PROLOGUE

A Historical Note on the "Discovery" of Startle Modification

HOWARD S. HOFFMAN

The term startle modification refers to the change in the amplitude and/or the latency of a startle reaction when the startle-eliciting signal has been preceded or accompanied by another (usually weaker) stimulus. In the early 1960s my students and I discovered or, as will be seen, rediscovered these effects when we found that in rats, the startle reaction to a sudden explosive sound could be virtually eliminated if another, barely audible, sound precedes the intense sound by about a tenth of a second (Hoffman and Searle 1965). We found this effect to be so impressive that we began what has for us proven to be more than 30 years of continuing investigations of its basic features.

At the time we started that work, very little of the contemporary research involved startle, and the primary source on this reaction was a slim volume entitled *The Startle Pattern* by Carney Landis and William A. Hunt (1939). This book described an extensive series of investigations by the authors in which high-speed cinematic photographs of both animal and human startle reactions were carefully analyzed. It is significant that the book made no mention of the phenomenon of startle modification, nor had the phenomenon been noted in any of the more contemporary research literature we were examining at the time.

It was a number of years after we had "discovered" startle modification that we were to learn that James Ison at the University of Rochester had independently and almost simultaneously discovered the same phenomenon. Furthermore, Ison's subsequent historical studies revealed that the phenomenon was originally discovered by Sechenov, a Russian scientist, almost 100 years earlier (Sechenov 1863/1965). During the ensuing century, startle modification had disappeared from the literature and been rediscovered at least four times. An account of those rediscoveries and an evaluation of their role in the history of psychology is provided in Ison and Hoffman (1983).

At the time of my own rediscovery I was a new assistant professor at Pennsylvania State University, and my students and I were investigating a set of behaviors that, technically, are described as "discriminated avoidance." Our subjects were laboratory rats and we had begun to cast about for a way to assess the emotional reactions that, theoretically, were thought to motivate the avoidance response. In the experiment we were conducting, a tone ending with an electrical shock was periodically presented to a rat that was confined in a small cage with a lever protruding from one of the walls. The conditions were such that if the rat pressed the lever during a tone but prior to the onset of shock, the tone immediately terminated and the shock was avoided. If, however, the rat failed to respond prior to shock onset, both the tone and the shock stayed on until a press occurred, whereupon both tone and shock were immediately turned off.

As we considered the ways we might assess the emotional aspects of our rat's behavior, I recalled an elegant study by Judson Brown and his colleagues. They reported that after a tone ending with a brief shock had been repeatedly presented to a rat, the animal's startle reaction to a sudden intense sound was larger (i.e., it was potentiated) if the sound was presented during the tone as compared with when it was presented in the absence of the tone (Brown, Kalish, & Farber 1951). It seemed possible that we might find it useful to employ the Brown, Kalish, and Farber procedures in our own work. More specifically, we thought we might be able to track the course of emotionality during our rat's avoidance behavior by occasionally presenting an intense sound during the tone and assessing the amplitude of the ensuing reaction. As it turned out, we never pursued this, because we were diverted by the study of startle itself once we began to assess it.

As we saw it, to study startle we had to solve two problems. We had to find a convenient way to measure response amplitude and we had to find a way to reliably produce an eliciting acoustic stimulus. Brown, Kalish, and Farber had used a spring-mounted mechanical postage scale to assess startle amplitude and they used a pistol shot to elicit the reaction. We wanted to use electronic gear to accomplish both of these ends.

Our solution to the problem of assessing startle was to build a small Plexiglas chamber and to mount it on compression springs that were fastened to a rigid superstructure. An aluminum rod with a small permanent magnet at its distal end was connected to the bottom of the chamber so that the magnet rode within an electrical coil. Movements of the chamber moved the magnet in the coil and generated an electrical current that was amplified and rectified and passed to a recording milliammeter. Because the output of the system was proportional to the rate at which magnetic lines of flux crossed the coil, the device was highly sensitive to the sudden ballistic-type movements involved in startle, but it was relatively insensitive to the gross, but more or less slow, movements involved in general activity.

