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Habituation Revisited: An Updated and Revised Description of the Behavioral Characteristics of Habituation

Catharine H. Rankin, **Thomas Abrams**, **Robert J. Barry**, **Seema Bhatnagar**, **David Clayton**, **John Colombo**, **Gianluca Coppola**, **Mark A. Geyer**, **David L. Glanzman**, **Stephen Marsland**, **Frances McSweeney**, **Donald A. Wilson**, **Chun-Fang Wu**, and **Richard F. Thompson**

Abstract

The most commonly cited descriptions of the behavioral characteristics of habituation come from two papers published almost 40 years ago (Thompson and Spencer, 1966; Groves and Thompson, 1970). In August 2007, the authors of this review, who study habituation in a wide range of species and paradigms, met to discuss their work on habituation and to revisit and refine the characteristics of habituation. This review offers a re-evaluation of the characteristics of habituation in light of these discussions. We made substantial changes to only a few of the characteristics, usually to add new information and expand upon the description rather than to substantially alter the original point.

In the 20th century, great progress was made in understanding the behavioral characteristics of habituation. A landmark paper published by Thompson and Spencer in 1966 clarified the definition of habituation, synthesized the research to date and presented a list of nine behavioral characteristics of habituation that appeared to be common in all organisms studied The history of habituation and the historical context of Thompson & Spencer's (1966) distillation are reviewed more fully in an article by Thompson (2009) that is included in this issue. This list was repeated and expanded upon by Groves and Thompson in 1970. These two papers are now citation classics and are considered to be the authorities on the characteristics of habituation. In August 2007, a group of 15 researchers (the authors of this review) who study habituation in a wide range of species and paradigms met to revisit these characteristics and refine them based on the 40 years of research since Thompson and Spencer 1966. The descriptions and characteristics from 1966 have held up remarkably well, and the revisions we have made to them were often for clarity rather than content. We made substantial changes to only a few of the characteristics, usually to add new information and expand upon the description rather than to substantially alter the original point. We restricted ourselves to an analysis of habituation; there was insufficient time for detailed discussions of the other form of non-associative learning “sensitization.” Thus this review is restricted to our discussions of habituation and dishabituation (as it relates directly to habituation).

Many people will be surprised to learn that, although habituation is termed ”the simplest form of learning” and is well studied behaviorally, remarkably little is known about the neural mechanisms underlying habituation. Researchers who work on this form of learning believe that because habituation allows animals to filter out irrelevant stimuli and focus selectively on

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Corresponding Author: Catharine H. Rankin Department of Psychology, University of British Columbia 2136 West Mall, Vancouver, BC V6H 1B3 Phone 604−822−5449 crankin@psych.ubc.ca.

important stimuli, it is a prerequisite for other forms of learning. Therefore, to fully understand the mechanisms of more complex forms of learning and cognition it is important to understand the basic building blocks of habituation. The objectives of this special issue are to re-ignite interest in studying the mechanisms of habituation and thereby to stimulate efforts to further our understanding of the neural basis of habituation.

In this review, we will first define habituation, then review and revise the nine characteristics of habituation that were originally determined by Thompson and Spencer in 1966 and that have been seen across all species studied. In addition, we describe a tenth characteristic that was added at the workshop. Finally we present several issues that were discussed extensively at the meeting and highlight how the view of habituation that arose from our discussions differs from the original characterization by Thompson and Spencer.

