

# Automatic and controlled attentional processes in startle eyeblink modification: Effects of habituation of the prepulse

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## Abstract

The effect of prehabituation of the prepulse on startle eyeblink modification was studied in two experiments. In Experiment 1, college student participants were either prehabituated or nonhabituated to a tone that served as a prepulse in a startle modification passive attention paradigm. Neither short lead interval (60 and 120 ms) prepulse inhibition (PPI) nor long lead interval (2,000 ms) prepulse facilitation (PPF) was affected by the prehabituation procedure. In Experiment 2, participants were presented with an active attention paradigm in which one of two tone prepulses was attended while the other was ignored. One group was prehabituated to the prepulses and the other was not. Unlike the results with the passive paradigm in Experiment 1, prehabituation did significantly diminish attentional modulation of PPI and PPF. These results are consistent with the hypothesis that passive PPI and PPF are primarily automatic processes, whereas attentional modulation involves controlled cognitive processing.

**Descriptors:** Prepulse inhibition, Prepulse facilitation, Skin conductance, Orienting, Attention, Habituation

In recent years the modification of the startle eyeblink response by nonstartling stimuli that precede the startle stimulus has shown promise as a tool for investigating both automatic and controlled attentional processes (for reviews see Blumenthal, 1999; Filion, Dawson, & Schell, 1998; Putnam & Vanman, 1999). The startle response is an automatic reflexive response mediated at the brain stem level (Davis, Gendelman, Tischler, & Gendelman, 1982; Davis, Walker, & Lee, 1999), but the magnitude of the blink can be modified reliably and predictably if a nonstartling stimulus (often called a prepulse) is presented prior to a startling stimulus. Specifically, the startle eyeblink is inhibited if the interval (referred to as the lead interval) between the prepulse and the startle stimulus is relatively short (between 30 and 300 ms), a process referred to as prepulse inhibition (PPI), whereas the startle eyeblink is facilitated (prepulse facilitation, PPF) if the interval is relatively long, that is, longer than 500 ms, at least if the startle stimulus and the prepulse are in the same modality.

PPI has been hypothesized to be automatic, or “hard wired,” because it is unlearned (Graham, Putnam, & Leavitt, 1975), requires only midbrain and lower brain structures (Leitner & Cohen, 1985), occurs in decorticate animals (Davis & Gendelman, 1977), and occurs in human adults while they are asleep (Silverstein, Graham, & Calloway, 1980). PPI has been hypothesized to be a result of basic sensory gating mechanisms that protect the processing of new stimuli (the prepulse) while screening out competing or nonrelevant (startling) stimuli (Braff & Geyer, 1990; Graham, 1975). Graham (1975) hypothesized that PPI is triggered by the onset transient of the prepulse and is an automatic gating process, whereas PPF is triggered by the sustained portion of a prepulse and reflects either or both a generalized orienting process and a “classical activation effect” (Graham, p. 243) facilitating sensory input and processing.

Although PPI and PPF were originally described as automatic processes, several studies have shown that voluntarily directing attention toward some aspect of the prepulse affects either or both PPI and PPF (Dawson, Hazlett, Filion, Nuechterlein, & Schell, 1993; DelPezzo & Hoffman, 1980; Filion, Dawson, & Schell, 1993, 1994; Hackley & Graham, 1987; Hazlett et al., 1998; Jennings, Schell, Filion, & Dawson, 1996; Putnam, 1990; Schell, Dawson, Hazlett, & Filion, 1995; Vanman, Böhmelt, Dawson, & Schell, 1996). In a series of studies (Dawson et al., 1993; Filion et al., 1993, 1994; Hazlett et al., 1998; Jennings et al., 1996; Schell et al., 1995), a tone length-judging task was used in which participants were presented with two tones of different pitch that served as prepulses for startle stimuli. Participants were asked to

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attend to one pitch of tone and to ignore the other, and to count the number of attended tones that were longer than usual (7 s vs. 5 s). We found consistently in healthy participants that short lead interval PPI at 120 ms (but not at shorter lead intervals such as 60 ms) and long lead interval PPF (2,000–4,500 ms) were greater during the attended prepulse than during the ignored prepulse. Based on data such as these, Dawson, Schell, Swerdlow, and Filion (1997, p. 262) hypothesized that PPI at the 60-ms lead interval is predominantly an automatic process, whereas PPI at 120 ms and PPF at longer lead intervals can be modulated by controlled attentional processes.

