane for smaller Anoles in the 30 and 120 sec ITI.

Additional Information

Since an effect of size was present in Experiment 1 and because size is correlated with age and sex in A. carolinensis (Fox & Dessauer, 1958), an estimate was determined for the proportion of males and females employed. Casual observation suggested that all of the larger Anoles were males and most of the smaller Anoles were subadult males and the rest were females. After completion of all the experiments, 43 animals were randomly chosen from approximately 100 animals and were inspected for the presence or absence of the male hemipenes, pointed or rounded head (female) and presence of a large anal fold (male). Inspection indicated that 79 % were males ($\underline{n} = 34$) and 21 % were females ($\underline{n} = 9$). Nineteen of the males ranged in size from 60-64 mm snout-vent length ($\underline{M} = 61.74$) and 15 males ranged from 51-58 mm ($\underline{M} = 54.93$), while females ranged from 50-55 mm ($\underline{M} = 51.67$). Therefore, of the Anoles less than 60 mm, 62.5 % were males and 37.5 % were females.

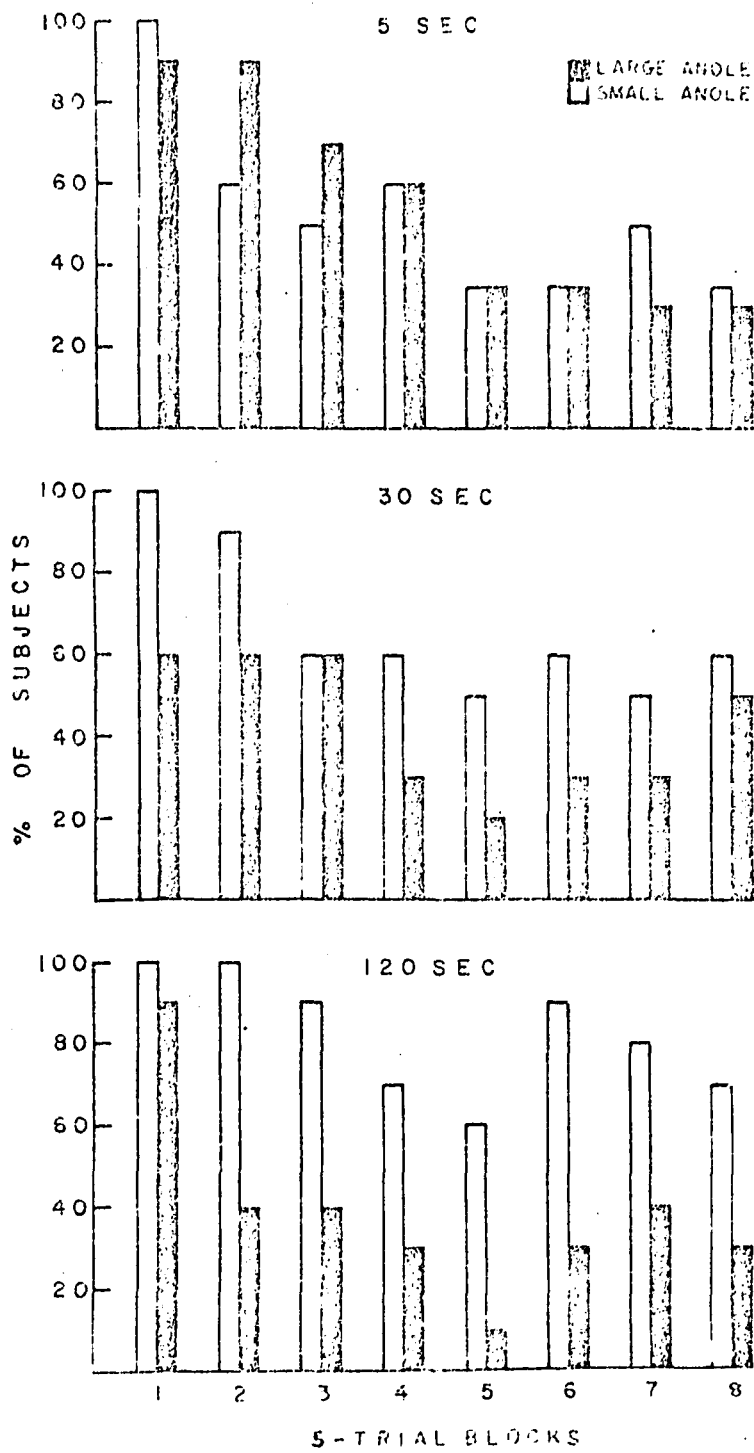


Fig. 8. Percentage of larger and smaller Anoles with open mouth as a function of intertrial interval.

Discussion

As expected, each response habituated which is what usually occurs when a response is repeatedly elicited (Harris, 1943; Thompson & Spencer, 1966). The observed decrement was not attributable to effector fatigue or sensory adaptation.

According to Thompson and Spencer, one of the parametric characteristics of habituation is that the more rapid the frequency of stimulation the more rapid and/or pronounced is habituation. In other words, shorter intertrial intervals will usually result in faster habituation (typically defined as the number of trials to criterion) and/or lower (asymptotic) levels of responding. This effect of shorter ITIs was partially supported in Experiment 1. That is, shorter ITIs resulted in lower levels of responding in the OKR and swimming response but not in the dewlap response. Rates of habituation (linear slopes) did not differ as a function of ITI in the OKR and swimming response, but did so in the dewlap response. Shorter ITIs were, however, frequently associated with faster rates of habituation.

That the effects of intertrial interval on the course of habituation were inconsistent in the present experiment is not unusual. Shorter ITIs have resulted in both lower asymptotic levels of responding (Askew, 1970; Barrass, 1961; Geer, 1966; Schaub, 1965; Thompson & Spencer, 1966; Winokur, Stewart, Stern & Pfeiffer, 1962) and also higher asymptotic levels (Davis, 1970; File, 1973a) than have longer ITIs, with no differences in the rate of habituation. Where faster rates of habituation have been reported for shorter ITIs than for longer ITIs, there were no differences in the asymp-

totic level of responding since the response level went to zero (Prechtel, 1958; Prosser & Hunter, 1936; Ratner, 1972; Ratner & Gilpin, 1974). It is not clear to what extent these inconsistencies are related to the different species and responses studied. The results of Experiment 1 suggest, however, that the differences in the effects of intertrial interval on habituation may be due to the response system.

Dewlap Response. The striking differences between larger and smaller Anoles in the dewlap response was totally unexpected. The reasons for this difference remain unclear but may be related to factors associated with the age or experience of the animals. Larger (>60 mm) A. carolinensis are typically older, sexually mature males (Fox & Dessauer, 1958; Gordon, 1956; Hamlett, 1952; Michael, 1972), while smaller animals are more likely immature males (50-55 mm) (Fox & Dessauer, 1958) or sexually mature females (45-55 mm) (Gordon, 1956; Hamlett, 1952; Michael, 1972). The size-sex relationship of animals used in the present experiments agrees well with the above studies. From the discussion that follows, it is suggested that perhaps the differences in habituation between the larger and smaller Anoles are related to the reproductive status of the animals.

The breeding season of A. carolinensis is usually between April and August (Cochran & Goin, 1970; Gordon, 1956; Greenberg & Noble, 1944), at which time adult males are particularly active in courtship (dewlap extension, strutting) and defending a territory (dewlap extension, mouth open, biting, bobbing). Female Anoles fight throughout the year (Greenberg & Noble, 1944). Adult males distin-

guish between females and juvenile males of a similar size (Greenberg & Noble, 1944) and change from a challenge (dewlap distension, bobbing, etc.) to a courtship pattern if the intruder is a female. Immature males, however, challenge indiscriminately other immature males and females, unless injected with testosterone (L. Evans, 1957). In which case, the injected males distinguished between the two and challenged the males and courted the females. Females injected with male hormones acted like males, in that, the injected females would court other females and challenge males (Greenberg & Noble, 1944). Thus for adult males it would appear that the dewlap response, as a component of a challenge display, functions to ward off a potential intruder (another male) and, as a component of the courtship pattern, functions to attract a possible mate (a female). Perhaps in females and immature males the dewlap functions mainly to ward off an intruder male or female. The differences appear to be related to the reproductive status of the males, since immature males resemble females in fighting behavior. This similarity between immature males and females and the difference from adult males parallels the results of Experiment 1. The extent to which the differences between adult males and smaller animals on habituation of the dewlap are related to reproductive status of the animals remains to be determined. Slower or no habituation in younger animals has also been reported for exploratory behaviors of rats (Bronstein, 1972; Feigley et al., 1972; Parsons et al., 1973), monkeys and chimpanzees (Green, 1965; Welker, 1956a, 1956b).

The initial increase in dewlap duration, although not found in the OKR or swimming response, is not unusual (Groves & Thompson,

1970; Thompson & Spencer, 1966) and has been found for many behaviors such as conspecific aggression in fish (Peeke et al., 1971; Peeke & Veno, 1973), prey catching in frogs and toads (Ewert & Ingle, 1972), escape reactions in leeches (Ratner, 1972) and the "mobbing" response of chaffinches shown towards a predator (Hinde, 1954a, 1954b, 1960). It seems reasonable that animals would increase responding to a potentially threatening stimulus once the stimulus is recognized as such. According to Groves and Thompson (1970), initial increases in responding (sensitization) are likely due to the intensity of the stimulus, with more intense stimuli leading to sensitization. If threatening stimuli are considered intense stimuli, the two above interpretations are not incompatible.

The finding that for larger animals there was no difference between ITIs in the level of responding requires further study. One possibility for the lack of differences is that the ITIs were not sufficiently different from each other. This is unlikely since the ITIs used are comparable to those found in the literature. Since there was no difference in responding when a stimulus was presented frequently (i.e., every 5 sec) or infrequently (i.e., every 120 sec), what may be important is not how often a threatening stimulus is encountered, but rather that when it is encountered an animal gives a response (even a "weak" one). "Weaker" dewlap responses (smaller in size) were noted frequently in later trials. It is possible that for some responses to threatening stimuli, the response would not rapidly reach a zero response level. This possibility requires investigation.

OKR. The OKR of turtles to a field of moving stripes (Hayes et

al., 1968) waned within 6 minutes of continuous rotation. Although the Hayes et al., procedure was different (restrained animals, 19 1-in. stripes, continuous rotation), their results are similar to the present findings in that most of the OKR decrement for Anoles occurred within the first 10-15 trials (5-7.5 minutes of rotation). It may be that OKR habituation in other reptiles would show a similar rapid decrement.

Swimming. The differences in habituation between the ITIs of the swimming response suggests that sufficient time was allowed for recovery between trials since the response level at each ITI remained fairly constant throughout trials 10-40. The swimming response presents somewhat of a problem in interpretation since A. carolinensis is not truly aquatic (Cochran & Goin, 1970; Smith, 1946). In addition, the swimming response involves movement of the whole body in contrast to the dewlap and OKR, where vision is the major sensory modality. The swimming response is probably not a dominant response in this species' behavioral repertoire and is unlikely to be a primary factor in survival.

The responses and ITI(s) to be used in the succeeding experiments were determined from the results of Experiment 1. The dewlap and OKR were selected as the best responses to be investigated because of (1) their possible functional significance in A. carolinensis, in contrast to the swimming response, (2) the available literature on the dewlap and OKR in A. carolinensis and other reptiles, as opposed to that of the swimming response and (3) the similarity between the dewlap and OKR habituation curves.

Experiment 2: Recovery and Retention of Habituation

An habituated response tends to recover over time and this spontaneous recovery is considered one of the major parametric characteristics of habituation (Thompson & Spencer, 1966). From the review of the literature presented in Chapter I, recovery and retention seem to be characteristics that may best differentiate various response systems. Experiment 2 was designed to investigate recovery and retention of habituation.

Recovery and Retention may vary with the extent of habituation in the previous session (Hinde, 1970b). If comparisons across responses in recovery and retention are to be meaningful, the extent of habituation should be as similar as possible. As evident from Experiment 1, the habituation curves for the dewlap response and OKR were similar, particularly under the 30 and 120 sec ITI condition and only then for larger animals. Thus to insure similarity in the extent of habituation, only larger animals were employed in Experiment 2 and only the two above responses were investigated.

Method

Subjects. Eighty Anolis carolinensis, ranging in size from 60-72 mm snout-vent length, were divided into four groups (20 per group) of comparable snout-vent length and were randomly assigned to one response and recovery period.

Procedure. A given animal was tested twice on only one response with either a 15 minute or 24 hour interval between sessions. Each session consisted of 40 trials, each trial of 30 seconds duration, with a 30 sec ITI. The order of testing responses and recovery in-

tervals was counterbalanced. The dewlap and OKR were elicited as in Experiment 1. When eliciting the dewlap response for any given animal, the same stimulus bird was employed for both sessions.

Treatment of Data. The habituation curves were analyzed on several dependent variables as follows: Amount of recovery (absolute recovery) refers to the difference in response level between the last trial of the first session and the first trial of the second session. Percentage recovery (relative recovery) is the amount of recovery divided by the amount of habituation in the first session. If the first trial of the second session was equal to or less than the last trial of the first session, the amount and percentage recovery were considered zero. The dependent variables defined above were determined for each Anole. Retention may be indicated by either (1) a lower response level in session 2 or (2) a faster rate of habituation in session 2.

Results

Figure 9 presents the mean response levels in 5-trial blocks for each response and recovery interval and session. Habituation occurred in each session of each response as evidenced from Figure 9.

Within each response, the 15 min and 24 hour group did not differ from each other on either Trials 1 or 40, TB-1 or TB-8 (all $t_s(38) < 1.11$, $p < .10$, two-tailed) or the total response curves (as determined by a two-way analysis of variance with repeated measures on trial blocks - dewlap: $F(1,38) = .26$, OKR: $F(1,38) = .05$) prior to the recovery interval. This absence of a

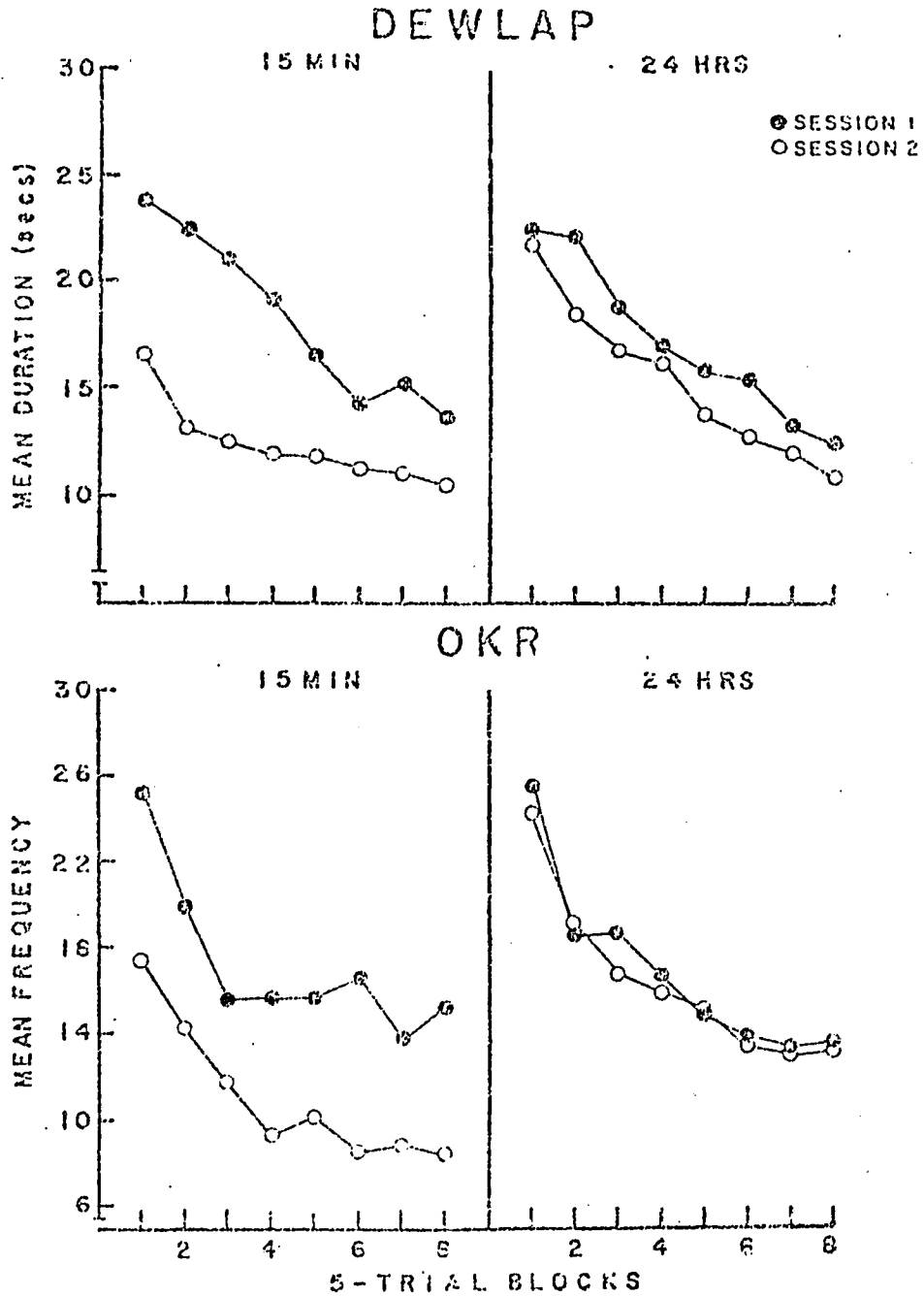


Fig. 9. Mean response levels for the dewlap response and OKR as a function of recovery interval.

difference was expected since each group within a response underwent the same treatment in the first session.

The amount and percentage recovery for each response as a function of recovery interval are given in Table 13. There was essentially complete recovery of the dewlap response (95.5 %) and substantial recovery of the OKR (80 %) after just 15 minutes rest.