Our solution to the problem of eliciting startle was not so elegant. We found that the maximum acoustic signals produced by our electronic signal generators were too weak to consistently elicit startle. We also found, however, that we could reliably evoke a response by discharging a condenser through the voice coil of an inexpensive 5-inch speaker. The problem here was that the speakers were fragile and would often blow out after only two or three discharges. Fortunately, however, we also found that every now and then we would come across a speaker that was so resistant to blowout that we could deliver thousands of startle-eliciting signals with no ill effects. We cherished those speakers and used them in our subsequent experiments.

Our "discovery" of startle modification occurred as we were engaged in our initial pilot work. We had noticed that when tested in the open environment of our laboratory, the startle reactions of our rats were highly variable. In an effort to obtain better control over these reactions, we enclosed our startle apparatus within an ice chest and arranged to introduce steady noise into the chest so as to mask extraneous environmental sounds.

As expected, responses were less variable when subjects were tested in the ice chest but to our surprise response amplitude turned out to be critically dependent on the nature of the acoustic conditions at the time that startle was evoked. With the background noise turned off, the ambient acoustic level within the chamber hovered about 58 dB SPL, with occasional peaks of about 70 dB. With the noise turned on, the ambient acoustic level within the chest was a steady 85 dB.

With the background noise turned off, responses to the acoustic bursts were of moderate amplitude. When the noise was turned on, however, responses to the same bursts were much larger. It should be noted that this was exactly the opposite of what we had expected would happen. We had assumed that the background noise would, in some measure, mask the startle-eliciting signals.

As a result, responses to those signals were smaller. Even more surprising was the observation that if we pulsed the background noise (one-half second on and one-half second off), the startle responses to the intense bursts all but disappeared. Figure 1 shows the trial by trial record of an individual rat when it was exposed to a sequence of startle-eliciting acoustic bursts spaced 10 s apart.

During the first ten bursts the background noise was off. The background noise was pulsed throughout the next ten trials and then it was made steady. Since, as indicated in Figure 1, manipulation of the background noise persisted in determining overall response amplitude and since the identical effects were easily obtained with other rats, it was apparent that we had stum-

Cambridge University Press
978-0-521-58046-5 - Startle Modification: Implications for Neuroscience, Cognitive Science, and Clinical Science
Edited by Michael E. Dawson, Anne M. Schell and Andreas H. Bohmelt
Excerpt
More information

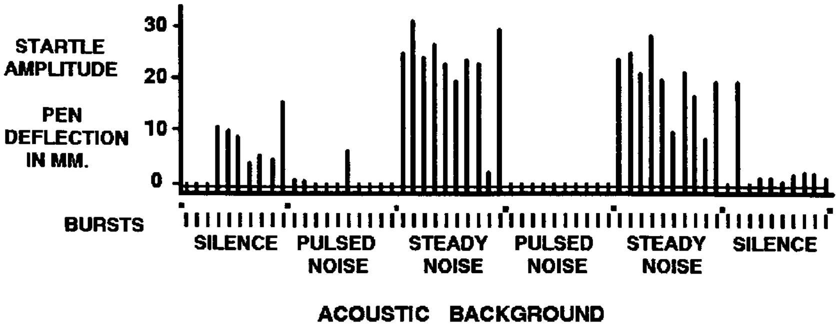

Figure 1. The effect of background acoustic stimulation on the startle reaction to an intense burst of noise. The record shows the sequence of startle reactions by a single rat that received a startle eliciting stimulus every 10 s. Throughout this session the acoustic background was changed (as indicated) shortly after every tenth startle-eliciting stimulus. (Adapted from Figure 1 in Hoffman and Fleshler, 1963. Copyright 1963 by The American Association for the Advancement of Science. Reprinted by permission.)

bled onto a robust and possibly quite important behavioral phenomenon. Accordingly, we abandoned our effort to employ startle as an index of the emotional factors in discriminated avoidance and turned our attention to the study of startle modification. In particular, we started a sequence of investigations designed to determine whether and how a single pulse of noise that was itself too weak to elicit startle might, nonetheless, influence the startle reaction to a subsequently presented intense acoustic burst.