The orienting response is often hypothesized to reflect largely controlled attentional processing of the orienting stimulus (e.g., Dawson, Schell, Beers, & Kelly, 1982; Kahneman, 1973; Öhman, 1992; Siddle & Spinks, 1992). According to this view, habituation of the orienting response reflects reduced controlled attentional processing of the stimulus, leaving primarily automatic processing of the stimulus intact. Consistent with this view, habituation of the orienting response has been shown to be associated with reduced allocation of controlled resources as indicated by secondary reaction time (Dawson, Filion, & Schell, 1989). According to this view, prehabituating a stimulus should interfere with its subsequent ability to function as a signal stimulus in any sort of controlled information processing task. For example, Lubow and Gewirtz (1995) pointed out that in human autonomic classical conditioning, prehabituating the stimulus is known to interfere with the stimulus functioning as a conditioned stimulus, a phenomenon known as *latent inhibition* (Lubow & Moore, 1959). Lubow and Gewirtz (1995) proposed that latent inhibition arises when stimuli are processed at only the automatic level, with controlled processing resources no longer being allocated; this proposal is consistent with the view of autonomic classical conditioning as generally involving controlled processes (Dawson & Schell, 1985; Dawson et al., 1982). Therefore, to the degree that PPI or PPF involves allocation of controlled resources to the prepulse, prehabituating of the prepulse should reduce the amount of PPI and PPF. On the other hand, automatic processes are not expected to habituate (Shiffrin, 1988). Thus, if PPI and PPF in passive attention paradigms are truly automatic, prehabituating a subject to the prepulse should have no effect on either. However, if they are influenced by controlled processes, prehabituating of the prepulse will decrease both.

There is considerable evidence that in nonhuman subjects (rats), prehabituating the prepulse does not reduce PPI, at least when the signal-to-noise ratio of the prepulse against background noise is well above threshold level (Gewirtz & Davis, 1995; Ison, Hammond, & Krauter, 1973; Russo, Reiter, & Ison, 1975; Wu, Kreuger, Ison, & Gerrard, 1984). Several investigators have reported that in human subjects PPI decreases over trial blocks in which prepulses and startle stimuli are paired (see Blumenthal, 1997, and Lipp & Siddle, 1998), but as Blumenthal (1997) pointed out, decrease over trials in PPI could be due to habituation of some aspect of the inhibitory processes initiated by the prepulse, or to habituation of the startle response itself, a suggestion supported by Lipp and Krinitzky (1998). Blumenthal (1997) found that if PPI was measured as a difference between the magnitude of blinks preceded by a lead stimulus and those that were not, expressed as a percentage of those that were not, PPI did not decrease over trials.

The effects of habituation of the prepulse on PPI have not been as extensively investigated in humans as in rats. Using a passive attention paradigm, Blumenthal (1997) found that PPI was not reduced by the presentation of prepulses alone prior to their pairing

with startle stimuli, consistent with the view that the inhibitory processes unique to PPI (as opposed to simple habituation of the startle response) do not show habituation; however, only six presentations of each type of prepulse occurred prior to pairing with the startle stimulus, which did not allow extensive opportunity for habituation to occur. Lipp and Krinitzky (1998) exposed subjects to four presentations of prepulse-startle pairings and four startle-alone presentations, and then to a variety of conditions including a habituation sequence of 24 prepulses presented alone. They found that habituation of the prepulse did not reduce subsequent PPI when the prepulse was again paired with the startle stimulus.

With respect to PPF in passive attention paradigms in humans, also theorized to be an automatic process, the effect of prehabituating of the prepulse has not been examined. Lipp and Siddle (1998), however, reported that such PPF does not decrease over trials of prepulse-startle pairings, consistent with the view of automaticity. The effects of prehabituating on attentional modulation of PPI and PPF, presumed to reflect controlled processes, have not been examined.

The present studies investigated the effects of prehabituating of the prepulse on both basic PPI and PPF and on attentional modulation of PPI and PPF. In both studies, sufficient prehabituating trials (30 of a single prepulse stimulus in Experiment 1 and 18 of each of two stimuli in Experiment 2) were given to allow the effects of a habituation process that was not rapid (requiring more than a few trials to occur) to manifest itself. In Experiment 1, PPI and PPF in a passive attention task were measured in a group of subjects who had been thoroughly prehabituating to the prepulse and a group who had not. In addition to startle eyeblink responses, skin conductance orienting responses (SCORs) elicited by the prepulses were measured to demonstrate that habituation had in fact occurred. Our hypothesis was that neither PPI nor PPF in the passive attention task would be affected by the habituation procedure.