TABLE 13

MEAN AND STANDARD DEVIATION RESPONSE LEVELS AND MEASURES OF RECOVERY FOR EACH RESPONSE AND RECOVERY INTERVAL

Response	Interval	Session 1		Session 2	Amt Habit	Amt Recov	% Recov
		T1 ^a	T40	T1			
Dewlap	15 min	17.85 (4.94)	14.05 (8.92)	20.05 (7.61)	6.30	7.40	95.5
	24 hr	16.50 (6.89)	13.55 (8.71)	23.10 (5.09)	6.65	9.90	133.8
OKR	15 min	30.10 (7.03)	14.75 (7.18)	21.35 (7.92)	15.35	8.85	80.0
	24 hr	29.00 (7.83)	12.40 (7.89)	29.50 (9.35)	16.90	17.10	106.5

^aM and (SD)

It is clear from Figure 9 that for both responses retention of habituation was evident after 15 minutes rest, while little or no retention was evident after 24 hours. This is further supported by the results summarized in Table 14. Note that there was a significant effect due to sessions for the 15 min recovery interval

TABLE 14

TWO-WAY ANALYSES OF VARIANCE WITH REPEATED MEASURES FOR EACH
RESPONSE AND RECOVERY INTERVAL AS A FUNCTION OF SESSIONS

Dewlap 15 Min Recovery Interval			
Source	<u>df</u>	<u>MS</u>	<u>F</u>
A (Sessions)	1	2798.97	28.11*
S (Subjects)	19	470.51	
Err (AS)	19	99.54	
B (Trial Blocks)	7	309.63	20.68*
AB	7	59.53	4.23*
Err (BS)	133	14.97	
Err (ABS)	133	14.09	

Dewlap 24 Hour Recovery Interval			
A (Sessions)	1	259.19	3.49
S (Subjects)	19	736.82	
Err (AS)	19	74.28	
B (Trial Blocks)	7	534.37	30.77*
AB	7	10.44	.79
Err (BS)	133	17.37	
Err (ABS)	133	13.19	

OKR 15 Min Recovery Interval			
A (Sessions)	1	2964.60	76.48*
S (Subjects)	19	212.15	
Err (AS)	19	38.77	
B (Trial Blocks)	7	455.08	28.49*
AB	7	21.61	1.51
Err (BS)	133	15.96	
Err (ABS)	133	14.30	

OKR 24 Hour Recovery Interval			
A (Sessions)	1	18.24	.45
S (Subjects)	19	294.04	
Err (AS)	19	40.75	
B (Trial Blocks)	7	602.55	34.55*
AB	7	6.14	.34
Err (BS)	133	17.44	
Err (ABS)	133	18.06	

* $p < .01$.

of both the dewlap response and OKR, thereby indicating retention. Sessions effect was nonsignificant for the 24 hour recovery interval of both responses which indicates that no retention was evident after 24 hours of rest. The Trial Blocks factor was significant for each response and recovery interval further substantiating that habituation occurred.

Rate of Habituation. Rates (slopes) of habituation were determined for each curve as in Experiment 1. The obtained F values for each degree fitted for each response and session may be found in Appendix D. Session 1 habituation curves for the 15 min and 24 hour recovery intervals of the dewlap response were linear, while all other curves were curvilinear. Log transformations were employed as in Experiment 1. The regression equations and standard errors of the slopes for the fitted curves are given in Table 15.

TABLE 15

REGRESSION EQUATIONS AND STANDARD ERRORS OF THE SLOPES
FOR EACH RESPONSE, RECOVERY INTERVAL AND SESSION

Response	Recovery Interval	Session 1		Session 2	
		Regression Equation	S.E. of Slope	Regression Equation	S.E. of Slope
Dewlap	15 min	$Y = 24.56 - .3041X$.0247	$Y = 18.94X^{-.1583}$.0187
	24 hr	$Y = 23.25 - .2923X$.0227	$Y = 29.16X^{-.2406}$.0226
OKR	15 min	$Y = 29.18X^{-.1999}$.0209	$Y = 23.33X^{-.2832}$.0217
	24 hr	$Y = 31.92X^{-.2411}$.0182	$Y = 31.16X^{-.2408}$.0221

The slopes and standard errors of the slopes of the linear component for each curve are presented in Table 16.

TABLE 16

SLOPES OF LINEAR COMPONENT AND STANDARD ERRORS OF THE SLOPES FOR EACH RESPONSE, RECOVERY INTERVAL AND SESSION

Response	Recovery Interval	Session 1		Session 2	
		Slope	S.E. of Slope	Slope	S.E. of Slope
Dewlap	15 min	-.3041	.0247	-.1355	.0221
	24 hr	-.2923	.0227	-.2903	.0228
OKR	15 min	-.2341	.0394	-.2356	.0261
	24 hr	-.3045	.0317	-.2898	.0369

Comparisons of the slopes of the linear components of session 1 with those of session 2 for each response and recovery interval yielded the t values listed in Table 17.

TABLE 17

t VALUES FOR DIFFERENCES BETWEEN THE SLOPES OF LINEAR COMPONENTS OF SESSION 1 AND SESSION 2 FOR EACH RESPONSE AND RECOVERY INTERVAL

Comparisons ^a	Recovery Interval	Dewlap	OKR
Session 1 linear slope vs Session 2 linear slope	15 min	5.09*	-.03
	24 hr	.06	.30

^adf = 78. *p < .01.

The session 1 linear slope differed from the session 2 linear slope in the dewlap response and only after 15 minutes of rest. However, the rate of habituation was slower in the second session (-.1355) than in the first session (-.3041). None of the other comparisons were significant. The lack of a difference in the rate of habituation for either response after 24 hours of rest is congruent with the absence of retention for both responses after 24 hours. To illustrate the rate and retention of habituation, the mean response levels for the 15 min recovery interval of the dewlap response and OKR are given in Figures 10 and 11 respectively.

The correlation coefficients (\underline{r}) and the coefficients of determination (\underline{r}^2) for the linear regression of each curve are listed in Table 18.

TABLE 18

CORRELATION COEFFICIENTS (\underline{r}) AND THE COEFFICIENTS OF DETERMINATION (\underline{r}^2) FOR EACH RESPONSE, RECOVERY INTERVAL AND SESSION

Response	Recovery Interval	Session 1		Session 2	
		\underline{r}	\underline{r}^2	\underline{r}	\underline{r}^2
Dewlap	15 min	-.8949	+.8008	-.7048	+.4968
	24 hr	-.9022	+.8139	-.8997	+.8094
OKR	15 min	-.6939	+.4816	-.8254	+.6814
	24 hr	-.8414	+.7079	-.7867	+.6189

Mouth Open. The data for mouth open were treated as in

DEWLAP 15 MIN

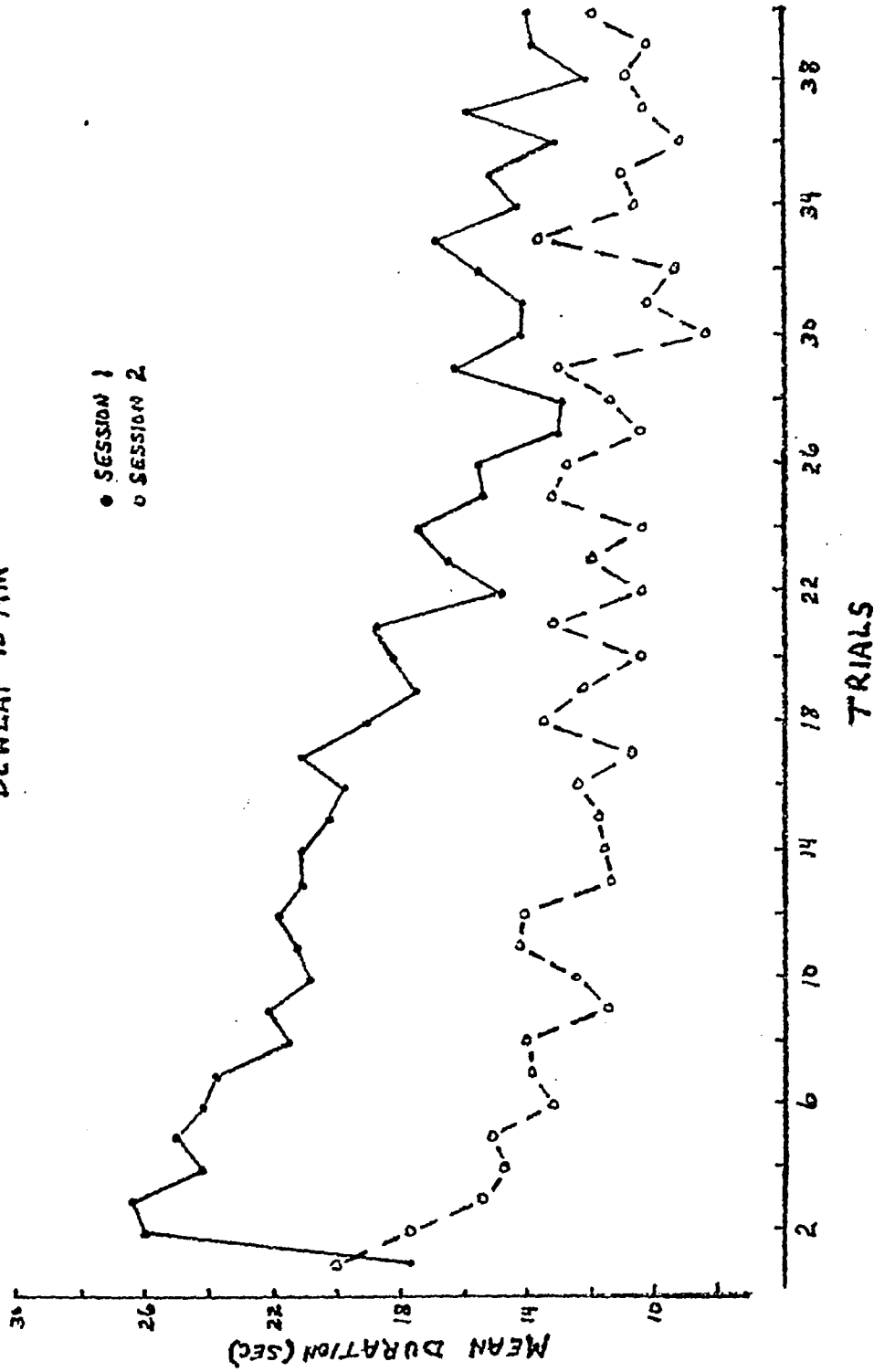


FIG. 10. Mean response levels of each session of the 15 minute recovery interval for the dewlap response.

OKR 15 MIN

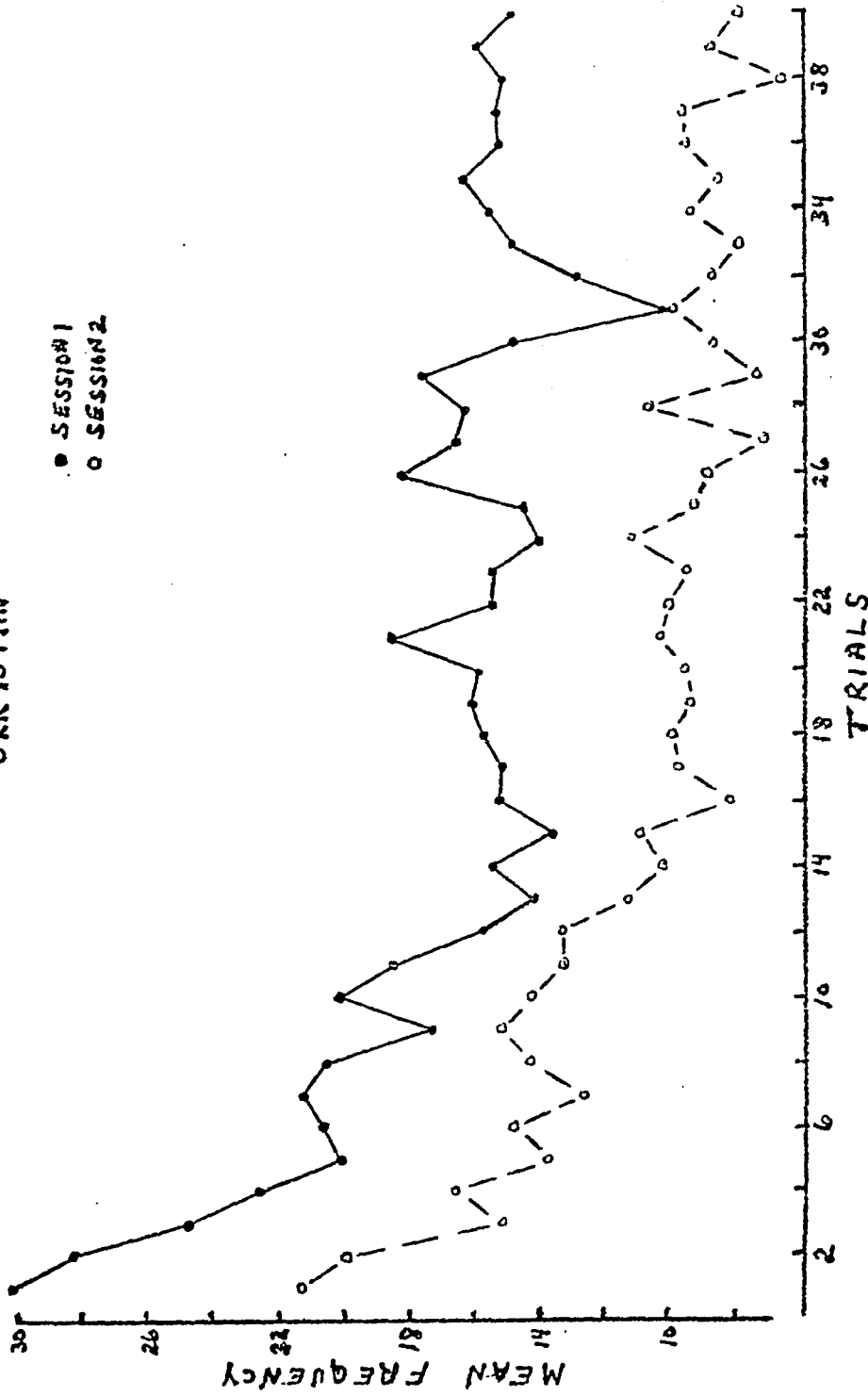


FIG. 11. Mean response levels of each session of the 15 minute recovery interval for the OKR.

Experiment 1. Figure 12 indicates for each session and recovery interval, the percentage of animals with a mouth open at least once in a 5-trial block. The percentage of animals with a mouth open decreased within each session and recovery interval. Fewer animals responded with a mouth open after 15 minutes rest, indicating retention. There was essentially no difference between session 1 and 2 in the percentage of Anoles responding with a mouth open after 24 hours of rest. These results parallel those for the dewlap response.

Discussion

The dewlap response and OKR habituated (as in Experiment 1) and substantially recovered from habituation after 15 minutes rest and completely recovered in 24 hours. No retention was evident for either response after 24 hours of rest.

The recovery intervals (15 min and 24 hours) did not differentiate between the dewlap response and OKR. The lack of retention after 24 hours may be due to the number of trials employed, since A. carolinensis required over 200 trials to learn an escape response (Powell, 1967). This possibility requires investigation. It may be that recovery and retention are not parameters that can differentiate between response systems. This possibility is not supported by the literature (cf. Hinde, 1970b and the review presented in Chapter I). Another alternative is that the dewlap and OKR are not completely different response systems, so that the course of habituation of both responses may be similar under some treatments (e.g., recovery intervals) but not others (e.g., inter-

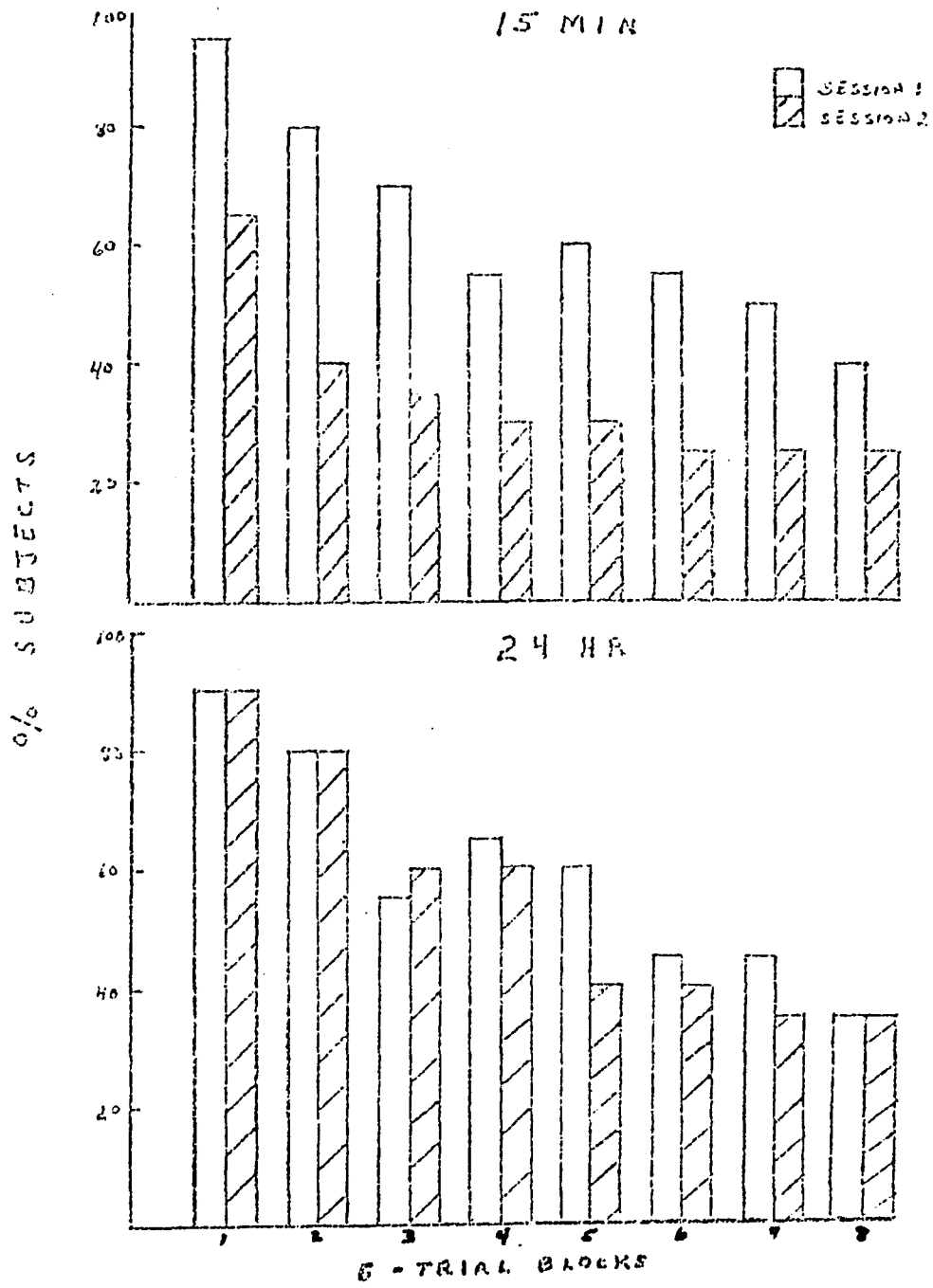


Fig. 12. Percentage of Anoles with open mouth for each session and recovery interval.

trial intervals). This alternative requires extensive investigation. Finally, the observed decrement for both responses during the first session may have resulted from effector fatigue and after 24 hours rest the fatigue dissipated which resulted in the similar response levels in session 2. However, in Experiment 1 effector fatigue was ruled out as the cause of the observed decrement.

Defensive reactions to threatening stimuli may be categorized into two general types: those that result in removal of the organism from the threatening situation or those that are attempts to frighten or ward off the threat. Withdrawal and escape reactions are of the first type, while mobbing and deimatic reactions are of the second type. The dewlap response, as studied in the present experiments, would also appear to be of the latter type. The mobbing response of chaffinches shown towards predator models habituates and rapidly recovers to about 60 % in 30 minutes, with retention of habituation evident for days (Hinde, 1954a, 1954b, 1960). The deimatic (frightening) reaction of mantids to a predator and possible predators (live birds) habituated in 30 3-min presentations. Recovery was complete after 2 and 6 days of rest, with evidence of retention of habituation at both intervals (Balderrama & Maldonado, 1971). In contrast, the dewlap response completely recovered within 15 minutes, with no retention after 24 hours.