The results of those initial investigations were reported in Hoffman and Searle (1965, 1968). It is, perhaps, of historical interest that in preparing those reports Searle and I used the term "prepulse" to describe the lead stimulus in our startle modification paradigms. Within a few years of those publications Francis Graham at the University of Wisconsin and James Ison at Rochester University independently began to publish reports of their own investigations of the startle modification effect, and it is, I suspect, also of historical interest that it was in one of those reports (Ison & Hammond, 1971) where the now popular expressions "prepulse inhibition" and "prepulse facilitation" were first used. Some of the results of the initial studies by both Graham and Ison were summarized in an early review paper (Hoffman & Ison, 1980).

As revealed in this volume, many new insights into and uses for startle modification have been developed in the decade and a half since Ison and I published our review. We ended that review with the following statement: "Clearly, the analysis of reflex modification offers an approach to a range of problems of utmost theoretical and practical importance. In some respects these preparations are comparable in their simplicity and reproducibility to the isolated systems studied by the physiologist. Yet in their appearance in the intact animal, even in the intact human animal, they are sensitive to the activity of more complex processes and offer another way to examine that activity and its determinants" (p. 187).

I can add only that it is a source of great satisfaction to me that the approaches and insights in the various chapters of the present volume are directed to the elaboration and extension of that enterprise.

CHAPTER ONE

Startle Modification: Introduction and Overview

MICHAEL E. DAWSON, ANNE M. SCHELL, AND ANDREAS H. BÖHMELT

ABSTRACT

Startle modification refers to a set of reliable and ubiquitous phenomena. Specifically, the startle modification phenomena include the inhibition and facilitation of the startle reflex by nonstartling stimuli that accompany or precede the startle-eliciting stimulus. This chapter introduces these phenomena through historical examples drawn from both the human and nonhuman animal literature. Both the inhibition and the facilitation of the startle reflex are illustrated. The standard terms used throughout this book – "startle stimulus," "lead stimulus," and "lead interval" – are defined by reference to these prototypical examples. Potential implications of startle modification phenomena are identified for cognitive science, neuroscience, and clinical science, with special emphasis on integrative implications. Finally, the book is outlined with reference to each of the subsequent chapters.

1. Introduction and Brief History

Reflexes are often considered simple, fixed, and invariant reactions to stimuli. However, it has been known for a number of years that reflexes are not fixed; rather, they are highly modifiable by a variety of events that occur concurrent with or immediately before the elicitation of the reflex. The amplitude of the patellar tendon "knee-jerk" reflex, for example, was shown over 100 years ago to vary systematically depending upon the time at which a voluntary motor response preceded the elicitation of the reflex (Bowditch & Warren, 1890). The amplitude of the human patellar reflex was facilitated if participants voluntarily clinched their hands in response to a bell simultaneously with the blow upon the tendon, but the reflex was inhibited, sometimes disappearing entirely, if the hand clinch occurred only a few hundred milliseconds before the patellar stimulation. This early study and several others that preceded and followed it are thoroughly reviewed by Ison and Hoffman (1983).

This research in combination with others suggested that "the myth of the knee-jerk as a simple spinal reflex is shattered. . . . data have been accumulating that the knee-jerk, and perhaps all 'simple' reflexes, *cannot be regarded as isolated units of function in the intact nervous system*" (Fearing, 1930, p. 277, emphasis in original). This book provides the first contemporary and comprehensive review of the proposition that reflexes are modified by ongoing psychophysiological processes, and hence can provide a window onto those processes.