## EXPERIMENT 1

### Methods

#### Participants

Fifty undergraduate students from Occidental College served as voluntary participants. Most received course credit for Introductory Psychology classes and all received \$5.00 for participating. Eleven participants were excluded from analysis because they failed to exhibit sufficient responsivity to the startle stimulus when it was presented alone (an average response of less than 1  $\mu$ V). These individuals were excluded because measuring PPI and PPF presumes that a blink is present in the absence of the prepulse, and for these individuals a blink was not reliably recorded. A total of 39 persons (10 men and 29 women) had usable data for the study.

#### Design

This experiment utilized a 2  $\times$  3 mixed design. The two variables were habituation group (prehabituating,  $n = 21$ , and nonhabituating,  $n = 18$ ) and lead interval (60, 120, and 2,000 ms following prepulse onset), which was varied within-subjects.

#### Procedure

Participants were first given an introduction to the experiment and were asked to sign an informed consent form. The experimental session began with the attaching of electrodes for the recording of skin conductance and startle eyeblink. Participants were then informed about the nature of the stimuli they were going to receive

and were told that their task was simply to sit quietly while the stimuli were presented. Following these instructions, they were presented with three startle-eliciting bursts of noise after which the main portion of the experimental session began.

The first phase of the experiment, habituation, consisted of either habituating or not habituating the participants to the prepulse. All participants were presented with 30 habituation stimuli (both tones and lights). Those who were habituated to the tone prepulse were presented with 30 trials of a 5-s 1000-Hz 75-dB (A) tone. Those who were not habituated to the tone prepulse were presented with the tone only three times (on habituation trials 6, 18, and 25). On the remaining 27 habituation trials they were presented with a yellow light for 5 s. Participants in each group were presented with five startle stimuli interspersed during inter-trial intervals (ITIs) throughout the habituation series. ITIs ranged from 25 to 35 s.

The second experimental phase, startle modification, involved 16 trials of prepulse presentations. This phase was divided into an early and a late block, each containing eight presentations of the prepulse. In each block, a startle stimulus was presented during six of the prepulses (probed trials) and two prepulses were presented without a startle stimulus (unprobed trials). Of the six probed trials in each block, two contained a startle probe at each of the three lead intervals: 60, 120, and 2,000 ms. The purpose of the probed trials was to measure startle blink modification during the processing of the tones, whereas the purpose of the unprobed trials was to measure the SCOR without contamination by startle stimuli. The probed and unprobed trials were intermixed so that presentation of the startle probes would be unpredictable to the subjects, and the order of presentation of the different conditions was counterbalanced across all participants.

Startle stimuli were also presented during six of the eight ITIs in each block, with no more than one stimulus presented during any ITI. The six ITI startle stimuli were presented at random intervals between 13 and 18 s into the interval. These ITI probes provided a reliable baseline measure with which to compute blink modification produced by the tone prepulses.

### Experimental Stimuli

The startle-eliciting stimuli were 105-dB (A) white noise bursts gated by a Coulbourn audio mixer/amplifier to be 40 ms in duration with a near instantaneous rise/fall time. The prepulse was a 75-dB (A) 1000 Hz tone 5 s in duration with a rise/fall time of 25 ms generated by a Coulbourn tone generator. All auditory stimuli were presented binaurally through TDH-49 headphones equipped with supra-aural cushions. Auditory stimulus intensities were calibrated on a Realistic Sound Level Meter (cat. No. 33-2055) using a Quest Electronics Earphone Coupler (model EC-9A) appropriate for the supra-aural headphones. The yellow light was presented on the backlit translucent screen of a box placed approximately 1.5 m in front of the subject just below eye level. The circular light pattern was 7.0 cm in diameter. The onsets, durations, and intervals between stimuli were computer controlled online.

### Acquisition and Scoring of Dependent Variables

The two primary dependent variables were magnitude of the SCORs elicited by prepulses on unprobed trials and change in startle blink magnitude occurring following prepulses. SCORs were recorded from the volar surface of the distal phalanges of the first and second fingers of the nonpreferred hand using 10-mm Ag/AgCl electrodes and 0.05 M NaCl paste (see Dawson, Schell, & Filion, in press). A constant 0.5 V was applied across the electrodes. The

skin conductance signal was amplified by a Grass 7P1 preamplifier and a 7DAE driver amplifier. On each unprobed trial, the SCOR was scored as any increase in skin conductance beginning within 1–3 s after tone onset, peaking by 12 s, and having an amplitude of at least 0.05  $\mu$ Siemens.