Substantial recovery of an OKR after a few minutes rest and complete recovery after 24 hours has also been found in turtles (Hayes et al., 1968). Hayes et al. found almost 50 % recovery of an OKR after 2 minutes rest and no retention of habituation after 24 hours. From these results and those of the present experiments,

it is suggested that OKR habituation in reptiles would occur rapidly in the early trials (Experiment 1) and would rapidly recover with minimal or no retention after 24 hours rest.

Experiment 3: Individual Consistency in Response Habituation

Experiments 1 and 2 were concerned with the effects of different treatments (intertrial intervals, recovery intervals) on each response as a means for determining the extent of similarities and differences in the habituation of those responses. The present experiment was concerned with individual consistency in habituation as another procedure for investigating similarities and differences between responses. This is discussed more fully below.

Individual differences in habituation are considered a major characteristic of habituation (Denny & Ratner, 1970; Ratner, 1970). The relatively few reports of individual differences in habituation indicate that, with repeated testing in the same situation, the differences may be relatively consistent (Bohlin, 1973; Cook, 1971; Gardner, 1968; Koepke & Pribram, 1966; Lát & Gollová-Hémon, 1969). However, "The question of whether individual differences in habituation are stable across different habituation tests using the same subjects is not yet answered" (Ratner, 1970, p. 58).

Although neither Thompson and Spencer (1966; Groves & Thompson, 1970) nor Askew and Leibrecht (1973) deal specifically with individual differences in habituation, it is theoretically important for both positions. The dual-process theory implies that an individual will, across responses, habituate in a similar manner because of the similarity of the underlying mechanisms. In contrast, Askew and Leibrecht imply that an individual would more likely habituate in a different manner from one response to another, depending upon the extent of the differences between the selection pressures that

operated on the habituation of those responses during the evolution of the species.

It should be noted that habituation is not necessarily a fixed property of an individual (Ratner, 1970), but rather is something that may occur when a response is repeatedly elicited. This is consistent with Askew and Leibrecht and suggests minimal or no individual consistency in habituation across responses.

Method

Subjects. Forty-six A. carolinensis (50-72 mm), 36 of which were selected from animals employed in Experiment 1 and 10 were naive, served as subjects. The 36 animals were chosen at random from each response group of Experiment 1. At least one month intervened between the time an animal was used in the first experiment and employed in the present experiment.

Procedure. Each animal was tested twice on both the dewlap and OKR with a 4 day (96 hr) interval between each test. Four days appeared to be sufficient time to allow for recovery with no retention since there was no retention of habituation after 24 hours in Experiment 2. Responses were elicited as in previous experiments. Each session consisted of 40 trials, each trial of 30 seconds duration, with a 5 sec ITI. A 5 sec ITI was employed because with that ITI both larger and smaller Anoles habituated on the dewlap response and OKR. In addition, there were no differences between the two sizes within a response under the 5 sec ITI condition (see Experiment 1, Figure 7). The order of testing responses was counterbalanced. An animal was tested on each response (both sessions) at

the same time of day \pm 5 minutes.

Results

The mean response levels for each session of the dewlap and OKR are shown in Figure 13. Habituation occurred in each session and response as can be seen in Figure 13. Note also that in Figure 13 there is no evidence of retention of habituation of the OKR after 4 days of rest. However, there is retention for the dewlap response. In Experiment 1, habituation of the dewlap response was related to the size of the Anoles. Experiment 2 employed only larger animals, while both larger and smaller Anoles were employed in the present experiment. Therefore, the possibility existed that perhaps retention of habituation of the dewlap response is also related to size. Thus the data were analyzed for smaller ($n = 27$) and larger ($n = 19$) animals, the results of which are presented in Figures 14 and 15 for smaller and larger Anoles, respectively, and in Table 19.

A two-way analysis of variance with repeated measures on both factors (Winer, 1971, p. 496) is presented in Table 19 for larger and smaller Anole. Retention of habituation of the dewlap response was evident for the smaller Anoles (Figure 14 and Table 19) and larger Anoles (Table 19). In addition, the Trial Blocks factor (B) was significant for both sizes, further substantiating that habituation occurred which is in agreement with the results of Experiment 1.

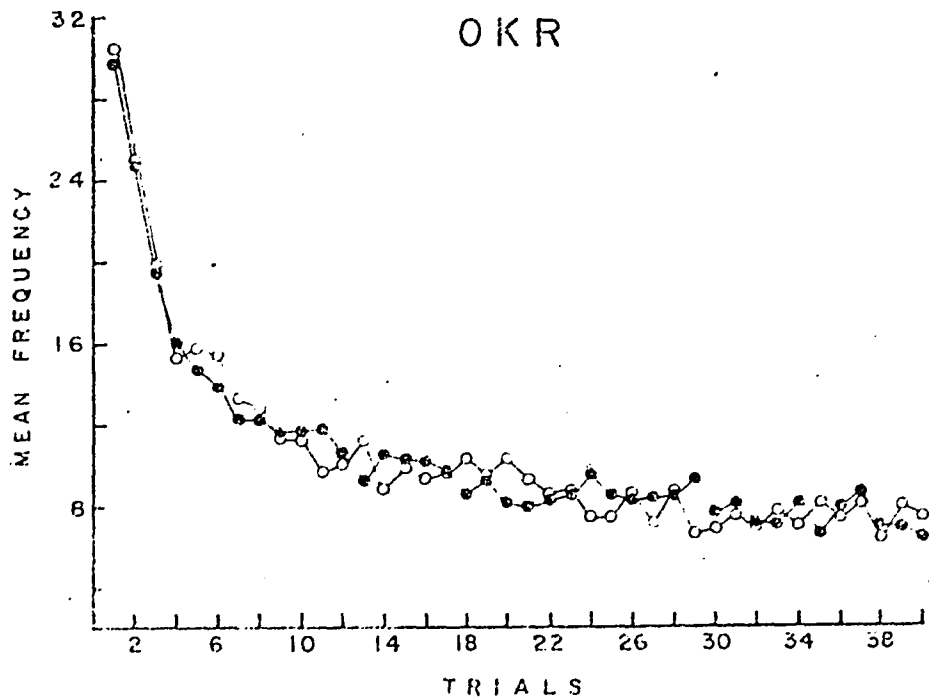
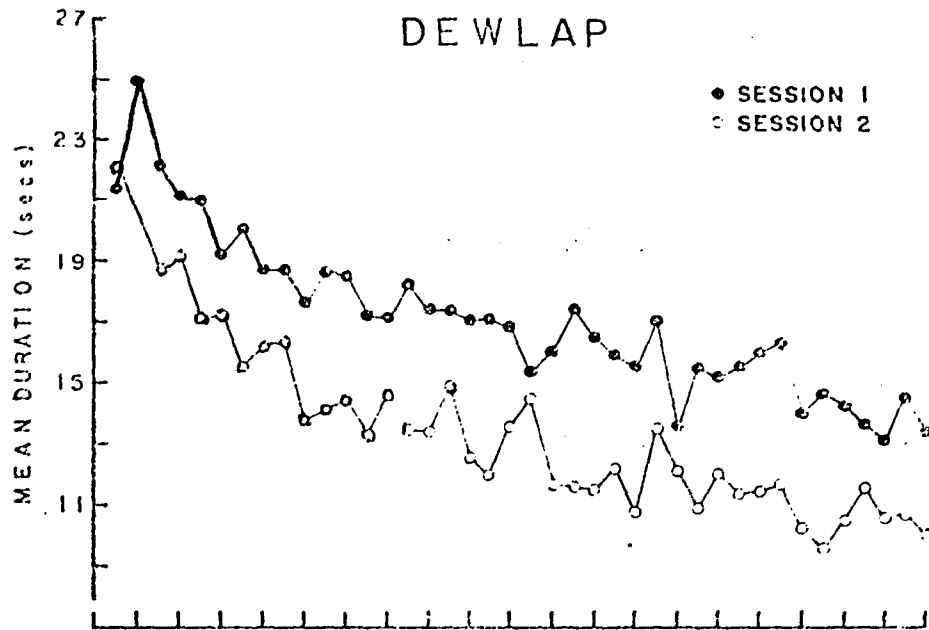


Fig. 13. Mean response levels for each session of the dewlap response and OKR.

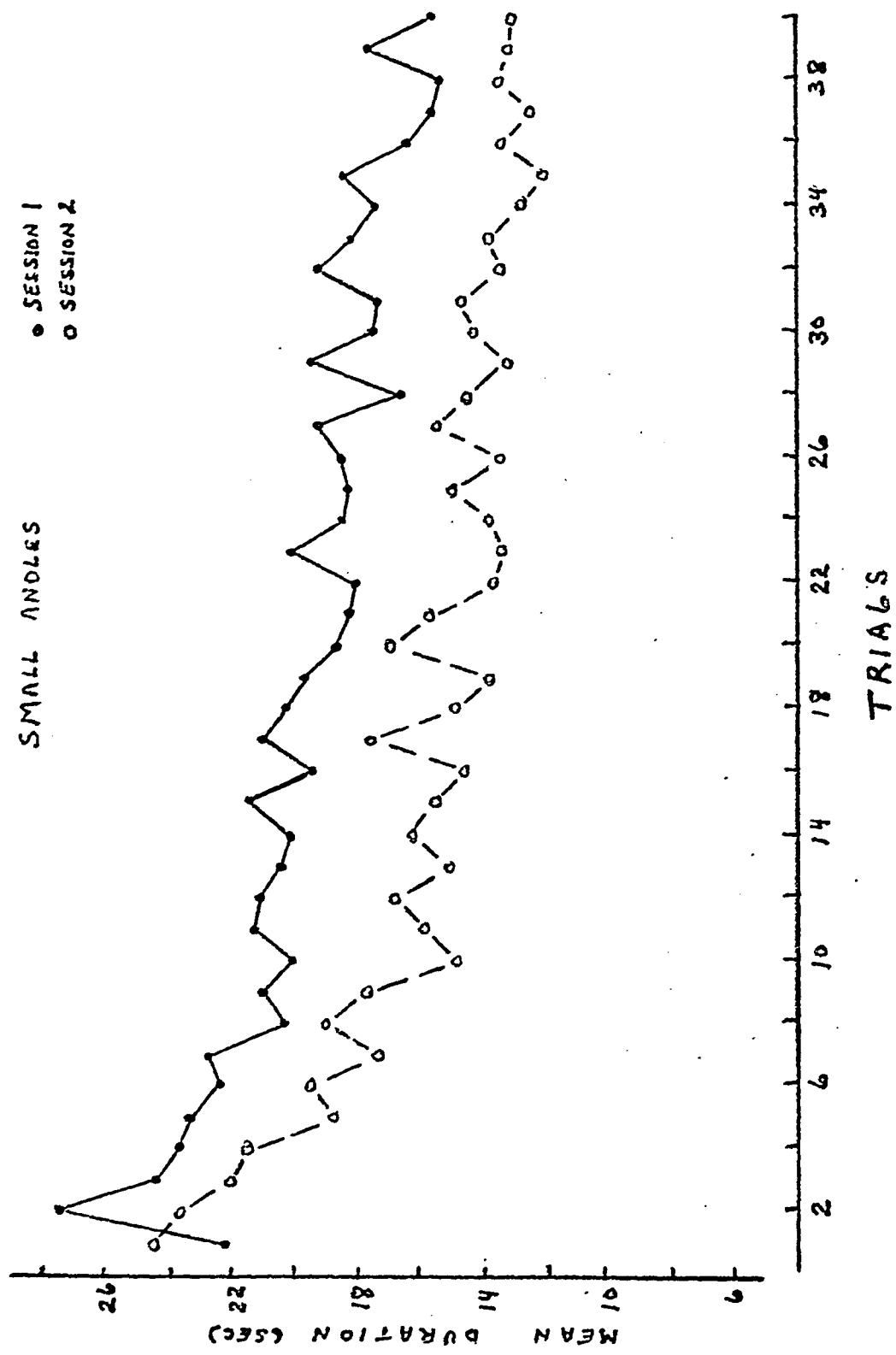


Fig. 14. Mean response levels for smaller Anoles for each session of the dewlap response

LARGE ANOLES

● SESSION 1
○ SESSION 2

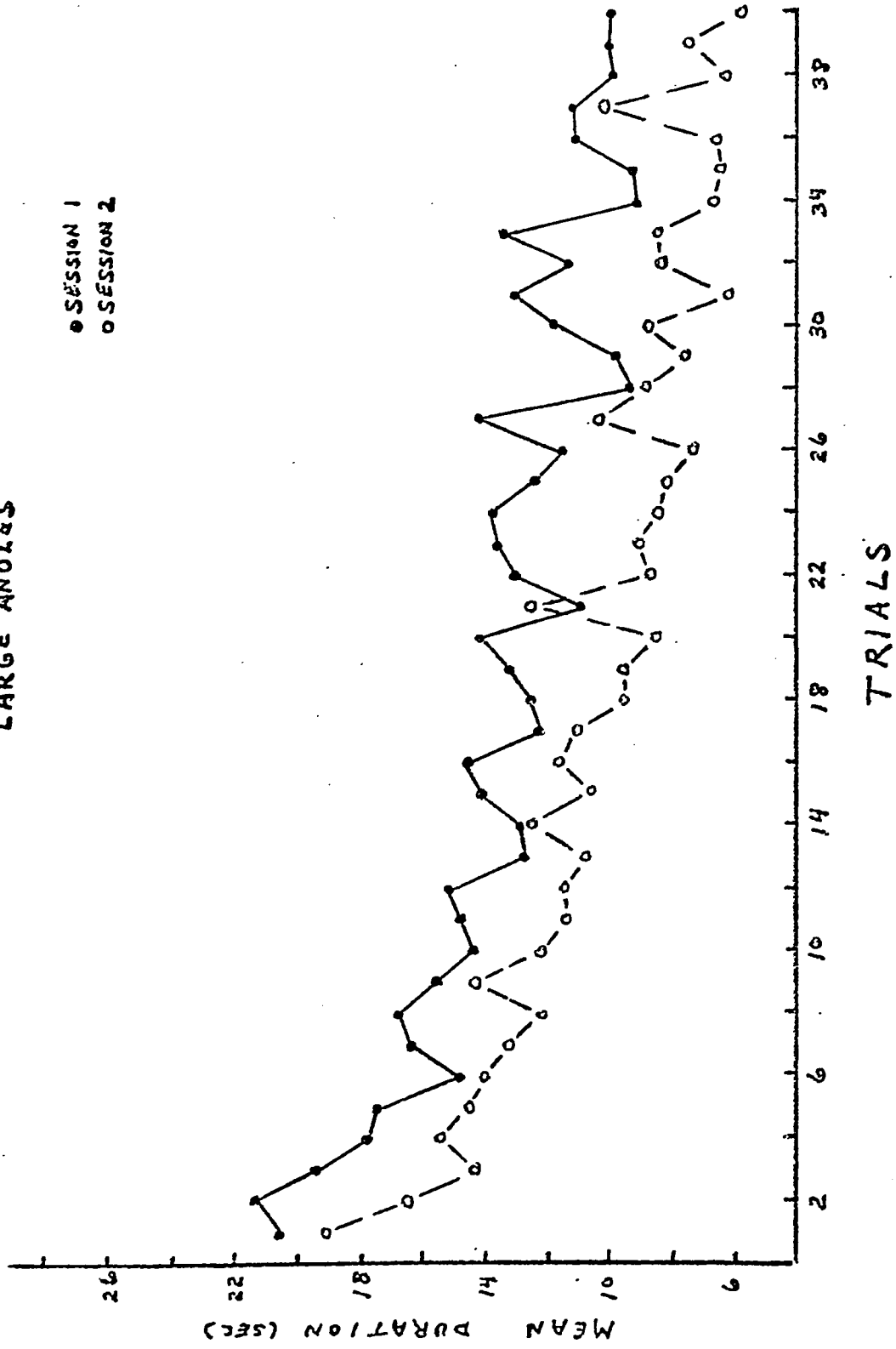


Fig. 15. Mean response levels for larger Anoles for each session of the delay response

TABLE 19

TWO-WAY ANALYSES OF VARIANCE WITH REPEATED MEASURES FOR THE
DEWLAP RESPONSE OF LARGER AND SMALLER ANOLES

Source	LARGER ^a ANOLES			SMALLER ^b ANOLES		
	<u>df</u>	<u>MS</u>	<u>F</u>	<u>df</u>	<u>MS</u>	<u>F</u>
A (Sessions)	1	722.93	5.74*	1	1666.16	11.78**
S (Subjects)	18	1069.14		26	1184.38	
Err (AS)	18	125.88		26	141.39	
B (Trial Blocks)	7	329.93	12.66**	7	389.78	19.98**
AB	7	2.76	.16	7	11.85	.88
Err (BS)	126	26.07		182	19.51	
Err (ABS)	126	16.87		182	13.39	

^a $\underline{n} = 19.$ ^b $\underline{n} = 27.$

* $\underline{p} < .05.$ ** $\underline{p} < .01.$

Prior habituation on one response may have affected the course of habituation on the other response even after 4 days of rest. This possibility was tested by comparing the session 1 response levels of those animals tested first on the dewlap response (or OKR) with those tested second on the dewlap response (or OKR). Two-way analyses of variance with repeated measures on one factor were employed for those comparisons and are presented in Table 20. The order of testing had no effect on habituation of the OKR, $\underline{F}(1,44) = .42$, but had an effect on the dewlap response, $\underline{F}(1,44) = 4.20$, $\underline{p} < .05$. Response level was lower for those animals tested

second on the dewlap response (Neuman-Keuls test, $p < .01$).

TABLE 20

TWO-WAY ANALYSES OF VARIANCE FOR COMPARISONS OF ANOLES TESTED
FIRST ON ONE RESPONSE WITH ANOLES TESTED
SECOND ON THE SAME RESPONSE

Source	df	DEWLAP		OKR	
		MS	F	MS	F
A (Order)	1	2577.27	4.20*	32.79	.42
Err (Bet)	44	614.09		78.93	
B (Trial Blocks)	7	314.36	15.53**	884.38	98.94**
AB	7	16.98	.84	5.87	.66
Err (W)	308	20.24		8.94	

* $p < .05$. ** $p < .01$.

Thus being tested first on the OKR had an effect on later habituation on the dewlap response, while being tested first on the dewlap response had no effect on later OKR habituation. The effect of order of testing on the dewlap response (Table 20) was further analyzed by making similar comparisons for larger and smaller Anoles as those made above. Table 21 summarizes the results of two-way analyses of variance with repeated measures on one factor for the effect of order of testing on the dewlap response for larger and smaller animals. Smaller Anoles were not affected by the order of testing, $F(1,25) = 0$, while larger Anoles were affected, $F(1,17) = 13.75$, $p < .01$. The overall response level for larger Anoles ($n = 11$) habituated second on the dewlap response was less than the response level of larger Anoles ($n = 8$) tested first on

the dewlap.