Definition of Habituation

Habituation is defined as a behavioral response decrement that results from repeated stimulation and that does not involve sensory adaptation/sensory fatigue or motor fatigue. Traditionally, habituation has been distinguished from sensory adaptation and motor fatigue by the process of dishabituation; however this distinction can also be made by demonstrating stimulus specificity (the response still occurs to other stimuli) and/or frequency-dependent spontaneous recovery (more rapid recovery following stimulation delivered at a high frequency than to stimulation delivered at a lower frequency). Behavioral responses that undergo habituation may include any final output of the nervous system including simple reflexes such as pupillary responses and sweating, and muscle contraction or even motor neuron activity. One additional example is hormone release, which is the final output of the neuroendocrine system; hormones have a persistent action in regulating many behaviors. Studies of habituation may also measure cellular or molecular responses or neuronal activity, including population activity, such as measured with EEG or functional imaging. These responses at the molecular, cellular or population levels may be monitored in an effort to identify underlying mechanisms or they may be used as indices of habituation. As with other forms of learning, even when changes in cellular or molecular processes do occur in parallel with habituation, dissociations may also be observed. Such dissociations occur because typically, no single mechanism necessarily accounts entirely for a specific type of learning.

Common characteristics of habituation

There are nine characteristics of habituation that are based on the characteristics described in Thompson and Spencer (1966); one additional characteristic was added as a result of our deliberations.

Characteristic #1

Original—“Given that a particular stimulus elicits a response, repeated applications of the stimulus result in decreased response (habituation). The decrease is usually a negative exponential function of the number of stimulus presentations.”

Revised—Repeated application of a stimulus results in a progressive decrease in some parameter of a response to an asymptotic level. This change may include decreases in frequency and/or magnitude of the response. In many cases, the decrement is exponential, but it may also be linear; in addition, a response may show facilitation prior to decrementing because of (or presumably derived from) a simultaneous process of sensitization.

The changes in the wording of characteristic #1 reflect the reality that responses have a number of parameters that can be altered by repeated stimulation such as response frequency, magnitude, duration etc, and that the decrement is not always best described as a negative exponential function. There are examples in Groves and Thompson (1970), where animals first show an increase in responsiveness (sensitization) and then later a decrease in responsiveness (habituation) to repeated stimulation. This type of curve reflects both a sensitizing and a habituation process, and would require more than a simple negative exponential to describe it; nevertheless it would still be considered an example of habituation. Recognition of these two processes prompted Groves and Thompson to develop what is widely known as the dual-process theory of response habituation.

Characteristic #2

Original—“If the stimulus is withheld, the response tends to recover over time (spontaneous recovery).”

Revised—If the stimulus is withheld after response decrement, the response recovers at least partially over the observation time (“spontaneous recovery”).

Other than a clarification of the timing (i.e. after response decrement) the only change here is that sometimes the response recovers completely, sometimes only partially within the time frame examined; however in both cases it is still considered spontaneous recovery.

Characteristic #3

Original—“If repeated series of habituation training and spontaneous recovery are given, habituation becomes successively more rapid (this phenomenon might be called potentiation of habituation).”

Revised—After multiple series of stimulus repetitions and spontaneous recoveries, the response decrement becomes successively more rapid and/or more pronounced (this phenomenon can be called potentiation of habituation).

Other than clarifying the wording there is no change to this characteristic.

Characteristic #4

Original—“Other things being equal, the more rapid the frequency of stimulation, the more rapid and/or more pronounced is habituation.”

Revised—Other things being equal, more frequent stimulation results in more rapid and/or more pronounced response decrement, and more rapid spontaneous recovery (if the decrement has reached asymptotic levels).

This characteristic was revised to reflect an observation made in many different organisms that spontaneous recovery is much more rapid following habituation at high stimulation frequencies than following habituation at low frequencies (e.g. rat startle response, Davis, 1970; depression at *Aplysia* sensory-motor synapses, which contributes to habituation of the defensive withdrawal reflex, Byrne 1982; *C. elegans* tap habituation, Rankin and Broster 1992). Using habituation to mechanosensory tap in *C. elegans* Rankin and Broster (1992) demonstrated that it was not the level of habituation that was achieved, the number of stimuli delivered or the number of missed stimuli before the recovery test that determined rate of recovery, but rather in all cases the frequency of stimulation during habituation training determined the rate of spontaneous recovery. An important caveat to this characteristic comes from Rankin and Broster (1992) who observed that the characteristic holds only if habituation has reached asymptotic levels.