Startle eyeblink was recorded from two 4-mm electrodes placed directly over the orbicularis oculi muscle. One electrode was placed 1 cm below the left pupil and the second was placed 1 cm laterally. The electromyographic (EMG) signal was recorded by a Grass 7P3 wide-band preamplifier/integrator. Eyeblink responses were digitized at a rate of 2000 Hz for 200 ms before and 300 ms following the presentation of each startle-eliciting stimulus. The amplitude of each response was scored in microvolts ( $\mu$ V) as the difference between the mean rectified EMG activity in the 200 ms preceding the onset of the startle stimulus and the mean rectified EMG activity in the 10 ms preceding and following the peak EMG activity following the startle stimulus. The peak of the response was defined as the highest microvolt average taken across three consecutive EMG samples (across a 1.5 consecutive ms time period).

The magnitude of each startle eyeblink elicited under a prepulse condition was expressed as a percent change score from the average magnitude of blinks elicited by the startling stimulus during the ITI. Separate ITI averages were computed for early and late trial blocks. That is, PPI or PPF =  $([\text{prepulse blink magnitude} - \text{average ITI blink magnitude}] / \text{average ITI blink magnitude}) \times 100$ . Thus, blink facilitation is represented by a positive percent change score while blink inhibition is represented by a negative percent change score.

### Results

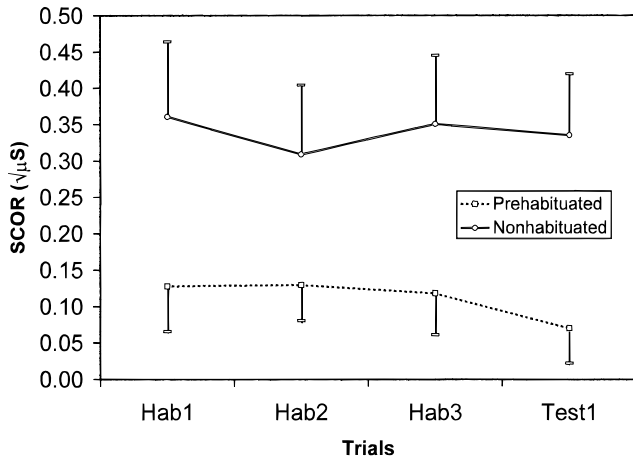
In all analyses of variance (ANOVAs) discussed, Greenhouse–Geisser corrections were used to adjust probabilities for repeated-measures effects with more than two levels. We report uncorrected degrees of freedom, corrected Type I error probabilities, and epsilon values. The data were cleaned of outliers on a trial-by-trial basis before statistical analysis; outlier data points were those more than 3 standard deviations above the mean of all subjects and at least 2 standard deviations removed from the next more central value. Fewer than 1% of data points were classified as outliers.

### SCORs

Data from habituation trials 6, 18, and 25 (on which tones were presented to all participants) and from the first unprobed trial of the probed trial series were selected to assess the effects of pre-habituation on the SCORs to the prepulses. The square root transformed skin conductance data were subjected to a Group  $\times$  Trials ANOVA. As can be seen in Figure 1, there was a significant effect of habituation to the prepulse on SCOR magnitude,  $F(1,36) = 11.61$ ,  $p < .002$ , with larger SCORs in the nonhabituated group than in the prehabituated group. However, neither the effect of Trials nor the Group  $\times$  Trials interaction was significant; over these points of comparison there was little change in SCOR magnitude. These results indicate that the prehabituation procedure was effective in reducing orienting to the prepulse. By the subsequent unprobed trials of the test trial series, the SCOR in the nonhabituated group had fallen to the level of that in the prehabituated group, to approximately that seen for the first test trial in Figure 1, and group differences were no longer significant.

### Eyeblink

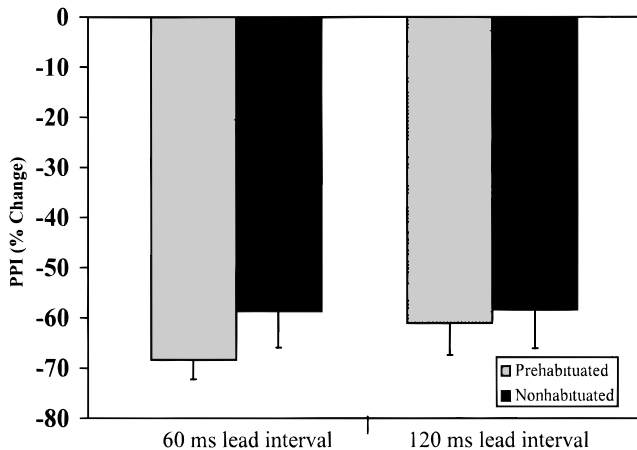
*Short lead interval prepulse inhibition.* Prepulse inhibition was analyzed by performing a Group  $\times$  Trial Block ANOVA on the