TABLE 21

TWO-WAY ANALYSES OF VARIANCE FOR LARGER AND SMALLER ANOLES
COMPARING SESSION ONE RESPONSE LEVELS OF DEWLAP
RESPONSE AS A FUNCTION OF ORDER OF TESTING

Source	LARGER ANOLE ^a			SMALLER ANOLE ^b		
	<u>df</u>	<u>MS</u>	<u>F</u>	<u>df</u>	<u>MS</u>	<u>F</u>
A (Order)	1	4859.62	13.75 [*]	1	1.19	.00
Err (Bet)	17	353.48		25	610.89	
B (Trial Blocks)	7	156.73	6.70 [*]	7	163.74	8.70 [*]
AB	7	20.83	.89	7	12.34	.66
Err (W)	119	23.41		175	18.81	

^an = 19. ^bn = 27. *p < .01.

Comparisons of session 1 with session 2 of the dewlap response indicated that retention was present after 4 days of rest for (1) smaller animals tested first on the dewlap response, $\underline{F}(1,13) = 4.74$, $\underline{p} < .05$, and those habituated second on the dewlap, $\underline{F}(1,12) = 10.76$, $\underline{p} < .01$, and (2) larger Anoles tested second on the dewlap, $\underline{F}(1,10) = 5.33$, $\underline{p} < .05$. However, larger animals tested first on the dewlap response showed no retention after 4 days, $\underline{F}(1,7) = 1.31$, which agrees with the results of Experiment 2 (viz., no retention after 24 hours rest).

The time of day (0900-1400 vs 1400-1900 hrs) had no effect on dewlap response, $\underline{F}(1,44) = 1.40$, or the OKR, $\underline{F}(1,44) = .23$.

Data for individual animals are presented below in an attempt to clarify the extent of the similarities and differences in

habituation of the dewlap response and OKR within individuals (intra-individual) and between individuals (inter-individual).

Analyses of Individual Data

Because of the non-normality of the data, Spearman rank order correlations were employed throughout. The below analyses focused upon Trials 1-15 since most of the response decrement for the dewlap and OKR occurred within those trials (cf. Figure 13).

Inter-individual Variability (Within Each Response). The means for each animal on the first block of 15 trials of session 1 were correlated with their means on the first block of 15 trials of session 2. The obtained r_s were $+.8257$ for the dewlap response, $t(44) = 9.71$, $p < .01$, two-tailed, and $+.6973$ for the OKR, $t(44) = 6.45$, $p < .01$, two-tailed. These significant correlations indicate that inter-individual differences were maintained at a similar rank order when animals were repeatedly tested on the same response. In other words, individuals seemed to maintain, from one session to the next, a constant level of responding relative to the other animals.

To further clarify the relationship between habituation on the dewlap response and habituation on the OKR, the first 15 trials of session 1 of the dewlap response and OKR are presented for each individual ($n = 46$) in Figures 16A (Ss 1-20), 16B (Ss 21-40) and 16C (Ss 41-46). Those curves that are for larger animals are indicated by an "L" located beneath the subject (Ss) number, all of the other curves are those of smaller Anoles.

Inter-individual variability is immediately obvious from these

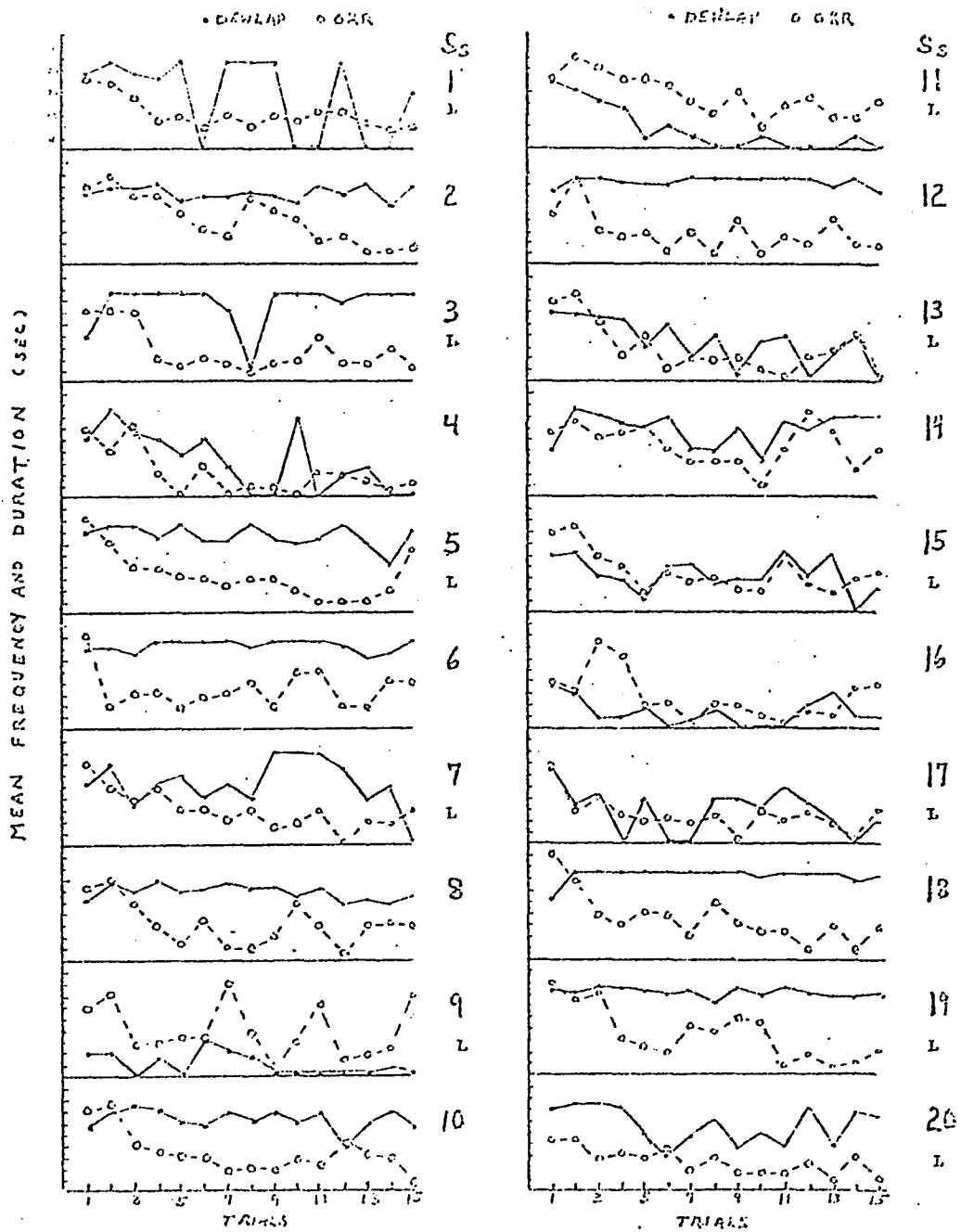


Fig. 16A. Response levels for each individual (Ss 1-20) on the first 15 trials of session 1 of the dewlap response and OKR.

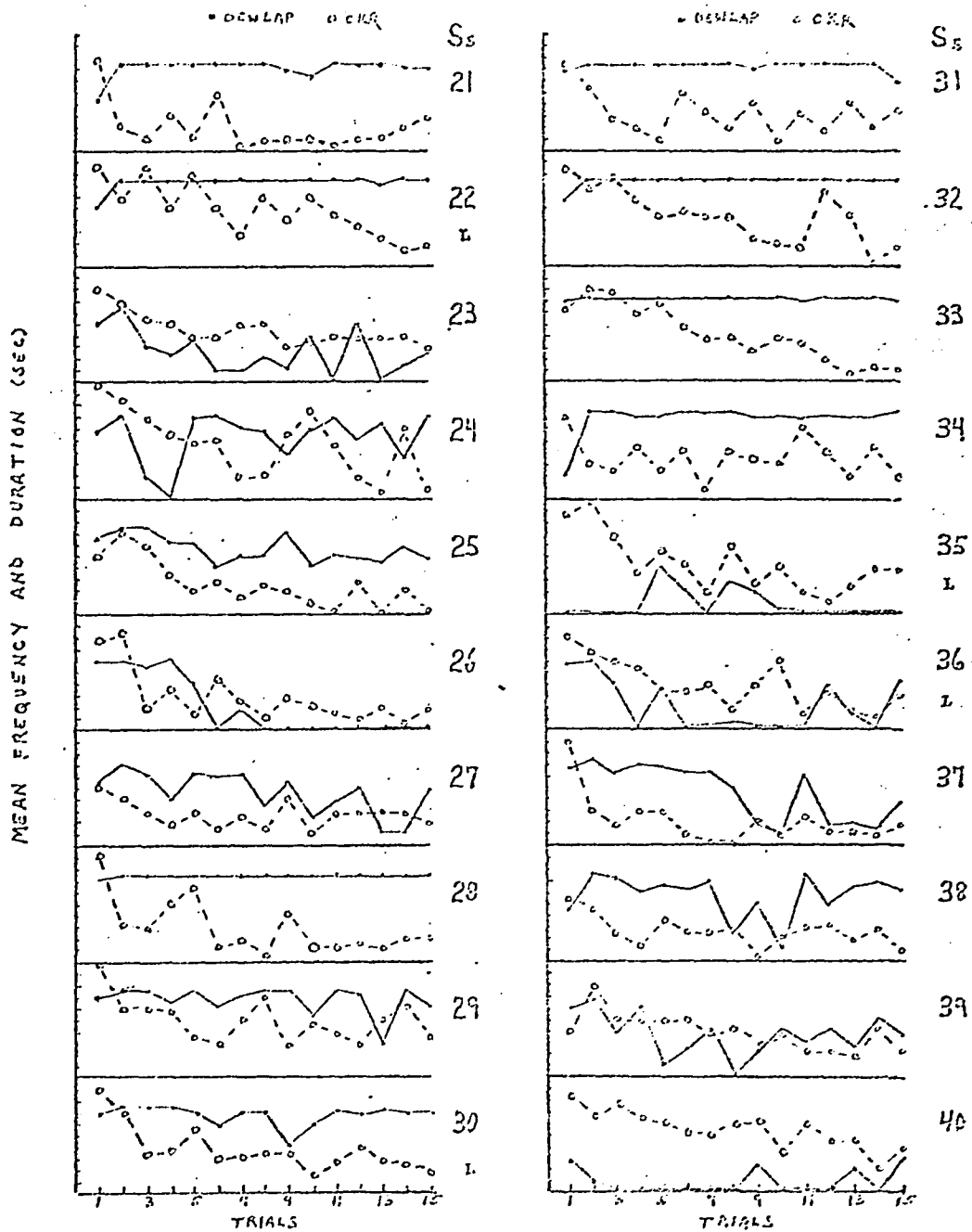


Fig. 16B. Response levels for each individual (Ss 21-40) on the first 15 trials of session 1 of the dewlap response and CKR.

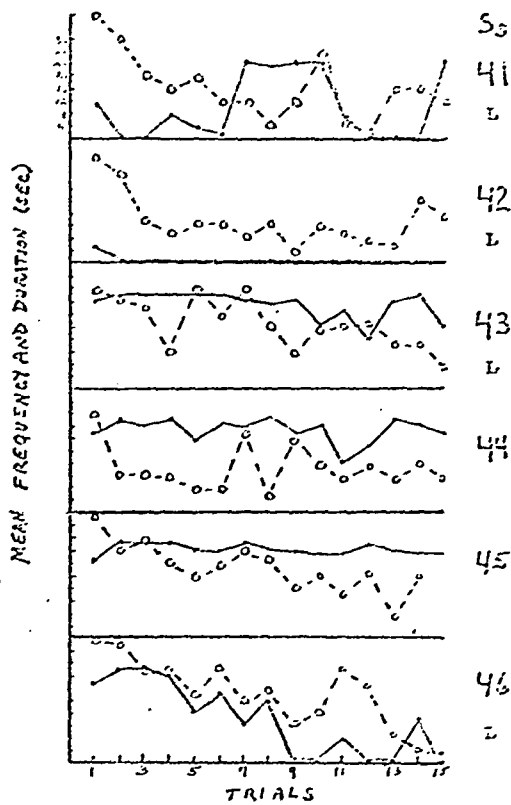


Fig. 160. Response levels for each individual (Ss 41-46) on the first 15 trials of session 1 of the dewlap response and OER.

figures and such variability is typical of habituation curves. There are various curve types or patterns of responding in the dewlap response from one animal to the next. Some animals (e.g., Ss 1, 20, 24) show marked fluctuations in dewlap responding, while others show minimal fluctuations (e.g., Ss 8, 19). Note that for some individuals ($\bar{n} = 20$), the dewlap response either did not decrement or only minimally decreased within 15 trials (e.g., Ss 6, 12, 21, 32, 45), while several animals responded at very low levels (e.g., Ss 9, 26, 35, 40, 42). In contrast, the inter-individual differences in the OKR were not as variable as those of the dewlap response. Note that the OKR curves show a similar decreasing pattern for each individual, except perhaps for Ss 16 and 20.

Intra-individual Variability (Between Responses). The means for each Anole on the first 15 trials of session 1 of the dewlap response were correlated with their corresponding means on session 1 of the OKR, yielding an $\underline{r} = +.0504$, $\underline{t} (44) = .358$. Thus individual animals varied unsystematically across responses in their initial levels of responding as compared to their consistency in responding from session 1 to session 2 of the same response (see above).

Inspection of the response patterns of the dewlap and OKR within each individual indicates that there is no systematic relationship between the two curves that is common to all animals. Within the same individual, the dewlap and OKR curves may be similar (e.g., Ss 4, 11, 13, 14, 23, 25, 39, 46) or different (e.g., Ss 3, 6, 12, 18, 28, 32) in form. For example, within Ss 11 and

13 the dewlap response and OKR show a similar decreasing pattern, while in Ss 18, 19 and 31-34 the dewlap response wanes slightly or not at all but the OKR decreases. Correlations between the first 15 trials of session 1 of the dewlap response and of the OKR (as shown in the previous figures) were computed for each individual and are listed in Table 22 below.

TABLE 22

EACH INDIVIDUAL ANOLE'S SPEARMAN RANK ORDER CORRELATION
BETWEEN THE FIRST 15 TRIALS OF THE DEWLAP AND OKR

Anole	$r^{a,b}$	Anole	r
1	+.4362	24	-.2554
2	+.2207	25	+.5998**
3	+.2712	26	+.5779**
4	+.3725	27	+.2683
5	+.4664*	28	-.4373
6	+.0156	29	+.1798
7	-.2446	30	+.2384
8	+.0337	31	-.4505*
9	+.5167**	32	-.4373
10	+.1054	33	+.1126
11	+.5933**	34	-.4549*
12	-.1429	35	+.2602
13	+.5018*	36	+.2932
14	+.3006	37	+.6348**
15	+.4360	38	+.2081
16	+.2919	39	+.2539
17	+.4098	40	+.1677
18	+.1139	41	-.1022
19	+.3007	42	+.4350
20	+.3415	43	+.2448
21	-.3560	44	-.2626
22	-.1270	45	+.2462
23	+.2538	46	+.7595***

^adf = 13. ^bt test of significance. *p < .10. **p < .05.

***p < .01, all ps two-tailed.

Six correlations were significant, while four correlations appro-

ached significance ($p < .10$). Neither size nor order of testing differentiated those ten animals with the significant correlations from the other Anoles.

For each animal, the slope of the linear component of the 40 trials of session 1 of the dewlap response were correlated with their corresponding linear slope on session 1 of the OKR. The correlation between the slopes of the linear component was not significant, $r = +.1897$, $t(44) = 1.28$.

The number of trials to asymptote (defined as the first trial, after Trial 1, at which the response level was equal to or less than the mean response level of the last 5 trials) were correlated across responses, yielding a nonsignificant $r = +.2245$, $t(44) = 1.53$.

Summary of Results of All Three Experiments

EXPERIMENT 1

	Dewlap	OKR	Swimming
General Results		Habituation occurs 5 sec \neq 30, 120 ITI Large = Small Ss	Habituation occurs Each ITI differed Large = small Ss
Larger Anoles	Habituation occurs Large = small Ss at 5 sec ITI Large \neq small Ss at 30, 120 sec		
Smaller	Habituation only at 5 sec ITI, none at 30, 120		

Note. Summary of results continued on following page.

Summary of Results of All Three Experiments (cont'd.)

EXPERIMENT 2			
	Dewlap	OKR	Swimming
General Results	Habituation occurs 95 % recovery in 15 minutes No retention in 24 hours	Habituation occurs 80 % recovery in 15 minutes No retention in 24 hours	Response not employed
Larger Anoles	Same as above	Same as above	X
Smaller Anoles	Not employed	Not employed	X

EXPERIMENT 3			
	Dewlap	OKR	Swimming
General Results	Habituation occurs	Habituation occurs No retention in 4 days No size difference No effect of order of testing	Response not employed
Larger Anoles	Effect of order of testing Ss tested first show no retention (4 days)	Same as above	X
Smaller Anoles	No effect of order of testing Retention after 4 days	Same as above	X

Discussion

As in the previous experiments, habituation occurred in both responses and sessions. Retention of habituation on the OKR was absent after 4 days of rest for larger and smaller Anoles. This lack of retention on the OKR agrees with the results of Experiment 2. Larger animals first habituated on the dewlap response (no intervening OKR experience) showed no retention of habituation, which also agrees with the results of Experiment 2 for the dewlap response. However, smaller Anoles retained habituation on the dewlap response even after 4 days of rest, which was totally unexpected given the findings of Experiment 2. Why this is so cannot be determined from the available data. Perhaps retention is influenced by the reproductive status of the animals, prior experience or other maturational changes. Maturation changes (e.g., development of adrenergic and cholinergic systems) have been suggested to account for the differences between younger and older rats in the habituation of exploratory behavior (Feigley et al., 1972) and its possible retention (Parsons et al., 1973). However, younger rats showed poorer retention of habituation than did older rats as compared to the better retention of younger Anoles in the present experiment. Larger Anoles have been observed to be in more exposed areas compared to females and subadult males which hide in dense vegetation (Gordon, 1956; Schoener, 1968). No retention of habituation of the dewlap response (after 24 hours or 4 days) may be advantageous for Anoles in exposed places, particularly if the dewlap is involved in several different behavior pat-

terns. This offers no explanation, however. It does suggest again the possible influence of reproductive state since defense of territory and courtship are correlated with size and reproductive status in A. carolinensis. Note, however, that the 4 day retention found for smaller Anoles is consistent with the long-term retention of other defensive reactions mentioned earlier (i.e., Balderama & Maldonado, 1971; Hinde, 1954b, 1960). Although there were no time of day effects on habituation, there may have been some seasonal effects on responding and retention since the experiments were conducted over a 7 month period. This possibility requires further investigation.