Hilgard (1933) devised a research paradigm based on the human startle eyeblink reflex to loud noise that is more relevant to present-day research than the knee-jerk paradigm employed by Bowditch and Warren. In this paradigm, simple stimuli (lights) rather than a motor response were used to modify the human startle eyeblink reflex elicited by a loud noise. The loud startling noise was preceded by a low-intensity light on some trials at various intervals, and not on other intermixed trials. When the light preceded the noise by very short intervals (e.g., 25 and 50 msec), the amplitude of the blink reflex to the noise was increased by approximately 150%; however, when the light preceded the noise by moderately short intervals (e.g., in the range of 100–300 msec), the blink reflex to the noise was inhibited to approximately half of its normal size. Thus, Hilgard concluded that "a faint stimulus, itself eliciting only minimal reflex reactions, may greatly exaggerate or depress the response to a more intense stimulus which follows it. By slight changes in the interval of time between the first and second stimulus, the reinforcing effect may be converted into an inhibitory effect" (1933, p. 86). The finding of facilitation or inhibition of the human acoustic startle eyeblink reflex by a prior occurring innocuous stimulus is an intriguing phenomenon that anticipates a large body of contemporary research.

Other historical examples of the modification of reflexes by simple stimuli preceding the elicitation of the reflex can be found in nonhuman animals. In one of the earliest and more interesting examples, Yerkes (1905) was puzzled by the fact that frogs did not respond behaviorally to sounds, and he wanted to experimentally determine whether frogs can hear. Therefore, he presented auditory stimuli (e.g., a bell) simultaneously with or shortly preceding a tactile stimulus (a tap to the head), which in turn elicited a leg withdrawal reflex. The results revealed that when the auditory stimulus occurred simultaneously with the tactile stimulus the withdrawal reflex was exaggerated, whereas on the contrary if the auditory stimulus preceded the reflex-eliciting tactile stimulus by several hundred milliseconds the reflex was partially inhibited. Yerkes concluded that "these experiments prove conclusively that sounds, although they do not call forth the reflex movement under consideration, modify in important ways the action of other stimuli" (p. 296).

Although there are obvious differences in the procedures employed by Hilgard and by Yerkes, both found that a weak innocuous stimulus has the power to significantly facilitate or inhibit an innate defensive reflex depending upon the time interval separating the two stimuli. The remarkable commonality of reflex modification effects observed across different species, different stimuli, and different response systems suggests the existence of processes of profound generalizability and importance.

Despite these early encouraging results, however, the study of reflex modification was largely ignored for several decades. Yerkes and Hilgard went on to distinguished careers, both becoming presidents of the American Psychological Association, but in research areas other than reflex modification. Ison and Hoffman (1983) suggested that the study of reflex modification was swept aside by the then burgeoning interest in classical Pavlovian conditioning (itself considered an associative reflex modification procedure) and learning theories in general.

Given the high level of interest in classical conditioning at the time, it is not surprising, therefore, that the return of research interest in reflex modification was in the context of understanding classical conditioning. Brown, Kalish, and Farber (1951), for example, classically conditioned fear in rats by pairing a neutral compound stimulus (light + buzzer) with an electric shock. In the experimental group, the onset of the light + buzzer was followed by the shock in 3 s, whereas the control group was presented the same stimuli but not in a paired arrangement. On interspersed trials during this procedure, a startle reflex was elicited by a loud noise in both groups 3 s after the onset of the light + buzzer (i.e., at the time the shock was due in the experimental group). The whole-body startle reaction (the magnitude of the jump of the rat as measured with a postage scale) was significantly larger in the experimental group than the control group. It was concluded that the pairing of the light + buzzer with the shock led to a conditioned fear state that facilitated the startle reaction to sound.

Brown et al. (1951) emphasized the importance of their findings as confirming Hull's (1943) theoretical prediction that conditioned fear has energizing properties. However, from today's perspective, the importance of the Brown et al. study is its demonstration of affective modulation of a startle reflex. Although Hullian theory has now gone the way of all grand learning theories, the affective modulation of the startle reflex has been confirmed many times in both human and nonhuman subjects and has become a commonly used paradigm with many important applications and implications.