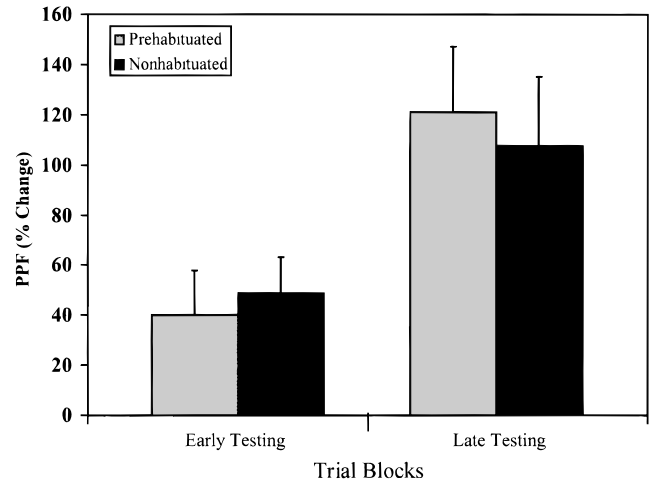
**Figure 1.** Skin conductance orienting responses (SCORs) during the habituation trial series and during startle eyeblink testing; bars indicate standard errors.

percent blink modification at lead intervals of 60 and 120 ms. Significant startle inhibition (PPI values significantly less than zero) occurred in both groups at both 60 and 120 ms during both early and late trial blocks. At neither lead interval did the effect of Group, Trial Block, nor the Group  $\times$  Trial Block interaction approach significance. As is clearly seen in Figure 2, both groups displayed equally well developed PPI at both lead intervals, and the degree of PPI did not decline over trial blocks, nor did pre-habituating affect PPI.

*Long lead interval prepulse facilitation.* A Group  $\times$  Trial Block ANOVA was used to analyze PPF scores at the 2,000-ms lead interval. There was a significant block effect,  $F(1,37) = 12.98$ ,  $p < .001$ , with PPF increasing over trial blocks for both groups, as seen in Figure 3. Neither the Group effect nor the Groups  $\times$  Trial Blocks interaction approached significance, indicating that the pre-habituating and nonhabituating prepulses were equally effective in producing blink facilitation at the 2,000-ms lead interval level. Significant startle facilitation (PPF values significantly greater than



**Figure 2.** Prepulse inhibition (PPI; percent change scores) at 60 and 120 ms during startle eyeblink testing; bars indicate standard errors.



**Figure 3.** Prepulse facilitation (PPF; percent change scores) at 2,000 ms during startle eyeblink testing; bars indicate standard errors.

zero) occurred in both groups during both early and late trial blocks.

*Intertrial interval blink magnitude.* To establish that the lack of group differences in PPI and PPF were not due to differential responsiveness to the startle stimuli, a Group  $\times$  Trial Block ANOVA of startle responses to the probes presented during the ITIs was performed. This ANOVA revealed that there was a significant difference between early and late blocks,  $F(1,37) = 22.88$ ,  $p < .001$ , with startle magnitude declining over blocks, but neither the Group effect nor the Group  $\times$  Block interaction approached significance.

**Discussion**

The results of Experiment 1 indicate that thorough habituation of the prepulse had no effect on PPI or PPF tested in a passive attention paradigm, consistent with the results of Blumenthal (1997) and Lipp and Krinitzky (1998), thus supporting the hypothesis that PPI and PPF are automatic processes under these conditions. Thorough habituation of the prepulse, as reflected by the reduced SCOR in the prehabituating group, did not create any reduction in PPI or PPF in comparison with a group that had not been habituated to the prepulse.

In Experiment 2 we investigated the effects of habituation of the orienting response to the prepulse on the attentional modulation of startle PPI and PPF. Because attentional modulation is hypothesized to reflect controlled processing mechanisms, our prediction was that the attentional modulation of PPI at the 120-ms lead interval and attentional modulation of PPF at the 2,000-ms lead interval with the tone length-judging task would be observed in nonhabituating participants but not in habituated participants.