For larger Anoles habituated first on the OKR, their session 1 response level on the dewlap was lower than the first session response level of larger animals habituated first on the dewlap. This suggests the possible influence of the prior OKR habituation experience for larger Anoles, which was not evident for smaller animals. Whether the lower response level is a function of being habituated specifically on the OKR remains an open question. It is possible that another intervening event (e.g., learning an escape response) might influence the dewlap response level. The retention evident in the second session may be an artifact of the combined influence of the prior OKR training and the "weaker" response levels given in session 1. This evidently requires clarification.

Thus within the dewlap response, retention may be related to factors associated with size differences. Reproductive status and maturational changes or experience were offered as possible fac-

tors. The OKR was not affected by size differences nor by prior habituation on the dewlap response. This suggests that the response systems are different.

Individuals were consistent when tested twice on the same response and this agrees with other findings (Cook, 1971; Gardner, 1968; Koepke & Pribram, 1966; Lat & Gollová-Hémon, 1969). Intra-individual differences were less consistent. Whereas within some individuals the dewlap response and OKR showed similar response patterns, in other individuals the patterns were different. There were basically two response patterns within individuals, either both responses showed a decreasing pattern or the OKR decreased while the dewlap did not. It is not clear why there was sensitization of the dewlap response in some animals but not in others. Size differences did not appear to be involved. Further investigations are evidently necessary.

Thus the results of the individual data neither refute nor confirm general process theories of habituation, but suggest that habituation within individuals is not necessarily similar from one response to another.

A final point that warrants mentioning and which has been indirectly alluded to earlier is that the size differences in the habituation of the dewlap response may be related to some ultimate evolutionary factors. What these factors might be is not known. One possibility suggested by Selander (1965) for birds and by Rand (1967) for lizards relates to inter-male competition for mates and the age of first breeding. Accordingly, a male lizard

will defend (a territory) when it would increase the likelihood of his contributing to the gene pool. Typically, a small male (younger) has little chance of defeating a larger (older) male, but is more likely to outlive the older male. It might be expected that younger males would concentrate on driving away other smaller males that would be competitors for the future territory and mates. In other words, younger males are less likely to compete successfully for mates with older experienced males and thus younger males that delay breeding may have an overall greater chance of passing on their genes. In addition, younger males may heighten their breeding success by experience in territorial and courtship behavior prior to breeding by eliciting responses from other males and females. Recall that young male A. carolinensis fight both males and females (L. Evans, 1957) indiscriminately unless treated with male hormones. This above possibility (selection for delayed age of first breeding) is complementary to the earlier suggestion that the differences found within the dewlap response may be related to the reproductive status of the animals.

CHAPTER IV

GENERAL DISCUSSION

The major purpose of this dissertation has been the development of a within-species comparative approach to habituation. This approach was derived from an alternative view of habituation (Askew & Leibrecht, 1973) to that of general process theories such as Thompson and Spencer (1966; Groves & Thompson, 1970). The critical assumption of the general process theories, as reflected in the dual-process theory, is that similarities in the characteristics of behavioral response habituation across various species and responses implies the operation of similar physiological processes and/or mechanisms. Differences in behavioral response habituation have been virtually ignored and basically unaccounted for. Comparative studies of habituation have not been typically employed. In contrast, the present dissertation was not designed to investigate the "mechanisms underlying habituation", but rather to study the similarities and differences in behavioral response habituation by means of a comparative method.

Similarities and differences in habituation were clearly evident in the responses studied. The most striking result was the differences between the dewlap and the other responses. Only in the habituation of the dewlap response were size differences present.

The extent to which the mechanisms underlying habituation, particularly in the dewlap response and OKR, are similar cannot of

course be ascertained from the above data. Rather, extensive neurophysiological investigations are required. Another difficulty in speculating about the possible similarities or differences in the mechanisms underlying habituation is in the meaning of mechanisms and/or processes. By mechanism or process, Thompson and Spencer (1966) are referring specifically to changes occurring at the cellular and synaptic level, while Askew and Leibrecht (1973) refer to changes occurring at all levels from synaptic to brain structures. The two orientations are not totally incompatible, if one assumes that the mechanisms of Thompson and Spencer may operate at various levels but that the levels may interact in different ways to produce different behavioral outcomes.

The present data do not refute nor confirm either orientation. Habituation of the OKR appears to be independent and different from that of the dewlap response (no effect of size or prior habituation) which would offer some support for Askew and Leibrecht, while the dewlap response may be influenced by prior habituation on the OKR in support of Thompson and Spencer. Analyses of individual data offer support for both positions. However, whether the mechanisms underlying habituation of the dewlap response and OKR are similar or not, it appears that the two responses are at least functionally distinct and that the course of habituation may be related to the response system.

The results of the present experiments suggest several possible lines of research that should be pursued. These lines of research are outlined next.

Future Research

Recovery and retention of habituation of the dewlap response in smaller animals should be investigated beyond a 4 day interval (Experiment 3).

The size differences in dewlap habituation (Experiment 1) and retention (Experiment 3) should be studied developmentally. Several developmental studies are possible: (a) a long-term developmental study in which the same animals are tested throughout their life span. Such a study would reveal how habituation of the dewlap changes with age. At each age tested, a comparable age-size group would be employed, one such group raised in the laboratory and another group recently captured in the field. Since Anoles may require several years to reach adulthood, another possible approach would involve (b) a short-term longitudinal study in combination with a cross-sectional approach. In other words, several age-size groups (hatchlings, immature males, young females) could be studied at the same time over a period of months rather than years. In conjunction with the above, it would be of value to (c) manipulate prior experience of contact with threatening stimuli. It was suggested earlier that the observed size differences on the dewlap response may be related to reproductive status. Therefore, it would be of importance to (d) manipulate reproductive status of immature males and females through hormonal treatment.

Since prior OKR habituation may affect dewlap habituation in larger Anoles, a study manipulating the type and recency of prior experience in larger Anoles should be conducted.

Information of the reactions of A. carolinensis to predators in the field is imperative. In addition, habituation should be studied in several other responses (e.g., reaction to live prey).

CHAPTER V

SUMMARY AND CONCLUSIONS

The present dissertation examined a within-species comparative approach to habituation as derived from an alternative approach to general process theories of habituation.

Several major theories of habituation were reviewed and were categorized as "general process" theories. General process theories attempt to explain habituation in different species and responses in terms of a limited set of "mechanisms" and/or "processes". The dual process theory of Thompson and Spencer (1966) and Groves and Thompson (1970) was examined because it is the most detailed and widely cited theory of habituation and because it best exemplifies the general process approach and the assumptions underlying general process theories of habituation.

From literature on intact organisms, Thompson and Spencer abstracted the most commonly observed characteristics of behavioral response habituation. There appeared to be virtually complete agreement across species and responses in the characteristics of habituation. For example, with repeated stimulation a response decreases; an habituated response recovers with rest; the faster the stimulation the faster or more pronounced is habituation. In total, "nine parametric characteristics" of habituation were abstracted from the literature. Similar characteristics were also demonstrated at the neuronal level. This led the dual-process theorists to suggest that similar or common physiological mecha-

nisms and/or processes underlying habituation in different species and responses. By focusing on similarities, Thompson and Spencer appear to have ignored the differences in behavioral response habituation. It was argued that, contrary to the general process approach exemplified by Thompson and his associates and other theorists reviewed, there are differences across (and within) species and responses and that the course of habituation may be related to the functional significance or nature of the response or response system.

The behavioral response habituation literature was reviewed in an attempt to assess the extent of species and response diversity in habituation. It was evident from that review that there are important species and response differences (and similarities) in habituation and that the course of habituation may indeed be related to the nature of the response system. The generality of the similarities in habituation at the behavioral level has been questioned previously (Askew, 1970; Hinde, 1970b).

The general process approach does not adequately deal with species and response diversity in behavioral response habituation or with the functional significance of a response. What appears to be needed is a conceptual framework within which species and response differences and similarities in habituation can be adequately assimilated and interpreted. Such an alternative conceptualization was outlined as presented by Askew and Leibrecht (1973). This alternative orientation views habituation within an evolutionary context. Accordingly, a response decrements as a result of

selection pressures favoring the development of habituatory mechanisms and processes underlying that response. The similarity in the habituation of responses across and within species implies the operation of similar selection pressures acting on those species and responses. The mechanisms and/or processes underlying habituation in those species and responses may or may not be similar in ways other than function. Differences in habituation across species and responses implies the operation of different selection pressures and the possibility of differences in the mechanisms and/or processes underlying habituation, although this need not be so.

The emphasis of the general process theories on the similarities in habituation across species and responses has hindered systematic comparative investigations of habituation as evidenced by the scarcity of such studies. In contrast, an evolutionary approach (Askew & Leibrecht, 1973) necessarily encourages comparative studies. A within-species comparative method was derived from this alternative perspective on habituation and was employed in the present dissertation. Basically, a within-species approach involves the investigation of similarities and differences in the habituation of various responses within a single species.

The lizard Anolis carolinensis was selected because of the paucity of habituation studies in reptiles. The background literature on A. carolinensis, its limited behavioral repertoire and the availability of related species for future comparative research provide further advantages in using this species. From pilot data

three responses were chosen for study: dewlap extension, optokinetic (OKR) and swimming response. Dewlap extension refers to the distension of the "throat fan" which was elicited by presenting a live house sparrow. OKR refers to distinct head movements (following) elicited by rotating a field of moving stripes, and swimming refers to an animal actively moving while in water. The dewlap response is involved in courtship and intraspecific fighting, while the OKR is probably involved in visually guided behaviors (e.g., prey capture). Behavioral experiments were conducted to investigate each of the following characteristics of habituation: effects of intertrial interval (ITI), spontaneous recovery and individual differences.

ITIs (5, 30 and 120 sec) had various effects (Experiment 1). The habituation curves for each ITI of the swimming response differed, while in the OKR the 5 sec ITI was different from the 30 and 120 sec ITI. There were no differences between ITIs of the dewlap response. However, comparisons of larger and smaller Anoles indicated that smaller animals did not habituate under the 30 and 120 sec ITI condition of the dewlap response, whereas no ITIs differed for larger Anoles. There were no size differences in the OKR or swimming response. Comparisons across responses indicated that the dewlap response in smaller Anoles differed from the OKR and swimming response under each ITI condition, but only under the 5 sec ITI condition for larger animals. The OKR did not differ from the swimming response for larger or smaller Anoles.

Larger animals were employed for studying spontaneous recovery

of the dewlap response and OKR in Experiment 2. After a 15 minute interval, recovery was virtually complete (95 %) for the dewlap response and was quite substantial (80 %) for the OKR, while retention (lower response level) was clearly evident. After a 24 hour interval, recovery was complete with no evidence of retention for either response.

Individual differences in habituation were consistent when animals were tested twice on the same response (Experiment 3). In contrast, there was less consistency across responses (dewlap and OKR). Approximately 57 % of the animals showed similar patterns of habituation on the dewlap response and OKR, while the rest did not. Further, smaller Anoles showed retention of habituation of the dewlap response after 4 days of rest and were not affected by the order of testing. Larger Anoles tested first on the dewlap response showed no retention on the dewlap habituation as opposed to larger animals tested second on the dewlap response.

It was suggested that perhaps reproductive status, prior experience or other maturational changes might account for the size differences in dewlap habituation. Several lines of future research were outlined.

REFERENCES

- Applewhite, P. B. Non-local nature of habituation in a rotifer and protozoan. Nature, 1968, 217, 287-288.
- Applewhite, P. B. Similarities in protozoan and flatworm habituation behaviour. Nature, New Biology, 1971, 230, 284-285.
- Applewhite, P. B., & Gardner, F. T. Theory of protozoan habituation. Nature, New Biology, 1971, 230, 285-287.
- Applewhite, P. B., & Morowitz, H. J. The micrometazoa as model systems for studying the physiology of memory. Yale Journal of Biological Medicine, 1966, 39, 90-105.
- Archer, J. Tests for emotionality in rats and mice: A review. Animal Behaviour, 1973, 21, 205-235.
- Askew, H. R. Effects of stimulus intensity and intertrial interval on habituation of the head-shake response in the rat. Journal of Comparative and Physiological Psychology, 1970, 72, 492-497.
- Askew, H. R., & Kurtz, P. J. Studies of the function of the abdominal rotation response in pupae of Tenebrio molitor. Behaviour, 1974, 50, 152-172.
- Askew, H. R., & Leibrecht, B. C. Evolution and general process theories of habituation (Report No. 1051). Washington, D. C.: U.S. Army Medical Research and Development Command, June, 1973.
- Askew, H. R., Leibrecht, B. C., & Ratner, S. C. Effects of stimulus duration and repeated sessions on habituation of the head-shake response in the rat. Journal of Comparative and Physiological Psychology, 1969, 67, 497-503.
- Askew, H. R., Musumeci, M., Sloane, L., & Stephan, L. Effects of prey movement and background on predatory behavior of chameleons. Psychonomic Science, 1970, 20, 171.
- Balderrama, N., & Maldonado, H. Habituation of the deimatic response in the mantid (Stagmatoptera biocellata). Journal of Comparative and Physiological Psychology, 1971, 75, 98-106.
- Barrass, R. A quantitative study of the behaviour of the male Mormoniella vitripennis (Walker) (Hymenoptera, Pteromalidae) towards two constant stimulus-situations. Behaviour, 1961, 18, 288-312.
- Bayard, J. The duration of tonic immobility in guinea pigs. Journal of Comparative and Physiological Psychology, 1957, 50, 130-133.

- Beach, F. A. The snark was a boojum. American Psychologist, 1950, 5, 115-124.
- Beach, F. A., & Jordan, L. Sexual exhaustion and recovery in the male rat. Quarterly Journal of Experimental Psychology, 1956, 8, 121-133.
- Berlyne, D. E. Conflict, arousal, and curiosity. New York: McGraw-Hill, 1960.
- Berlyne, D. E., & Slater, J. Perceptual curiosity, exploratory behavior, and maze learning. Journal of Comparative and Physiological Psychology, 1957, 50, 228-232.
- Bindra, D., & Spinner, N. Response to different degrees of novelty: The incidence of various activities. Journal of Experimental Analysis of Behavior, 1958, 1, 341-350.
- Bishop, P. D., & Kimmel, H. D. Retention of habituation and conditioning. Journal of Experimental Psychology, 1969, 81, 317-321.
- Bitterman, M. E. Toward a comparative psychology of learning. American Psychologist, 1960, 15, 704-712.
- Bitterman, M. E. Phyletic differences in learning. American Psychologist, 1965, 20, 396-410. (a)
- Bitterman, M. E. The evolution of intelligence. Scientific American, 1965, 212, 92-100. (b)
- Black, R. W., Fowler, R. L., & Kimbrell, G. Adaptation and habituation of heart rate to handling in the rat. Journal of Comparative and Physiological Psychology, 1964, 57, 422-425.
- Blizard, D. A. Situational determinants of open-field behaviour in Mus musculus. British Journal of Psychology, 1971, 62, 245-252.
- Blizard, D. A., & Wertz, R. Cardiac activity in the mouse: Strain differences. Journal of Comparative and Physiological Psychology, 1971, 77, 337-344.
- Bohlin, G. The relationship between arousal level and habituation of the orienting reaction. Physiological Psychology, 1973, 1, 308-312.
- Bolles, R. C. Grooming behavior in the rat. Journal of Comparative and Physiological Psychology, 1960, 53, 306-310.

- Bolles, R. C., & Seelbach, S. E. Punishing and reinforcing effects of noise onset and termination for different responses. Journal of Comparative and Physiological Psychology, 1964, 58, 127-131.
- Bols, R. J., & Wong, R. Gerbils reared by rats: Effects on adult open-field and ventral marking activity. Behavioral Biology, 1973, 9, 741-748.
- Boneau, C. A. The effects of violations of assumptions underlying the t test. Psychological Bulletin, 1960, 57, 49-64.
- Box, G. E. P. Some theories on quadratic forms applied in the study of analysis of variance problems: I. Effects of inequality of variance in the one-way classification. Annals of Mathematical Statistics, 1954, 25, 290-302.
- Bronstein, P. M. Open-field behavior of the rat as a function of age: Cross-sectional and longitudinal investigations. Journal of Comparative and Physiological Psychology, 1972, 80, 335-341.
- Bronstein, P. M. Replication report: Age and open-field activity of rats. Journal of Comparative and Physiological Psychology, 1973, 32, 403-406.
- Brookshire, K. H., & Rieser, T. C. Temporal course of exploratory activity in three inbred strains of mice. Journal of Comparative and Physiological Psychology, 1967, 63, 549-551.
- Brown, D. M. B., & Noakes, D. L. Habituation and recovery of aggressive display in paradise fish (Macropodus opercularis (L.)). Behavioral Biology, 1974, 10, 519-525.
- Brown, J. H. Acquisition and retention of nystagmic habituation in cats with distributed acceleration experience. Journal of Comparative and Physiological Psychology, 1965, 60, 340-343.
- Brown, J. H. Interacting vestibular stimuli and nystagmic habituation. Acta Oto-Laryngologica, 1966, 62, 341-350.
- Bruner, J., & Kehoe, J. Long-term decrements in the efficacy of synaptic transmission in molluscs and crustaceans. In G. Horn & R. A. Hinde (Eds.), Short-term changes in neural activity and behaviour. New York: Cambridge University Press, 1970.
- Buchwald, J. S., & Humphrey, G. L. An analysis of habituation in the specific sensory systems. In H. Stellar & J. Sprague (Eds.), Progress in physiological psychology. New York: Academic Press, 1972.

- Burghardt, G. Effects of prey size and movement on the feeding behavior of the lizards Anolis carolinensis and Eumeces fasciatus. Copeia, 1964, 576-578.
- Burnham, R. W. Repeated auditory stimulation of the startle response in the guinea pig. Journal of Psychology, 1939, 7, 79-89.
- Butler, R. A. Discrimination learning by rhesus monkeys to visual-exploration motivation. Journal of Comparative and Physiological Psychology, 1953, 46, 95-98.
- Butler, R. A. The reaction of rhesus monkeys to fear-provoking stimuli. Journal of Genetic Psychology, 1964, 104, 321-330.
- Butler, R. A., & Alexander, H. M. Daily patterns of visual exploratory behavior in the monkey. Journal of Comparative and Physiological Psychology, 1955, 48, 247-249.
- Butler, R. A., & Harlow, H. F. Persistence of visual exploration in monkeys. Journal of Comparative and Physiological Psychology, 1954, 47, 258-263.
- Candland, D. K., & Nagy, Z. M. The open field: Some comparative data. Annals of the New York Academy of Sciences, 1969, 159, 831-851.
- Candland, D. K., Pack, K. D., & Matthews, T. J. Heart rate and defecation frequency as measures of rodent emotionality. Journal of Comparative and Physiological Psychology, 1967, 64, 146-150.
- Carlton, P. L. Brain acetylcholine and habituation. In P. B. Bradley & M. Fink (Eds.), Progress in brain research. Vol. 28. Anticholinergic drugs and brain functions in animals and man. Amsterdam: Elsevier, 1968.
- Carlton, P. L., & Vogel, J. R. Habituation and conditioning. Journal of Comparative and Physiological Psychology, 1967, 63, 348-351.
- Carr, R. M., & Brown, W. L. The effect of the introduction of novel stimuli upon manipulation in rhesus monkeys. Journal of Genetic Psychology, 1959, 94, 107-111.
- Casarett, A. P. Swim-tank measurement of radiation induced behavioral incapacitation. Psychological Reports, 1973, 33, 731-736.
- Castellucci, V., Pinsker, H., Kupfermann, I., & Kandel, E. Neuronal mechanisms of habituation and dishabituation of the gill withdrawal reflex in Aplysia. Science, 1970, 167, 1745-1748.