Characteristic # 5

Original—“The weaker the stimulus, the more rapid and/or more pronounced is habituation. Strong stimuli may yield no significant habituation.”

Revised—Within a stimulus modality, the less intense the stimulus, the more rapid and/or more pronounced the behavioral response decrement. Very intense stimuli may yield no significant observable response decrement.

This revised characteristic has no conceptual changes; the wording has been revised to make the meaning clearer.

Characteristic # 6

Original—“The effects of habituation training may proceed beyond the zero or asymptotic response level.”

Revised—The effects of repeated stimulation may continue to accumulate even after the response has reached an asymptotic level (which may or may not be zero, or no response). This effect of stimulation beyond asymptotic levels can alter subsequent behavior, for example, by delaying the onset of spontaneous recovery.

This characteristic was revised first to clarify that this statement refers to asymptotic levels of response that are zero or greater and second, that continuing to receive habituation stimuli after the organism has reached asymptotic response levels might have effects on later behavior that can be revealed with the proper tests. Using habituation to mechanosensory tap in *C. elegans*, Rankin and Broster (1992) showed that the higher the number of habituating stimuli the later the onset of spontaneous recovery (once spontaneous recovery began however it proceeded at the normal rate for the frequency of the training stimuli).

Characteristic # 7

Original—“Habituation of response to a given stimulus exhibits stimulus generalization to other stimuli.”

Revised—Within the same stimulus modality, the response decrement shows some stimulus specificity. To test for stimulus specificity/stimulus generalization, a second, novel stimulus is presented and a comparison is made between the changes in the responses to the habituated stimulus and the novel stimulus. In many paradigms (e.g. developmental studies of language acquisition) this test has been improperly termed a dishabituation test rather than a stimulus generalization test, its proper name.

This characteristic is a critical aspect of habituation that can be used to distinguish it from more general sensory adaptation or motor fatigue (which should generalize across a broad range of stimuli within a sensory modality). This change reflects a shift in focus from stimulus generalization to stimulus specificity. The notion of stimulus specificity is consistent with the notion that habituation functions to reduce the response to innocuous stimuli while still leaving the organism responsive to novel stimuli. In contrast stimulus generalization (even within the same sensory modality) is consistent with the idea that habituation is happening centrally rather than in primary sensory afferents. A clarification of this characteristic was deemed an important aspect of this revision because this characteristic has been incorrectly labeled dishabituation in many types of studies and should more properly be termed generalization.

Characteristic # 8

Original—“Presentation of another (usually strong) stimulus results in recovery of the habituated response (dishabituation).”

Revised—Presentation of a different stimulus results in an increase of the decremented response to the original stimulus. This phenomenon is termed “dishabituation.” It is important to note that the proper test for dishabituation is an increase in response to the original stimulus and not an increase in response to the dishabituating stimulus (see point #7 above). Indeed, the dishabituating stimulus by itself need not even trigger the response on its own.

Although traditionally a strong stimulus has been used to produce dishabituation there is some discussion in the literature that any different stimulus can serve to dishabituate a response (i.e. Wagner, 1979). In a study of the defensive gill and siphon withdrawal response in *Aplysia* Marcus, Nolen, Rankin and Carew (1988) showed that a touch or a weak electric shock produced better dishabituation than did a strong shock.

Characteristic #9

Original—“Upon repeated application of the dishabituatory stimulus, the amount of dishabituation produced habituates (this phenomenon might be called habituation of dishabituation).”

Revised—Upon repeated application of the dishabituating stimulus, the amount of dishabituation produced decreases (this phenomenon can be called habituation of dishabituation).

Again, in this case the only change was a clarification of the wording.

Characteristic # 10

Additional—Some stimulus repetition protocols may result in properties of the response decrement (e.g. more rapid rehabituation than baseline, smaller initial responses than baseline, smaller mean responses than baseline, less frequent responses than baseline) that last hours, days or weeks. This persistence of aspects of habituation is termed long-term habituation.