**EXPERIMENT 2**

**Methods**

*Participants*

Thirty-eight undergraduate students from Occidental College served as voluntary participants (21 men and 17 women). Most received

course credit for Introductory Psychology classes and all received some monetary bonus for participating. Data from one participant were lost due to experimenter error, three participants were excluded from analysis because they failed to exhibit sufficient responsiveness to the startle stimulus when it was presented alone, and two participants were excluded because they were unable to discriminate perceptually between the two tone prepulses.

### Design

This experiment used a  $2 \times 2 \times 3$  mixed design. The three variables were habituation group (prehabituated, nonhabituated), prepulse (attended, ignored), and lead interval (60, 120, and 2,000 ms). The prepulse and lead interval variables were varied within-subjects.

### Procedure

Participants were informed about the nature of the stimuli that they were to receive and the task that they were to perform. They were told that throughout the experiment they would receive four stimuli, a green and a yellow light and a high-pitched and a low-pitched tone. They were instructed that most of these stimuli would be 5 s long, but that some would be 7 s long, and that their task was to count the number of lights of one color and tones of one pitch that were longer; the other light and the other tone could be ignored. They were asked to monitor either the high-pitched tone and the yellow light, or the low-pitched tone and the green light. A small sign was placed above the light presentation box to remind them which stimuli should be attended. Participants were informed that if their count of longer attended stimuli was accurate at the end of the experiment, they would earn \$5.00; if their count was off by one, they would earn \$4.00; if their count was off by two, they would earn \$3.00, and so on. They were also told that occasional brief loud noises would be presented, but that these did not require any response. Finally, they were told that before the task began, they would be presented with samples of all of the stimuli that they would receive, so that they could become familiar with the long and short versions of each tone and light, and the loud noise.

Participants were then presented with three startle-eliciting bursts of noise, followed by 5-s and 7-s versions of the high- and low-pitched tones and the yellow and green lights. The main portion of the experimental session then began.

The first phase of the experiment, habituation, consisted of either habituating or not habituating the participants to the prepulses. All participants were presented with a total of 40 habituation stimuli (both tones and lights in a random order). Participants who were habituated to the tone prepulses were presented with 36 tones (18 high and 18 low in a counterbalanced order) and four lights (two yellow and two green). Four high and four low tones were 7 s instead of the standard 5 s. The two yellow lights occurred on Trials 15 and 37, while the two green lights occurred on Trials 4 and 23; one light of each color was longer than usual. Participants who were not habituated to the tone prepulses were presented with 36 lights (18 yellow and 18 green) and four tones (two high and two low). Eight of the lights (four yellow and four green) were 7 s instead of the standard 5 s. The two high-pitched tones occurred on Trials 5 and 25 and the two low pitched tones on Trials 12 and 34; one tone of each pitch was longer than usual. ITIs ranged from 25 to 35 s for both groups, and the startle stimulus was presented during eight of the ITIs.

The second experimental phase, startle modification, involved 32 trials of tone presentations. No break in the presentation of trials

occurred between the habituation phase and the testing phase.<sup>1</sup> This testing phase was divided into an early and a late block, each containing eight presentations of each of the tone prepulses. In each block, six of the presentations of each prepulse were probed with the startle stimulus and two were unprobed. Of the six probed trials of each prepulse in each block, two contained a startle probe at each of the three lead intervals: 60, 120, and 2,000 ms. Of the eight tones of each pitch in each block, two were 7 s in duration. The high- and low-pitched tones of 5 s and 7 s and probed and unprobed trials were intermixed so that presentation of the attended and unattended prepulses and the startle probes would be unpredictable to the subjects. Startle stimuli were also presented during 12 of the 16 ITIs in each block, with no more than one startle probe presented during any ITI.

### Experimental Stimuli

The same experimental stimuli were used as in Experiment 1, with the exception that two tones (800 Hz and 1200 Hz) and two lights (yellow and green) were used.

### Acquisition and Scoring of Dependent Variables

The SCOR and the eyeblink response were acquired and scored as in Experiment 1. Again, fewer than 1% of startle magnitude data points were classified as outliers. Each subject was also given an accuracy score on the length-judging task. For each subject, nine attended stimuli were 7 s rather than 5 s. Subjects responding with the correct number at the end of the testing trial series were given an error score of 0; subjects being off in their count by one (responding with eight or ten) were given an error score of 1, and so on.