- Chow, K., & Leiman, A. L. The photo-sensitive organs of crayfish and brightness learning. Behavioral Biology, 1972, 7, 25-35.
- Clark, R. B. Habituation of the polychaete Nereis to sudden stimuli. 1. General properties of the habituation process. Animal Behaviour, 1960, 8, 82-91. (a)
- Clark, R. B. Habituation of the polychaete Nereis to sudden stimuli. 2. Biological significance of habituation. Animal Behaviour, 1960, 8, 92-103. (b)
- Clayton, F. L., & Hinde, R. A. The habituation and recovery of aggressive display in Betta splendens. Behaviour, 1968, 30, 96-106.
- Cochran, D. M., & Goin, C. J. The new field book of reptiles and amphibians. New York: Putnam's Sons, 1970.
- Cohen, D. H., & MacDonald, R. L. Some variables affecting orienting and conditioned heart-rate responses in the pigeon. Journal of Comparative and Physiological Psychology, 1971, 74, 123-133.
- Collette, B. B. Correlations between ecology and morphology in Anoline lizards from Havana, Cuba and southern Florida. Bulletin of the Museum of Comparative Zoology, Harvard, 1961, 125, 136-162.
- Collins, W. E. Primary, secondary, and caloric nystagmus of the cat following habituation to rotation. Journal of Comparative and Physiological Psychology, 1964, 57, 417-421.
- Collins, W. E. Influence of head position on the habituation of vertical vestibular nystagmus in the cat. Journal of Comparative and Physiological Psychology, 1969, 67, 156-159.
- Cook, A. Habituation in a freshwater snail (Limnaea stagnolis). Animal Behaviour, 1971, 19, 463-474.
- Crampton, G. H., & Schwam, W. J. Effects of arousal reaction on nystagmus habituation in the cat. American Journal of Physiology, 1961, 200, 29-33.
- Crampton, G. H., & Schwam, W. J. Turtle vestibular responses to angular acceleration with comparative data from cat and man. Journal of Comparative and Physiological Psychology, 1962, 55, 315-321.
- Crews, D. Coition-induced inhibition of sexual receptivity in female lizards (Anolis carolinensis). Physiology and Behavior, 1973, 11, 463-468.

- Davis, M. Effects of interstimulus interval length and variability on startle-response habituation in the rat. Journal of Comparative and Physiological Psychology, 1970, 72, 177-192. (a)
- Davis, M. Interstimulus interval and startle response habituation with a "control" for total time during training. Psychonomic Science, 1970, 20, 39-41. (b)
- Davis, M. Differential retention of sensitization and habituation of the startle response in the rat. Journal of Comparative and Physiological Psychology, 1972, 78, 260-267.
- Dennenberg, V. H., Ross, S., & Blumenfield, M. Behavioral differences between mutant and nonmutant mice. Journal of Comparative and Physiological Psychology, 1963, 56, 290-293.
- Denny, M. R., & Leckart, B. T. Alternation behavior: Learning and extinction one trial per day. Journal of Comparative and Physiological Psychology, 1965, 60, 229-232.
- Denny, M. R., & Ratner, S. C. Comparative psychology: Research in animal behavior (Rev. ed.). Homewood, Ill.: Dorsey Press, 1970.
- Dessauer, H. C. Seasonal changes in the gross organ composition of the lizard, Anolis carolinensis. Journal of Experimental Zoology, 1955, 128, 1-12.
- Dodge, R., & Louttit, C. M. Modification of the pattern of the guinea pig's reflex response to noise. Journal of Comparative Psychology, 1926, 6, 267-285.
- Doty, B. A., Jones, C. N., & Doty, L. A. Learning set formation by mink, ferrets, skunks and cats. Science, 1967, 155, 1579-1580.
- Douglas, R. J. Pavlovian conditioning and the brain. In R. A. Boakes & M. S. Halliday (Eds.), Inhibition and learning. New York: Academic Press, 1972.
- Doyle, G., & Yule, E. P. Grooming activities and freezing behaviour in relation to emotionality in albino rats. Animal Behaviour, 1959, 7, 18-22.
- Drees, O. [Investigations on the innate behavior of jumping spiders (Salticidae).] Zeitschrift für Tierpsychologie, 1952, 9, 169-207. (In German)
- Dyal, J. A., & Hetherington, K. Habituation in the polychaete Hesperonoe adventor. Psychonomic Science, 1968, 13, 263-264.

- Ehrlich, A. Response to novel objects in three lower primates: Greater galago, slow loris and owl monkey. Behaviour, 1970, 37, 55-63.
- Eibl-Eibesfeldt, I. Ethology, the biology of behavior. New York: Holt, Rinehart & Winston, 1970.
- Eisenstein, E., & Peretz, B. Comparative aspects of habituation in invertebrates. In H. V. S. Peeke & M. J. Herz (Eds.), Habituation (Vol. II). Physiological substrates. New York: Academic Press, 1973.
- Evans, L. T. Behavior of castrated lizards. Journal of Genetic Psychology, 1936, 48, 217-221. (a)
- Evans, L. T. Social behavior of the normal and castrated lizard, Anolis carolinensis. Science, 1936, 83, 104. (b)
- Evans, L. T. A study of a social hierarchy in the lizard, Anolis carolinensis. Journal of Genetic Psychology, 1936, 48, 88-111. (c)
- Evans, L. T. The effect of hormones upon juvenile lizards, Anolis carolinensis. Anatomical Record, 1957, 128, 545.
- Evans, S. M. Learning in the polychaete Nereis. Nature, 1965, 207, 1420.
- Evans, S. M. Non-associative behavioural modifications in the polychaete Nereis diversicolor. Animal Behaviour, 1966, 14, 107-119.
- Evans, S. M. Habituation of the withdrawal response in Nereid polychaetes. 1. The habituation process in Nereis diversicolor. Biological Bulletin, 1969, 137, 95-104. (a)
- Evans, S. M. Habituation of the withdrawal response in Nereid polychaetes. 2. Rates of habituation in intact and decerebrate worms. Biological Bulletin, 1969, 137, 105-117. (b)
- Ewert, J., & Ingle, D. Excitatory effects following habituation of prey-catching activity in frogs and toads. Journal of Comparative and Physiological Psychology, 1971, 77, 369-374.
- Fearing, F. The retention of the effects of repeated elicitation of the post-rotational nystagmus in pigeons. I. The retention of the effects of "massed" stimulation. Journal of Comparative Psychology, 1940, 30, 31-40.

- Fearing, F. The retention of the effects of repeated elicitation of the post-rotational nystagmus in pigeons. II. The retention of the effects of "distributed" stimulation. Journal of Comparative Psychology, 1941, 31, 47-56.
- Feigley, D. A., Parsons, P. J., Hamilton, L. W., & Spear, N. E. Development of habituation to novel environments in the rat. Journal of Comparative and Physiological Psychology, 1972, 79, 443-452.
- Figler, M. H. The relation between eliciting stimulus strength and habituation of the threat display in the male Siamese fighting fish, Betta splendens. Behaviour, 1972, 42, 63-96.
- File, S. E. Inter-stimulus interval and the rate of behavioural habituation. Quarterly Journal of Experimental Psychology, 1973, 25, 360-367. (a)
- File, S. E. Long-term retention of behavioural habituation in the rat. Animal Behaviour, 1973, 21, 585-589. (b)
- File, S. E., & Russell, I. S. Specificity and savings of behavioural habituation over a series of intra- and inter-modal stimuli. Quarterly Journal of Experimental Psychology, 1972, 24, 465-473.
- Fox, W., & Dessauer, H. C. Photoperiodic stimulation of appetite and growth in the male lizard, Anolis carolinensis. Journal of Experimental Zoology, 1957, 134, 557-575.
- Fox, W., & Dessauer, H. C. Growth rates in captive male green anoles. Herpetologica, 1958, 14, 196-197. (a)
- Fox, W., & Dessauer, H. C. Response of the male reproductive system of lizards (Anolis carolinensis) to unnatural day-lengths in different seasons. Biological Bulletin, 1958, 115, 421-439. (b)
- Franzisket, L. Characteristics of instinctive behaviour and learning in reflex activity of the frog. Animal Behaviour, 1963, 11, 318-324.
- French, G. M. Locomotor effects of regional ablations of frontal cortex in rhesus monkeys. Journal of Comparative and Physiological Psychology, 1959, 52, 18-24.
- French, G. M., & Harlow, H. F. Locomotor reaction decrement in normal and brain-damaged rhesus monkeys. Journal of Comparative and Physiological Psychology, 1955, 48, 496-501.

- Furchtgott, E., Wechkin, S., & Dees, J. W. Open-field exploration as a function of age. Journal of Comparative and Physiological Psychology, 1961, 54, 386-388.
- Gallegher, J. E., Herz, M. J., & Peeke, H. V. S. Habituation of aggression: The effects of visual social stimuli on behavior between adjacently territorial convict cichlids (Cichlasoma nigrofasciatum). Behavioral Biology, 1972, 7, 359-368.
- Gallup, G. G., Jr., Nash, R. F., & Ellison, A. L., Jr. Tonic immobility as a reaction to predation: Artificial eyes as a fear stimulus for chickens. Psychonomic Science, 1971, 23, 79-80.
- Galvani, P. F. Air-puff-elicited startle: Habituation over trials and measurements of a hypothetical emotional response. Behavior Research Methods and Instrumentation, 1970, 2, 232-233.
- Gammon, W. D., Singer, J. J., & Michels, K. M. Visual exploratory behavior in the squirrel monkey (Saimiri sciureus). Perceptual and Motor Skills, 1972, 34, 715-718.
- Garcia, J., & Koelling, R. A. Relation of cue to consequence in avoidance learning. Psychonomic Science, 1966, 4, 123-124.
- Garcia, J., McGowan, B. K., & Green, K. F. Biological constraints on learning. In A. H. Black & W. F. Prokasy (Eds.), Classical conditioning II: Current research and theory. New York: Appleton-Century-Crofts, 1972.
- Gardner, B. T. Hunger and characteristics of the prey in the hunting behavior of the salticid spiders. Journal of Comparative and Physiological Psychology, 1966, 62, 475-478.
- Gardner, L. E. Retention and overhabituation of a dual-component response in Lumbricus terrestris. Journal of Comparative and Physiological Psychology, 1968, 66, 315-319.
- Gardner, W. M., & Melvin, K. B. Note on long-term habituation of freezing responses of bobwhite quail to a hawk. Perceptual and Motor Skills, 1971, 33, 555-558.
- Geer, J. H. Effect of interstimulus interval and rest period length upon habituation of the orienting response. Journal of Experimental Psychology, 1966, 72, 617-619.
- Gibson, J. J. The senses considered as perceptual systems. New York: Houghton Mifflin, 1966.
- Gilman, T. T., Marcuse, F. L., Moore, A. U. Animal hypnosis: A study in the induction of tonic immobility in chickens. Journal of Comparative and Physiological Psychology, 1950, 43, 99-111.

- Glickman, S. E., & Hartz, K. E. Exploratory behavior in several species of rodents. Journal of Comparative and Physiological Psychology, 1964, 58, 101-104.
- Glickman, S. E., & Sroges, R. W. Curiosity in zoo animals. Behaviour, 1966, 26, 151-188.
- Goodman, D. A., & Weinberger, N. M. Habituation in "lower" tetrapod vertebrates: Amphibia as vertebrate model systems. In H. V. S. Peeke & M. J. Herz (Eds.), Habituation (Vol I). Behavioral studies. New York: Academic Press, 1973.
- Goodrick, C. L. Exploration activity and emotionality of albino and pigmented mice: Inheritance and effects of test illumination. Journal of Comparative and Physiological Psychology, 1973, 84, 73-81.
- Gordon, R. The biology and biodemography of Anolis carolinensis carolinensis Voigt. (Doctoral dissertation, Tulane University, 1956). Dissertation Abstracts, 1956, 17, 698. (University Microfilms No. 20,303.
- Graham, F. K. Habituation and dishabituation of responses innervated by the autonomic nervous system. In H. V. S. Peeke & M. J. Herz (Eds.), Habituation (Vol. I). Behavioral studies. New York: Academic Press, 1973.
- Graham, F. K., & Clifton, R. K. Heart-rate change as a component of the orienting response. Psychological Bulletin, 1966, 65, 305-320.
- Green, P. C. Influence of early experience and age on expression of affect in monkeys. Journal of Genetic Psychology, 1965, 106, 157-171.
- Greenberg, B., & Noble, G. K. Social behavior of the American chameleon (Anolis carolinensis Voigt). Physiological Zoology, 1944, 17, 393-439.
- Greene, W. A., & Kimmel, H. D. Habituation of large and small GSRs. Psychological Reports, 1966, 19, 587-591.
- Griffin, J. P. Neurophysiological studies into habituation. In G. Horn & R. A. Hinde (Eds.), Short-term changes in neural activity and behaviour. New York: Cambridge University Press, 1970.
- Griffiths, W. J. Response of wild and domestic rats to forced swimming. Psychological Reports, 1960, 6, 39-49.
- Groves, P. M., & Lynch, G. S. Mechanisms of habituation in the brain stem. Psychological Review, 1972, 79, 237-244.

- Groves, P. M., & Thompson, R. F. Habituation: A dual-process theory. Psychological Review, 1970, 77, 419-450.
- Grunt, J. A., & Young, W. C. Psychological modification of fatigue following orgasm (ejaculation) in the male guinea pig. Journal of Comparative and Physiological Psychology, 1952, 45, 508-510.
- Hamlett, G. W. Notes on breeding and reproduction in the lizard Anolis carolinensis. Copeia, 1952, 183-185.
- Harlow, H. F. Learning and satiation of response in intrinsically motivated complex puzzle performance by monkeys. Journal of Comparative and Physiological Psychology, 1950, 43, 289-294.
- Harlow, H. F., Blazek, N. C., & McClearn, G. E. Manipulatory motivation in the infant rhesus monkey. Journal of Comparative and Physiological Psychology, 1956, 49, 444-448.
- Harris, J. D. Habitatory response decrement in the intact organism. Psychological Bulletin, 1943, 40, 385-423.
- Haslerud, G. M. The effect of movement of stimulus objects upon avoidance reactions in chimpanzees. Journal of Comparative Psychology, 1938, 25, 507-528.
- Hayes, W. N., Hertzler, D. R., & Hogberg, D. K. Visual responsiveness and habituation in the turtle. Journal of Comparative and Physiological Psychology, 1968, 65, 331-335.
- Hayes, W. N., & Ireland, L. C. Optokinetic response of the guinea pig. Journal of Comparative and Physiological Psychology, 1969, 68, 199-202.
- Hayes, W. N., & Ireland, L. C. A study of visual orientation mechanisms in turtles and guinea pigs. Brain, Behavior and Evolution, 1972, 5, 226-239.
- Hayes, W. N., & Saiff, E. I. Visual alarm reactions in turtles. Animal Behaviour, 1967, 15, 102-106.
- Hernández-Peón, R. Neurophysiological correlates of habituation and other manifestations of plastic inhibition (internal inhibition). Electroencephalography and Clinical Neurophysiology, 1960, Suppl. 13, 101-114.
- Hinde, R. A. Factors governing the changes in strength of a partially inborn response, as shown by the mobbing behaviour of the chaffinch (Fringilla coelebs). I. The nature of the response, and an examination of its course. Proceedings of the Royal Society of London, Series B, 1954, 142, 306-330. (a)

- Hinde, R. A. Factors governing the changes in strength of a partially inborn response, as shown by the mobbing behaviour of the chaffinch (Fringilla coelebs). II. The waning of the response. Proceedings of the Royal Society of London, Series B, 1954, 142, 331-359. (b)
- Hinde, R. A. Factors governing the changes in strength of a partially inborn response, as shown by the mobbing behaviour of the chaffinch (Fringilla coelebs). III. The interaction of short-term and long-term incremental and decremental effects. Proceedings of the Royal Society of London, Series B, 1960, 153, 398-420.
- Hinde, R. A. Animal behaviour: A synthesis of ethology and comparative psychology (2nd ed.). New York: McGraw-Hill, 1970. (a)
- Hinde, R. A. Behavioural habituation. In G. Horn & R. A. Hinde (Eds.), Short-term changes in neural activity and behaviour. New York: Cambridge University Press, 1970. (b)
- Hinde, R. A., & Tinbergen, N. The comparative study of species-specific behavior. In A. Roe & G. G. Simpson (Eds.), Behavior and evolution. New Haven: Yale University Press, 1958.
- Hine, B., & Paolino, R. M. Increases in heart rate accompanying decreases in activity and defecation: Support for a dual-process theory of habituation? Behavioral Biology, 1972, 7, 427-433.
- Hirsch, J., Lindley, R. H., & Tolman, E. C. An experimental test of an alleged innate sign stimulus. Journal of Comparative and Physiological Psychology, 1955, 48, 278-280.
- Hodos, W., & Campbell, C. B. G. Scala naturae: Why there is no theory in comparative psychology. Psychological Review, 1969, 76, 337-350.
- Hoffman, H. S., & Fleshler, M. Startle reaction: Modification by background acoustic stimulation. Science, 1963, 141, 928-930.
- Hoffman, H. S., Marsh, R. R., & Stein, N. Persistence of background acoustic stimulation in controlling startle. Journal of Comparative and Physiological Psychology, 1969, 68, 280-283.
- Hoffman, H. S., & Stitt, C. Behavioral factors in habituation of acoustic startle reactions. Journal of Comparative and Physiological Psychology, 1969, 68, 276-279.

- Hogan, J. A. An experimental study of conflict and fear: An analysis of behavior of young chicks toward a mealworm. Part I. The behavior of chicks which do not eat the mealworm. Behaviour, 1965, 25, 45-97.
- Hollis, J. H. Habitatory response decrement in pupae of Tenebrio molitor. Animal Behaviour, 1963, 11, 161-163.
- Horn, G. Neural mechanisms of habituation. Nature, 1967, 215, 707-711.
- Horridge, G. A. Optokinetic memory in the crab, Carcinus. Journal of Experimental Biology, 1966, 44, 233-245. (a)
- Horridge, G. A. Optokinetic memory in the locust. Journal of Experimental Biology, 1966, 44, 255-261. (b)
- Horvath, T., Kirby, H. W., & Smith, A. A. Rats' heart rate and grooming activity in the open field. Journal of Comparative and Physiological Psychology, 1971, 76, 449-453.
- Howard, I. P. Orientation and motion in space. In E. C. Carterette & M. P. Friedman (Eds.). Handbook of perception (Vol. 1). Biology of perceptual systems. New York: Academic Press, 1973.
- Howarth, E. Activity decrements and recovery during repeated day to day exposure to the same environment. Journal of Comparative and Physiological Psychology, 1962, 55, 1102-1104.
- Hughes, R. N. Exploration in three laboratory rodents. Perceptual and Motor Skills, 1969, 28, 90.
- Humphrey, G. The nature of learning in its relation to the living system. New York: Harcourt, Brace, 1933.
- Ingle, D. Reduction of habituation of prey-catching activity by alcohol intoxication in the frog. Behavioral Biology, 1973, 8, 123-129.
- Ireland, L. C., & Hayes, W. N. Factors influencing induction and duration of oculomotor reflex rebound in the guinea pig. Journal of Comparative and Physiological Psychology, 1973, 82, 159-164.
- Ireland, L. C., Hayes, W. N., & Ladden, L. H. Relation between frequency and amplitude of visual alarm reactions in Pseudemys scripta. Animal Behaviour, 1969, 17, 386-388.
- Jacobson, A. L. Learning in flatworms and annelids. Psychological Bulletin, 1963, 60, 74-94.