This additional characteristic was added to acknowledge evidence for long-term habituation in a number of systems including *Aplysia* (Castellucci, Carew and Kandel, 1978; Ezzadine and Glanzman 2003), *C. elegans* (Rose , Kaun, Chen and Rankin, 2003), rats (Bhatnagar, Huber, Nowak and Trotter, 2002) and humans (Maschke, Drepper, Kindsvater, Kolb, Diener and Timmann, 2000). This additional characteristic has been recognized for many years and was referred to by Thorpe (1956) when he defined habituation as “a relatively permanent waning of a response as a result of repeated stimulation”. In this revised view of habituation, we recognize that habituation comes in at least two forms, short-term habituation and long-term habituation. The distinction is the duration of the effects of training and the demonstrated (or assumed) necessity of changes in protein synthesis that underlie long-term habituation.

Our Perspective on Habituation

Our perspective on habituation differs somewhat from the earlier formulation in several important ways. In the 1966 and 1970 papers the focus was primarily on reflexes; since then however many types of response properties in diverse preparations have been quantified under the rubric of habituation including responses that are not reflexes. These preparations include, but are not limited to: the habituation to the sensory property or properties of a reinforcer in operant conditioning paradigms as described by Frances McSweeney (Murphy and

McSweeney, 2009, this issue) and habituation of a hypothalamic-pituitary-adrenal axis response to stress described by Seema Bhatnagar (Grissom and Bhatnagar, 2009, this issue). Many studies have been published on correlates of habituation such as decrement of event-related potentials (i.e. Robert Barry, 2009, this issue) or decrement of responses measured by positron emission tomography or functional magnetic resonance imaging.

We treat “generalization” differently than the earlier papers (focusing on stimulus specificity rather than stimulus generalization) and emphasize stimulus specificity of habituation and frequency-dependent spontaneous recovery as two ways to distinguish habituation from adaptation or fatigue. We felt it important to emphasize that there are several ways to distinguish habituation from sensory adaptation or fatigue. The traditional way to make this distinction is to use dishabituation but, given that we do not fully understand the relationship between the mechanisms of habituation and dishabituation, it seems useful to have other methods to identify when habituation has occurred, especially in a system in which dishabituation is not observed (i.e. Rankin and Wicks 2000; Wright, 1998). Finally, we explicitly introduce the notion of long-term habituation, which is the expression of long lasting memory for habituation training. In our view, long-term habituation is not merely the extension in time of the processes that mediate short-term habituation. Rather, we believe that long-term habituation is likely to involve qualitatively different cellular mechanisms than those involved in short-term habituation, as well as a more prolonged time course.

The question of mechanisms of habituation was also hotly debated and several of the articles in this issue explicitly discuss possible mechanisms underlying this form of learning. It is clear from looking at the broad range of areas covered by the articles in this issue that to call habituation a “simple” form of learning is a misnomer – what is simple is the acquisition of habituation. Nervous systems are constantly evaluating incoming stimuli and filtering out stimuli that are not important as well as cataloguing and using stimuli that are important (i.e. those stimuli that signal things that are good or bad for the survival of the organism). Habituation paradigms are often simple and effortless: anytime we put an animal into a test chamber we first allow it to “habituate” to the environment; when we put a cannula into an animal or an electrode cap onto one, an animal will need to habituate to the surgically added device. If we repeatedly play a loud noise to an animal it will “habituate.” What the diversity of the articles in this issue indicates is that underlying this simple concept of “habituation” is a rich collection of cellular mechanisms that are differentially recruited in different parts of the nervous system, in different types of neurons, and by different stimulus paradigms. We believe that the results of future research in this area will extend the hypothesis that there are a large number of cellular mechanisms that underlie the deceptively simple forms of learning termed “habituation” by identifying novel mechanisms that can mediate this process. The challenge for neuroscientists now is to continue to identify the mediatory mechanisms for habituation and to determine when, where and how these mechanisms are activated.

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