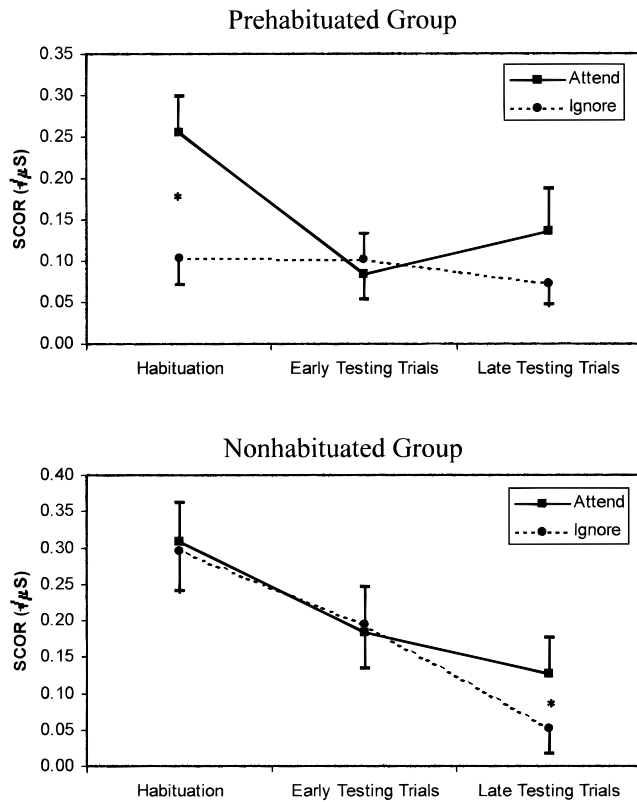
### Results

In all ANOVAs discussed, Greenhouse–Geisser corrections were used to adjust probabilities for repeated measures effects with more than two levels. We report uncorrected degrees of freedom, corrected Type I error probabilities, and epsilon values.

### SCORs

A Groups (prehabituated, nonhabituated)  $\times$  Prepulse (attended, ignored)  $\times$  Trial Block (habituation, early testing, late testing) ANOVA was carried out on SCOR magnitude to compare orienting in the two groups during the habituation trial series and during the early and late trial blocks of the startle modification testing trial series. The trials used from the habituation trial series were those on which all subjects received the tone stimuli. Group means for both prepulses over blocks are shown in Figure 4. The effect of prepulse type was significant,  $F(1,30) = 6.07, p < .02$ , with SCORs being larger to the attended prepulse, as would be expected. The significant trial block effect,  $F(2,60) = 16.95, p < .001, \epsilon = 0.8615$ , reflects the overall decline in SCOR magnitude over trial blocks. The Group  $\times$  Trial Block interaction was also significant,  $F(2,60) = 4.25, p < .03, \epsilon = 0.8615$ . As can be seen in Figure 4, the pattern of orienting across phases of the experiment was different in the two groups. The prehabituated group showed lower

<sup>1</sup> In pilot work we had initially habituated subjects to all four stimuli (lights and tones) and only then given the task instructions as to which stimuli should be attended. However, the break in the flow of trials and the instructions themselves caused a marked dishabituation of the SCOR, undoing the difference between the habituated and nonhabituated groups that had developed in the SCOR to the tone prepulses during habituation.



**Figure 4.** Skin conductance orienting responses (SCORs) to attended and ignored prepulses during the habituation trial series and during startle eyeblink testing; bars indicate standard errors.

responding during the habituation trials on which both groups received the tone prepulses than did the nonhabituated group. The difference between the groups for the average SCOR (averaging over the attended and nonattended tones) during habituation was significant,  $t(30) = 2.20, p < .04$  (two-tailed). This lower responding in the prehabituated group was also seen during the early block of PPI testing,  $t(30) = 2.28, p < .03$  (two-tailed). Only in the late trial block of testing did the two groups show equivalent degrees of habituation of the SCOR to the tone prepulses.