The most recent reemergence of interest in reflex modification in the 1960s was initially motivated by an attempt to replicate the Brown et al. effect (see Prologue). Fortunately, while conducting pilot studies, Hoffman and his colleagues serendipitously noticed that the rat acoustic startle reaction was highly modifiable by mild sounds even without being paired with shock. Hoffman and Wible (1969) then systematically studied startle in rats to a loud noise (130 dB) preceded by a weaker noise (75 dB) at onset to onset intervals ranging from 100 to 6000 msec. The preceding noise was presented as a discrete 20-msec pulse or as a continuous stimulus throughout the interval. The authors observed reflex inhibition at the short lead intervals and facilitation at the long lead intervals, but the inhibition effect was strongest with the brief discrete preceding noise and the facilitation was evident only with the continuous preceding noise that was maintained throughout the entire lead interval. Hoffman and Wible suggested that two aspects of the preceding stimulus control startle amplitude. The transient *onset* of the leading stimulus can trigger a short latency, brief inhibitory effect at short lead intervals, whereas the *continuous* presence of the stimulus can have a long-lasting amplifying effect at long lead intervals. This hypothesis has been a fertile seed that has flourished and continues to bear fruit to this day, as will become clear in later chapters.

Hoffman's research influenced the independent research programs of other investigators, most notably Ison and Graham. Ison and his students soon demonstrated that the acoustic startle reflex in rats could be inhibited by stimuli in multiple sensory systems, and was not specific to an auditory refractory process (Buckland, Buckland, Jamieson, & Ison, 1969; Ison, Hammond, & Krauter, 1973), and they also examined various parametric effects with the human eyeblink reflex (e.g., Krauter, Leonard, & Ison, 1973). Graham and her students quickly followed with a systematic series of studies that demonstrated that the human acoustic startle eyeblink reflex was reliably inhibited by a mild tone presented 60–240 msec prior to the startle loud noise and was facilitated if the same mild tone was presented several seconds prior to the startling noise (Graham, 1975; Graham, Putnam, & Leavitt, 1975), and they have since gone on to study preattentive, attentive, and arousal processes with startle modification and other psychophysiological measures (Graham, 1997).

In summary, numerous studies have demonstrated that relatively small changes in environmental stimuli produce large changes in subsequently elicited reflexes, with the interval separating the stimuli being a critical determiner of the direction of the effect. The present book contains chapters that focus separately on short and long intervals precisely because the processes that modify and modulate reflexes appear to be quite different at these intervals.

In the remainder of this chapter we will describe the reflex modification paradigm and phenomena in more formal terms, suggest standard terminology to describe the reflex modification paradigm, and, most important, discuss why researchers from diverse scientific disciplines find the reflex modification phenomena worthy of renewed attention and research. We then conclude with an outline of this book, briefly indicating how each chapter contributes an important part of the story of the psychological and physiological significance of startle modification.

2. Startle Reflex Modification: Paradigms and Terminology

Rather than discuss modification of reflexes in general, one particular type of reflex is emphasized here and throughout the book, that is, the acoustic startle reflex. Many of the prototypical paradigms described above (e.g., Hilgard, 1933; Brown et al., 1951; Hoffman & Wible, 1969) measured the acoustic startle reflex and its modification. Whenever an exception to this general rule is made by reference to other reflexes, this will be made clear. Although it is empirically and theoretically important to know whether other types of reflexes are similarly modified, this is not the focus of the present book. Therefore, in the subsequent material we will refer to startle reflex modification or simply startle modification rather than the more general term reflex modification.

Given the large and rapidly growing body of startle modification research, it is impossible for one volume to adequately cover both human and nonhuman research on this topic. We chose to focus primarily but not exclusively on human research. The human acoustic startle reflex, as originally captured with high-speed motion pictures by Landis and Hunt (1939), consists of a series of involuntary muscle movements. Landis and Hunt reported that the fastest, most reliable, and most resistant to habituation component of the human startle reflex was the eyeblink reaction. For these reasons, and because it is relatively easy to measure and quantify, the eyeblink response is the most commonly used measure of startle in human research today.

In the previous section we presented prototypical examples of startle modification, some with short interstimulus intervals (e.g., in a few hundred milliseconds as in Hilgard, 1933) and others with long interstimulus intervals (e.g., several seconds as in Brown et al., 1951). Figure 1.1 depicts diagrammatically the basic procedures and results of the startle modification paradigm.

The startle modification paradigm consists of two stimuli and the interval separating their onsets. Various terms have been used in the literature to