- Jeffrey, W. E., & Cohen, L. B. Habituation in the human infant. In H. W. Reese (Ed.), Advances in child development and behavior (Vol. 6). New York: Academic Press, 1971.
- Jolly, A. Prosimians' manipulation of simple object problems. Animal Behaviour, 1964, 12, 560-570.
- Joslin, J., Fletcher, H., & Emlen, J. A comparison of the responses to snakes of lab- and wild-reared rhesus monkeys. Animal Behaviour, 1964, 12, 348-352.
- Kandel, E., & Spencer, W. A. Cellular neurophysiological approaches in the study of learning. Psychological Review, 1968, 48, 65-134.
- Kay, H., & Birren, J. E. Swimming speed of the albino rat: II. Fatigue, practice, and drug effects on age and sex differences. Journal of Gerontology, 1958, 13, 378-385.
- Kessen, W., Haith, M. M., & Salapatek, P. H. Human infancy: A bibliography and guide. In P. H. Mussen (Ed.), Manual of child psychology. New York: Wiley, 1970.
- Kimble, D. P., & Ray, R. S. Reflex habituation and potentiation in Rana pipiens. Animal Behaviour, 1965, 13, 530-533.
- Kimmel, H. D. Habituation, habitability, and conditioning. In H. V. S. Peeke & M. J. Herz (Eds.), Habituation (Vol. I). Behavioral studies. New York: Academic Press, 1973. (a)
- Kimmel, H. D. Reflex habituality as a basis for differentiating between classical and instrumental conditioning. Conditional Reflex, 1973, 8, 10-27. (b)
- Kimmel, H. D., & Goldstein, A. J. Retention of habituation of the GSR to visual and auditory stimulation. Journal of Experimental Psychology, 1967, 73, 401-404.
- King, J. A. Swimming and reaction to electric shock in two subspecies of deermice (Peromyscus maniculatus) during development. Animal Behaviour, 1961, 9, 142-150.
- Koepke, J. E., & Pribram, K. H. Habituation of GSR as a function of stimulus duration and spontaneous activity. Journal of Comparative and Physiological Psychology, 1966, 61, 442-448.
- Konorski, J. Integrative activity of the brain. Chicago: University of Chicago Press, 1967.
- Korn, J. H., & Moyer, K. E. Habituation of the startle response and of the heart rate in the rat. Canadian Journal of Psychology, 1966, 20, 183-190.

- Kramer, T. J., & Wright, J. W. Effects of bilateral frontal lesions in habituation of the head-shake response in the rat. Physiology and Behavior, 1971, 7, 211-214.
- Krasne, F. B. Escape from recurring tactile stimulation in Bran-
chiomma vesiculosum. Journal of Experimental Biology, 1965, 42, 307-322.
- Krasne, F. B., & Roberts, A. Habituation of the crayfish escape response during release from inhibition induced by picrotoxin. Nature, 1967, 215, 769-770.
- Krasne, F. B., & Woodsmall, K. S. Waning of the crayfish escape response as a result of repeated stimulation. Animal Behaviour, 1967, 17, 416-424.
- Kuenzer, P. P. [Behavior-physiological investigations on the twitch of the earthworm.] Zeitschrift für Tierpsychologie, 1958, 15, 31-49. (In German)
- Kupfermann, I., Castellucci, V., Pinsker, H., & Kandel, E. Neuronal correlates of habituation and dishabituation of the gill withdrawal reflex in Aplysia. Science, 1970, 167, 1743-1745.
- Kupfermann, I., Pinsker, H., Castellucci, V., & Kandel, E. Central and peripheral control of gill movements in Aplysia. Science, 1971, 174, 1252-1256.
- Lagerspetz, K. Y. H., & Kivivuori, L. The rate and retention of the habituation of the shadow reflex in Balanus improvisus (Cirripedia). Animal Behaviour, 1970, 18, 616-620.
- Lát, J., & Gollová-Hémon, E. Permanent effects of nutrition and endocrinological intervention in early ontogeny on the level of nonspecific excitability and on lability (emotionality). Annals of the New York Academy of Sciences, 1969, 159, 710-720.
- Leaton, R. N. Long-term retention of the habituation of lick suppression in rats. Journal of Comparative and Physiological Psychology, 1974, 87, 1157-1164.
- Leibrecht, B. C. Habituation, 1940-1970: Bibliography and key word index. Psychonomic Monograph Supplements, 1972, 4(11, Whole No. 59).
- Leibrecht, B. C. Dishabituation of the head-shake response in the rat. Behavioral Biology, 1973, 9, 467-477.
- Leibrecht, B. C. Habituation: Supplemental bibliography. Physiological Psychology, 1974, 2, 401-419.

- Leibrecht, B. C., & Askew, H. R. Habituation of the head-shake response in the rat: Recovery, transfer, and changes in topography. Journal of Comparative and Physiological Psychology, 1969, 69, 699-708.
- Leibrecht, B. C., & Kemmerer, W. S. Varieties of habituation in the chinchilla (Chinchilla lanigera). Journal of Comparative and Physiological Psychology, 1974, 86, 124-132.
- Lewis, D. Quantitative methods in psychology. New York: McGraw-Hill, 1960.
- Licht, P. Reproduction in lizards: The influence of temperature on photoperiodism in testicular recrudescence. Science, 1967, 154, 1668-1670.
- Licht, P. Environmental control of animal testicular cycles in the lizard Anolis carolinensis. II. Temperature thresholds for photoperiodism. Journal of Experimental Zoology, 1969, 172, 311-322.
- Licht, P. Regulation of the annual testis cycle by photoperiod and temperature in the lizard Anolis carolinensis. Ecology, 1971, 52, 240-252.
- Lindquist, E. F. Design and analysis of experiments in psychology and education. New York: Houghton Mifflin, 1953.
- Lorenz, K. The comparative method in studying innate behaviour patterns. Symposia of the Society for Experimental Biology, 1950, 4, 221-268.
- Lorenz, K. Evolution and modification of behavior. Chicago: University of Chicago Press, 1965.
- Lorenz, K. Innate bases of learning. In K. H. Pribram (Ed.), On the biology of learning. New York: Harcourt, Brace & World, 1969.
- Lovibond, S. H. Habituation of the orienting response to multiple stimulus sequences. Psychophysiology, 1969, 5, 435-438.
- Lubow, R. E. Latent inhibition. Psychological Bulletin, 1973, 79, 398-407.
- Lukowiak, K., & Jacklet, J. W. Habituation and dishabituation: Interactions between peripheral and central nervous systems in Aplysia. Science, 1972, 178, 1306-1308.
- Maldonado, H. A learning process in the praying mantis. Physiology and Behavior, 1972, 9, 435-445.

- Marler, P., & Hamilton, W. J. Mechanisms of animal behavior. New York: Wiley, 1966.
- Martin, R. C., & Melvin, K. B. Fear responses of Bobwhite quail (Colinus virginianus) to a model and a live red-tailed hawk (Buteo jamaicensis). Psychologische Forschung, 1964, 27, 323-336.
- Mayr, E. Behavior and systematics. In A. Roe & G. G. Simpson (Eds.), Behavior and evolution. New Haven: Yale University Press, 1958.
- Mayr, E. Animal species and evolution. Cambridge: Harvard University Press, 1963.
- Melvin, K. B., & Cloar, F. T. Habituation of responses of quail (Colinus virginianus) to a hawk (Buteo swainsoni): Measurement through an 'innate suppression' technique. Animal Behaviour, 1969, 17, 468-473.
- Melzack, R. On the survival of mallard ducks after "habituation" to the hawk-shaped figure. Behaviour, 1961, 17, 9-16.
- Melzack, R., Penick, E., & Beckett, A. The problem of "innate fear" of the hawk shape: An experimental study with mallard ducks. Journal of Comparative and Physiological Psychology, 1959, 52, 694-698.
- Menzel, E. W., Jr., Davenport, R. K., Jr., & Rogers, C. M. Some aspects of behavior toward novelty in young chimpanzees. Journal of Comparative and Physiological Psychology, 1961, 54, 16-19.
- Messinger, J. B. Learning in the cuttlefish, Sepia. Animal Behaviour, 1973, 21, 801-826.
- Meyerriecks, A. J. Green anole threatens wasp. Copeia, 1960, 60.
- Michael, E. D. Growth rates in Anolis carolinensis. Copeia, 1972, 575-577.
- Miller, J. D., & Murray, F. S. Guinea pig's immobility response to sound: Threshold and habituation. Journal of Comparative and Physiological Psychology, 1966, 61, 227-233.
- Mittelstaedt, H. Basic control patterns of orientational homeostasis. Symposium of the Society for Experimental Biology, 1964, 18, 365-386.
- Montgomery, K. C. The relation between exploratory behavior and spontaneous alternation in the white rat. Journal of Comparative and Physiological Psychology, 1951, 44, 582-589.

- Montgomery, K. C. The effect of the hunger and thirst drives upon exploratory behavior. Journal of Comparative and Physiological Psychology, 1953, 46, 315-319. (a)
- Montgomery, K. C. Exploratory behavior as a function of "similarity" of stimulus situations. Journal of Comparative and Physiological Psychology, 1953, 46, 129-133. (b)
- Moyer, K. E. Startle response: Habituation over trials and days, and sex and strain differences. Journal of Comparative and Physiological Psychology, 1963, 56, 863-865.
- Murray, S. G., & King, J. E. Snake avoidance in feral and laboratory reared squirrel monkeys. Behaviour, 1973, 47, 281-289.
- Nicol, J. A. C. The responses of Franchiomma vesiculosum (Montagu) to photic stimulation. Journal of the Marine Biological Association, U. K., 1950, 29, 303-320.
- Noble, G. K., & Bradley, H. T. The mating behavior of lizards: Its bearing on the theory of sexual selection. Annals of the New York Academy of Sciences, 1933, 35, 25-100.
- Noirot, E. Changes in responsiveness to young in the adult mouse. I. The problematrical effect of hormones. Animal Behaviour, 1964, 12, 52-58.
- Noirot, E. Changes in responsiveness to young in the adult mouse. III. The effect of immediately preceding performances. Behaviour, 1965, 24, 318-325.
- Nyström, M. Extinction, disinhibition and spontaneous recovery of the pecking response in young herring gulls. Behaviour, 1973, 45, 271-281.
- O'Brien, R. M., & Corron, C. D. Retention of habituation of exploratory behavior. Psychonomic Science, 1970, 18, 23-24.
- Oldham, J., & Morlock, H. The effects of open-field size on activity in the Mongolian gerbil. Psychonomic Science, 1970, 20, 290.
- Olson, R. D., & May, J. G. Habituation and sensitization of an innate fear response in Carassius auratus. Psychological Reports, 1973, 32, 799-802.
- Osborn, D., Blair, H. J., Thomas, J., & Eisenstein, E. M. The effects of vibratory and electrical stimulation on habituation in the ciliated protozoan, Spirostomum ambiguum. Behavioral Biology, 1973, 8, 655-664.

- Pare, W. P. Relationship of various behaviors in the open-field test of emotionality. Psychological Reports, 1964, 14, 19-22.
- Parsons, P. J., Fagan, T., & Spear, N. E. Short-term retention of habituation in the rat: A developmental study from infancy to old age. Journal of Comparative and Physiological Psychology, 1973, 84, 545-553.
- Patterson, D. J. Habituation in a protozoan, Vorticella convallaria. Behaviour, 1973, 45, 304-311.
- Pavlov, I. P. Conditioned reflexes. London: Oxford University Press, 1927.
- Pearl, J. Avoidance learning in rodents: A comparative study. Psychological Reports, 1963, 12, 139-145.
- Peeke, H. V. S. Habituation of conspecific aggression in the three-spined stickleback (Gasterosteus aculeatus L.). Behaviour, 1969, 35, 135-156.
- Peeke, H. V. S., Herz, M. J., & Gallagher, J. E. Changes in aggressive interaction in adjacently territorial convict cichlids (Cichlasoma nigrofasciatum): A study of habituation. Behaviour, 1971, 40, 43-54.
- Peeke, H. V. S., & Peeke, S. C. Habituation of conspecific aggressive responses in the Siamese fighting fish (Betta splendens). Behaviour, 1970, 36, 232-246.
- Peeke, H. V. S., & Peeke, S. C. Habituation in fish with special reference to intraspecific aggressive behavior. In H. V. S. Peeke & M. J. Herz (Eds.), Habituation (Vol. I). Behavioral studies. New York: Academic Press, 1973.
- Peeke, H. V. S., & Veno, A. Stimulus specificity of habituated aggression in the stickleback (Gasterosteus aculeatus). Behavioral Biology, 1973, 8, 427-432.
- Peeke, H. V. S., Wyers, E. J., & Herz, M. J. Waning of the aggressive response to male models in the three-spined stickleback (Gasterosteus aculeatus L.) Animal Behaviour, 1969, 17, 224-228.
- Petrinovich, L. A species-meaningful analysis of habituation. In H. V. S. Peeke & M. J. Herz (Eds.), Habituation (Vol. I). Behavioral studies. New York: Academic Press, 1973.
- Petrinovich, L., & Peeke, H. V. S. Habituation to territorial song in the white-crowned sparrow (Zonotrichia leucophrys). Behavioral Biology, 1973, 8, 743-748.

- Pinsker, H. M., Hening, W. A., Carew, T. J., & Kandel, E. R. Long-term sensitization of a defensive withdrawal reflex in Aplysia. Science, 1973, 182, 1039-1042.
- Pinsker, H. M., Kupfermann, I., Castellucci, V., & Kandel, E. R. Habituation and dishabituation of the gill-withdrawal reflex in Aplysia. Science, 1970, 167, 1740-1742.
- Polyak, S. The vertebrate visual system. Chicago: University of Chicago Press, 1957.
- Powell, R. W. Avoidance and escape conditioning in lizards. Psychological Reports, 1967, 20, 583-586.
- Precht, H., & Freytag, G. [On the aspects of fatigue and inhibition of innate behavior in jumping spiders (Salticidae). Also a contribution to the problem of instinct.] Behaviour, 1958, 13, 143-211. (In German)
- Precht, H. F. R. The directed head turning response and allied movements of the human baby. Behaviour, 1958, 13, 212-240.
- Pribram, K. H. The limbic systems, efferent control of neural inhibition and behavior. In W. R. Adey & T. Tokizane (Eds.), Progress in brain research (Vol. 27). Structure and function of the limbic system. Amsterdam: Elsevier, 1967.
- Prosser, C. L., & Hunter, W. S. The extinction of startle responses and spinal reflexes in the white rat. American Journal of Physiology, 1936, 117, 609-618.
- Rabedeau, R., & Miles, R. C. Response decrement in visual exploratory behavior. Journal of Comparative and Physiological Psychology, 1959, 52, 364-367.
- Rand, A. S. The adaptive significance of territoriality in Iguanid lizards. In W. W. Milstead (Ed.), Lizard ecology: A symposium. Columbia: University of Missouri Press, 1967.
- Ratner, S. C. Habituation: Research and theory. In J. Reynierse (Ed.), Current issues in animal learning. Lincoln: University of Nebraska Press, 1970.
- Ratner, S. C. Habituation and retention of habituation in the leech (Macrobdella decora). Journal of Comparative and Physiological Psychology, 1972, 81, 115-121.
- Ratner, S. C., & Gardner, L. E. Variables affecting responses of earthworms to light. Journal of Comparative and Physiological Psychology, 1968, 66, 239-243.

- Ratner, S. C., & Gilpin, A. R. Habituation and retention of habituation of responses to air puff of normal and decerebrate earthworms. Journal of Comparative and Physiological Psychology, 1974, 86, 911-918.
- Ratner, S. C., & Stein, D. G. Responses of worms to light as a function of intertrial interval and ganglion removal. Journal of Comparative and Physiological Psychology, 1965, 59, 301-305.
- Ratner, S. C., & Thompson, R. W. Immobility reactions (fear) of domestic fowl as a function of age and prior experience. Animal Behaviour, 1960, 8, 186-191.
- Rilling, S., Mittelstaedt, H., & Roeder, K. D. Prey recognition in the preying mantis. Behaviour, 1959, 14, 164-184.
- Rodgers, W. L., Melzack, R., & Segal, J. R. "Tail flip response" in goldfish. Journal of Comparative and Physiological Psychology, 1963, 56, 917-923.
- Roe, A., & Simpson, G. G. Behavior and evolution. New Haven: Yale University Press, 1958.
- Rovner, J. S. An analysis of display in the Lycosid spider (Lycosa rabida Walckenaer): A quantitative study. Animal Behaviour, 1968, 16, 358-369.
- Rushforth, N. B. Behavioral studies of the coelenterate Hydra pirardi Brien. Animal Behaviour, Suppl., 1965, 1, 30-42.
- Rushforth, N. B., Burnett, A. L., & Maynard, R. Behavior in hydra: Contraction responses of Hydra pirardi to mechanical and light stimuli. Science, 1963, 139, 760-761.
- Rushforth, N. B., Krohn, I. T., & Brown, L. K. Behavior in hydra: Inhibition of the contraction responses of Hydra pirardi. Science, 1964, 145, 602-604.
- Russell, E. M. Changes in the behavior of Lebistes reticulatus upon a repeated shadow stimulus. Animal Behaviour, 1967, 15, 574-585.
- Russell, E. M., & Pearce, G. A. Exploration of novel objects by marsupials. Behaviour, 1971, 40, 312-322.
- Schaub, R. E. The effect of interstimulus interval on GSR adaptation. Psychonomic Science, 1965, 2, 361-362.
- Schein, M. W., & Carter, C. S. Sexual behaviour and novel stimuli in male Japanese quail (Coturnix coturnix Japonica). Animal Behaviour, 1972, 20, 383-385.

- Schiller, P. H. Innate constituents of complex response in primates. Psychological Review, 1952, 59, 177-191.
- Schoener, T. W. The Anolis lizards of Bimini: Resource partitioning in a complex fauna. Ecology, 1968, 49, 704-726.
- Scourse, N. J. S., & Hinde, R. A. Habituation to auditory stimuli in mice. Behaviour, 1973, 47, 1-13.
- Selander, R. K. On mating systems and sexual selection. American Naturalist, 1965, 99, 129-141.
- Seligman, M. E. P. On the generality of the laws of learning. Psychological Review, 1970, 77, 406-418.
- Sexton, O. J. Differential predation by the lizard, Anolis carolinensis, upon unicoloured and polycoloured insects after an interval of no contact. Animal Behaviour, 1964, 12, 101-110.
- Sexton, O. J., Hoger, C., & Ortleb, E. Anolis carolinensis: Effects of feeding on reaction to aposematic prey. Science, 1966, 153, 1140.
- Shapiro, S., & Schuckman, H. Habituation and covariation of the components of the threat display in Betta splendens. Psychological Reports, 1971, 28, 827-837.
- Sharpless, S. K. Reorganization of function in the nervous system - use and disuse. Annual Review of Physiology, 1964, 26, 357-388.
- Shepherd, P. Control of head movement in the locust, Schistocerca gregaria. Journal of Experimental Biology, 1974, 60, 735-767.
- Shettleworth, S. J. Conditioning of domestic chicks to visual and auditory stimuli and control of conditioned fear by sound. In M. E. P. Seligman & J. L. Hager (Eds.), Biological boundaries of learning. New York: Appleton-Century-Crofts, 1972.
- Simpson, G. G. Behavior and evolution. In A. Roe & G. G. Simpson (Eds.), Behavior and evolution. New Haven: Yale University Press, 1958. (a)
- Simpson, G. G. The study of evolution: Methods and present status of theory. In A. Roe & G. G. Simpson (Eds.), Behavior and evolution. New Haven: Yale University Press, 1958. (b)
- Smith, H. M. Handbook of lizards. Ithaca, New York: Comstock, 1946.

- Smith, K. U., & Bojar, S. The nature of optokinetic reactions in mammals and their significance in the experimental analysis of the neural mechanisms of visual functions. Psychological Bulletin, 1938, 35, 193-219.
- Sokolov, E. N. Neuronal models and the orienting reflex. In M. A. B. Brazier (Ed.), The central nervous system and behavior. New York: Josiah Macey, Jr. Foundation, 1960.
- Sokolov, E. N. Higher nervous system functions: The orienting reflex. Annual Review of Physiology, 1963, 25, 545-580. (a)
- Sokolov, E. N. Perception and the conditioned reflex. New York: Pergamon Press, 1963, (b)
- Stephens, C. L. Progressive decrements in the activity of Aplysia neurons following repeated intracellular stimulation: Implications for habituation. Journal of Experimental Biology, 1973, 58, 411-422. (a)
- Stephens, C. L. Relative contribution of synaptic and non-synaptic influences to response decrements in a post-synaptic neurone. Journal of Experimental Biology, 1973, 59, 315-321. (b)
- Symmes, D. Anxiety reduction and novelty as goals of visual exploration by monkeys. Journal of Genetic Psychology, 1959, 94, 181-198.
- Szlep, R. Change in the response of spiders to repeated web vibrations. Behaviour, 1964, 23, 203-238.
- Tauber, E., & Atkin, A. Optomotor responses to monocular stimulation: Relation to visual system organization. Science, 1968, 160, 1365-1367.
- Tauber, E., & Koffler, S. Optomotor responses in human infants to apparent motion: Evidence of innateness. Science, 1966, 152, 382-383.
- Thompson, R. F., Groves, P. M., Teyler, T. J., & Roemer, R. A. A dual-process theory of habituation: Theory and behavior. In H. V. S. Peeke & M. J. Herz (Eds.), Habituation (Vol. I). Behavioral studies. New York: Academic Press, 1973.
- Thompson, R. F., & Spencer, W. A. Habituation: A model phenomenon for the study of neuronal substrates of behavior. Psychological Review, 1966, 73, 16-43.
- Thompson, R. W., & Lippman, L. G. Exploration and activity in the gerbil and rat. Journal of Comparative and Physiological Psychology, 1972, 80, 439-448.

- Thompson, W. R. Exploratory behavior as a function of hunger in "bright" and "dull" rats. Journal of Comparative and Physiological Psychology, 1953, 46, 323-326.
- Thorpe, W. H. Learning and instinct in animals. Cambridge: Harvard University Press, 1963.
- Tinbergen, N. The study of instinct. New York: Oxford University Press, 1951.
- Valle, F. B. Rats' performance on repeated tests in the open field as a function of age. Psychonomic Science, 1971, 23, 333-335.
- Vinogradova, O. S. Registration of information and the limbic system. In G. Horn & R. A. Hinde (Eds.), Short-term changes in neural activity and behaviour. New York: Cambridge University Press, 1970.
- Vowles, D. M., & Prewitt, E. Stimulus and response specificity in the habituation of anti-predator behaviour in the ring dove (Streptopelia risoria). Animal Behaviour, 1971, 19, 80-86.
- Walker, I. Habituation to disturbance in the fiddler crab (Uca annulipes) in its natural environment. Animal Behaviour, 1972, 20, 139-146.
- Wall, P. D. Habituation and post-tetanic potentiation in the spinal cord. In G. Horn & R. A. Hinde (Eds.), Short-term changes in neural activity and behaviour. New York: Cambridge University Press, 1970.
- Walls, G. L. The vertebrate eye and its adaptive radiation. Bloomfield Hills, Michigan: Cranbrook Press (Cranbrook Institute of Science), 1942.
- Walls, G. L. The evolutionary history of eye movements. Vision Research, 1962, 2, 69-80.
- Weisbard, C., & Graham, F. K. Heart-rate changes as a component of the orienting response in monkeys. Journal of Comparative and Physiological Psychology, 1971, 76, 74-83.
- Welker, W. I. Effects of age and experience on play and exploration of young chimpanzees. Journal of Comparative and Physiological Psychology, 1956, 49, 223-226. (a)
- Welker, W. I. Some determinants of play and exploration in chimpanzees. Journal of Comparative and Physiological Psychology, 1956, 49, 84-89. (b)

- Welker, W. I. Variability of play and exploratory behavior in chimpanzees. Journal of Comparative and Physiological Psychology, 1956, 49, 181-185. (c)
- Welker, W. I. Escape, exploratory, and food-seeking responses of rats in a novel situation. Journal of Comparative and Physiological Psychology, 1959, 52, 106-111.
- Wells, M. J., & Wells, J. Repeated presentation experiments and the function of the vertical lobe in octopus. Journal of Experimental Biology, 1957, 34, 469-477.
- Wells, M. J., & Young, J. Z. Changes in textural preferences in octopus after lesions. Journal of Experimental Biology, 1968, 49, 401-412.
- Westerman, R. A. Somatic inheritance of habituation of responses to light in planarians. Science, 1963, 140, 676-677.
- Wicklegren, B. G. Habituation of spinal motoneurons. Journal of Neurophysiology, 1967, 30, 1404-1423. (a)
- Wicklegren, B. G. Habituation of spinal interneurons. Journal of Neurophysiology, 1967, 30, 1424-1438. (b)
- Wilcock, J. Water escape in weanling rats: A link between behaviour and biological fitness. Animal Behaviour, 1972, 20, 543-547.
- Wilcoxon, H. C., Dragoin, W. B., & Kral, P. A. Illness-induced aversions in rat and quail: Relative salience of visual and gustatory cues. Science, 1971, 171, 826-828.
- Williams, C. D., Zerof, S. A., & Carr, R. M. Exploratory behavior of the crosses of three strains of rats. Journal of Comparative and Physiological Psychology, 1962, 55, 121-122.
- Wilson, C. J., & Groves, P. M. Refractory period and habituation of acoustic startle response in rats. Journal of Comparative and Physiological Psychology, 1973, 83, 492-498.
- Wilz, K. J., & Bolton, R. L. Exploratory behavior in response to the spatial arrangement of familiar stimuli. Psychonomic Science, 1971, 24, 117-118.
- Winer, B. J. Statistical principles in experimental design (2nd ed.). New York: McGraw-Hill, 1971.
- Winokur, G., Stewart, M., Stern, J., & Pfeiffer, E. A dynamic equilibrium in GSR habituation: The effect of interstimulus interval. Journal of Psychosomatic Research, 1962, 6, 117-122.

- Winston, H. D. Heterosis and learning in the mouse. Journal of Comparative and Physiological Psychology, 1964, 57, 279-283.
- Wolda, H. Response decrement in the prey-catching activity of Notonecta glauca L. (Hemiptera). Archives Néerlandaises de Zoologie, 1961, 14, 61-89.
- Wolin, L. R., Ordy, J. M., & Dillman, A. Monkeys' fear of snakes: A study of its basis and generality. Journal of Genetic Psychology, 1963, 103, 207-226.
- Wood, D. C. Electrophysiological correlates of the response decrement produced by mechanical stimuli in the protozoan, Stentor coeruleus. Journal of Neurobiology, 1970, 2, 1-11. (a)
- Wood, D. C. Parametric studies of the response decrement produced by mechanical stimuli in the protozoan, Stentor coeruleus. Journal of Neurobiology, 1970, 1, 345-360. (b)
- Wood, D. C. Stimulus specific habituation in a protozoan. Physiology and Behavior, 1973, 11, 349-354.
- Woods, P. J. Behavior in a novel situation as influenced by the immediately preceding environment. Journal of the Experimental Analysis of Behavior, 1962, 5, 185-190.
- Wyers, E. J., H. V. S. Peeke, & Herz, M. J. Behavioral habituation in invertebrates. In H. V. S. Peeke & M. J. Herz (Eds.), Habituation (Vol. I). Behavioral studies. New York: Academic Press, 1973.
- Young, W. C., & Grunt, J. A. The pattern and measurement of sexual behavior in the male guinea pig. Journal of Comparative and Physiological Psychology, 1951, 44, 492-500.
- Zeiner, A. R., & Peeke, H. V. S. Habituation of response to distress cries in the rat: Measurement by an innate suppression technique. Communications in Behavioral Biology, 1969, 3, 249-252.
- Zimbardo, P. G., & Montgomery, K. C. Effects of "free-environment" rearing upon exploratory behavior. Psychological Reports, 1957, 3, 589-594.
- Zimny, G. H., Pawlick, G. F., & Saur, D. P. Effects of stimulus order and novelty on orienting responses. Psychophysiology, 1969, 6, 166-173.
- Zimny, G. H., & Schwabe, L. W. Stimulus change and habituation of the orienting response. Psychophysiology, 1966, 2, 103-115.

APPENDIX A

INTERRATER RELIABILITY FOR EACH RESPONSE

Judges	Dewlap ^a	OKR ^a	Swimming ^a
Experimenter and:			
Judge 1	+ .9854	+ .9411	+ .9636
Judge 2	+ .8984	+ .9326	+ .9858
Judge 3	+ .9786	+ .9855	+ .9813

^an = 30.

APPENDIX B

SUMMARY OF ANALYSES OF VARIANCE FOR HABITUATION CURVES
OF EXPERIMENT 1 FITTED TO FIRST AND SECOND
DEGREE WITH ORTHOGONAL POLYNOMIALS

DEWLAP							
Source	df	5 Sec ITI		30 Sec ITI		120 Sec ITI	
		MS	F	MS	F	MS	F
Total	39	394.4		224.83		238.42	
Between	39	378.8		209.51		225.42	
1°	1	533.9	26.39*	456.26	122.87*	223.48	29.93*
Error (1°)	38	2.0		3.71		7.47	
Balance	1	14238.6	6997.48*	7714.76	2646.64*	8567.74	1767.66*
2°	1	1.4	.71	33.25	11.41*	104.42	21.54*
Error (2°)	37	2.0		2.91		4.85	

OKR							
Source	df	5 Sec ITI		30 Sec ITI		120 Sec ITI	
		MS	F	MS	F	MS	F
Total	39	219.3		367.82		379.14	
Between	39	200.2		348.94		360.77	
1°	1	370.8	37.92*	522.18	92.64*	437.82	59.68*
Error (1°)	38	9.8		5.64		7.34	
Balance	1	7438.5	1498.31*	13086.5	2983.61*	13632.2	3213.75*
2°	1	187.9	37.84*	51.91	11.84*	121.82	28.72*
Error (2°)	37	4.9		4.39		4.24	

SWIMMING							
Source	df	5 Sec ITI		30 Sec ITI		120 Sec ITI	
		MS	F	MS	F	MS	F
Total	39	26.2		46.59		81.10	
Between	39	21.8		42.47		77.10	
1°	1	76.7	31.95*	70.13	29.50*	68.45	29.62*
Error (1°)	38	2.4		2.38		2.31	
Balance	1	775.2	454.38*	1586.24	1211.49*	2938.31	2427.06*
2°	1	28.2	16.52*	41.89	31.99*	43.02	35.54*
Error (2°)	37	1.7		1.31		1.21	

*p < .01.

APPENDIX C

SUMMARY OF ANALYSES OF VARIANCE FOR HABITUATION CURVES
FOR EACH RESPONSE, RECOVERY INTERVAL AND SESSION OF
EXPERIMENT 2 FITTED TO FIRST AND SECOND
DEGREE WITH ORTHOGONAL POLYNOMIALS

DEWLAP 15 MIN						
Source	df	Session 1		Session 2		
		MS	F	MS	F	
Total	39	360.47		163.13		
Between	39	344.60		158.08		
1°	1	493.02	148.87*	97.84	37.53*	
Error (1°)	38	3.31		2.61		
Balance	1	12946.5	4029.02*	6067.45	3078.08*	
2°	1	6.95	2.16	26.15	13.26*	
Error (2°)	37	3.21		1.97		

DEWLAP 24 HR						
Total	39	319.89		259.41		
Between	39	305.59		245.18		
1°	1	455.19	168.49*	449.08	161.44*	
Error (1°)	38	2.70		2.78		
Balance	1	11462.8	4188.79*	9112.29	3970.74*	
2°	1	1.40	.51	2.08	9.06*	
Error (2°)	37	2.74		2.29		

Note. Appendix D continued on following page.

* $p < .01$.

OKR 15 MIN					
Source	df	Session 1		Session 2	
		MS	F	MS	F
Total	39	318.62		137.55	
Between	39	303.07		126.43	
1°	1	292.12	35.31*	295.74	81.27*
Error (1°)	38	8.27		3.64	
Balance	1	11527.7	2672.43*	4634.88	2470.17*
2°	1	154.79	35.89*	68.86	36.69*
Error (2°)	37	4.31		1.88	

OKR 24 HR					
Total	39	309.93		296.80	
Between	39	292.02		278.26	
1°	1	494.32	92.15*	447.66	61.73*
Error (1°)	38	5.36		7.25	
Balance	1	10894.6	3051.47*	10404.4	2131.12*
2°	1	71.74	20.09*	94.93	19.44*
Error (2°)	37	3.57		4.88	

*p < .01.

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A Comparison of the Habituation of Three Responses in the Lizard, Anolis carolinensis.

Dissertation directed by John W. Wright, Ph.D. and Peter Borchelt, Ph.D.

A within-species comparative approach, derived from an alternative viewpoint to that of general process theories of habituation, was employed in studying the habituation of three responses in the lizard, Anolis carolinensis ("American chameleon").

Habituation studies frequently employ a single response or response system given to either one stimulus or various stimuli. In contrast, a within-species comparative approach involves the investigation of similarities and differences in the habituation of various responses within a single species.

A. carolinensis was selected because of the paucity of habituation studies in reptiles. From pilot data, three responses were chosen for study: dewlap extension, optokinetic response (OKR) and swimming. Dewlap extension refers to the distension of the "throat (gular) fan" located beneath the throat of A. carolinensis and was elicited from an Anole by exposing it to a live house sparrow. OKR refers to distinct lateral head movements (following) elicited by rotating counterclockwise a field of stripes, and swimming refers to an animal actively moving while in water. The dewlap response

is involved in courtship and intraspecific fighting, while the OKR is probably involved in visually guided behaviors (e.g., prey capture). The duration of swimming and dewlap extension and the frequency of head following in the direction of the moving stripes (OKR) were recorded by hand, while all stimulus presentations and intertrial intervals were electromechanically programmed. Interrater reliabilities were $+0.97$, $+0.96$ and $+0.98$ for the dewlap, OKR and swimming responses, respectively.

Behavioral experiments were conducted to investigate the effects of intertrial interval (ITI), spontaneous recovery and individual differences in habituation across responses (Experiments 1, 2 and 3, respectively). For each response, a habituation session consisted of 40 trials, each trial of 30 sec duration.

In Experiment 1, ITIs (5, 30 and 120 sec) had various effects. The habituation curves for each ITI of the swimming response differed, while in the OKR the 5 sec ITI was different from the 30 and 120 sec ITI. There were no differences between ITIs of the dewlap response. However, comparisons of larger and smaller Anoles indicated that smaller animals did not habituate under the 30 and 120 sec ITI condition of the dewlap response, while no ITIs differed for larger Anoles. There were no size differences in the OKR or swimming response. Comparisons across responses indicated that the dewlap response of smaller Anoles differed from the OKR and swimming response under each ITI condition, while for larger animals the dewlap response differed from the OKR and swimming response only under the 5 sec ITI condition. The OKR did not differ from the swimming response for larger or smaller Anoles.

Larger animals were employed for studying spontaneous recovery of the dewlap response and OKR in Experiment 2. After a 15 minute interval, recovery was virtually complete (95%) for the dewlap response and was substantial (80%) for the OKR, while retention (lower response level) was clearly evident in both responses. After a 24 hour interval, recovery was complete with no evidence of retention for either response.

Individual differences in habituation were consistent when animals were tested twice on the same response (Experiment 3). In contrast, there was less consistency ($r = +.05$) across responses (dewlap and OKR). Approximately 57% (26/46) of the animals showed similar decreasing patterns of habituation on the dewlap response and OKR, while the rest (20/46) did not. Further, smaller Anoles showed retention of habituation of the dewlap response after 4 days of rest and were not affected by the order of testing. Larger Anoles tested first on the dewlap response showed no retention of dewlap habituation as opposed to larger animals tested second on the dewlap response.

The reasons for the observed size differences in dewlap habituation remain unknown at this time. Reproductive state, prior experience and/or other maturational changes may be involved.

In addition to demonstrating, for the first time, habituation in a reptile other than turtles, the present dissertation offers an alternative method for testing theories of habituation.

VITA

David Joseph Gubernick, son of Irving and Frances Darmiento Gubernick, entered into the world on the morning of April 21, 1944, in Yonkers, New York. He attended Cardinal Hayes High School, Bronx, New York and was graduated in June 1962.

He entered Westchester Community College, Valhalla, New York, in September 1964 and received an Associate of Arts degree in June 1966. He then entered the State University College of New York at New Paltz and received the Bachelor of Arts, cum laude, in June 1968.

In September 1968, he was accepted as a psychology student in the Graduate School of Arts and Sciences of Fordham University. After a two year delay serving in the United States Army, he returned to continue his education and received the Degree of Master of Arts from Fordham University in February 1972. He was awarded a Teaching Fellowship in the Psychology Department during the academic year 1972-1973. He has studied in the General-Theoretical psychology program, specializing in experimental-animal behavior under the comentorship of Professors John W. Wright and Henry R. Askew and later Peter Borchelt.