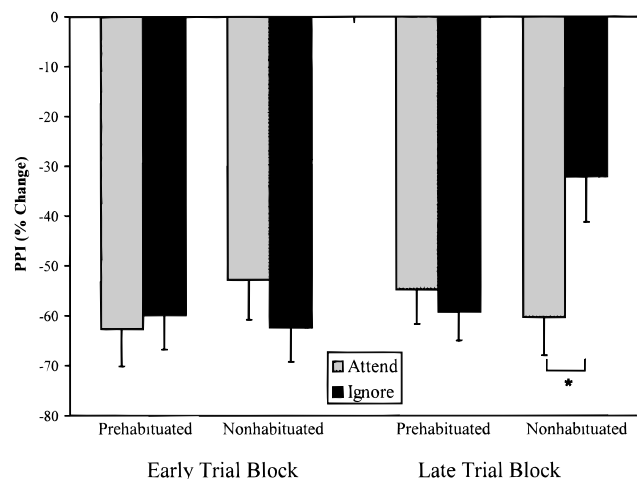
Within-subject planned comparisons determined that in the prehabituated group, significantly greater responding to the attended as opposed to the ignored prepulse occurred during the habituation trials,  $t(16) = 3.48, p < .003$  (two-tailed); after that point, during the testing trial series, SCOR amplitude declined greatly and discrimination did not approach significance. In the nonhabituated group, although SCORs to both the attended and ignored prepulses were large during the habituation trial series, discrimination did not occur, nor did it occur during the early block of the testing trial series. Discrimination was significant during the late trial block of testing,  $t(14) = 2.36, p < .04$  (two-tailed).

#### Eyeblink

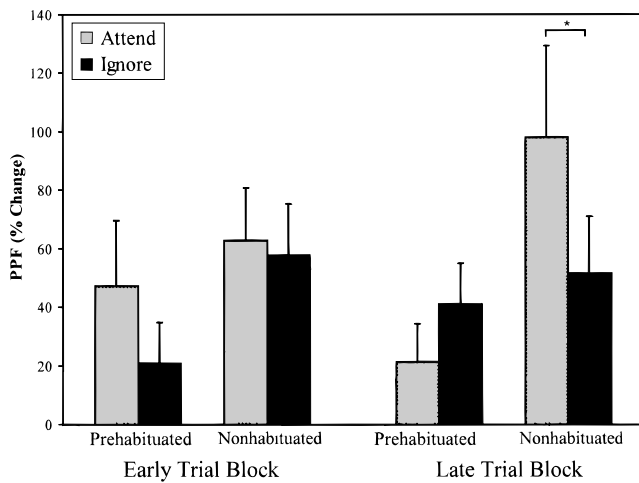
**Short lead interval prepulse inhibition.** A Groups  $\times$  Prepulse  $\times$  Trial Blocks ANOVA was carried out to examine PPI at both the 60-ms lead interval and at the 120-ms lead interval. For the 60-ms lead interval, no main effects or interactions approached significance. PPI was statistically different from zero in both groups during both trial blocks during the testing trial series.

For PPI at the 120-ms lead interval, only the Groups  $\times$  Prepulse  $\times$  Trial Blocks interaction was significant,  $F(1,30) = 7.86, p < .01$ . PPI was statistically different from zero in both groups during both trial blocks. Within-subject planned comparisons indicated that in the prehabituated group, there was no significant difference in PPI during the attended and ignored prepulses in either trial block, as seen in Figure 5. In the nonhabituated group, PPI did not differ between the attended and ignored prepulses during the early trial block, but attentional modulation, defined as the difference between values during attended and ignored prepulses, was significant during the late trial block,  $t(14) = 2.36, p < .04$  (two-tailed). During the late trial block, attentional modulation of PPI was significantly greater in the nonhabituated group than in the prehabituated group,  $t(30) = 2.64, p < .02$  (two-tailed). As can be seen in Figure 5, the greater modulation of PPI in the nonhabituated group compared with the habituated group appears to be due primarily to the lower PPI during the ignored prepulse in the nonhabituated than the habituated group,  $t(30) = 2.55, p < .02$  (two-tailed). The difference between the groups in PPI during the attended prepulse was not significant.

**Long lead interval prepulse facilitation.** A Groups  $\times$  Prepulse  $\times$  Trial Blocks ANOVA was carried out to examine PPF at the 2,000-ms lead interval. The Groups  $\times$  Prepulse  $\times$  Blocks interaction was significant,  $F(1,30) = 10.74, p < .003$ . Means for the two groups for attended and ignored prepulses in both trial blocks are shown in Figure 6. In the nonhabituated group, PPF was significantly different from zero during both prepulses in both trial blocks. In the prehabituated group, PPF was significantly different from zero only during the ignored prepulse during the late trial block. Within-subject planned comparisons indicated that in the prehabituated group, there was no significant difference in the amount of PPF between the attended and ignored prepulses in either trial block. In the nonhabituated group, PPF did not differ between the attended and ignored prepulses during the early trial block, but attentional modulation was significant during the late trial block,  $t(14) = 2.18, p < .05$  (two-tailed). Attentional modulation of PPF was significantly greater in the nonhabituated group than in the prehabituated group during the late trial block,  $t(30) =$



**Figure 5.** Prepulse inhibition (PPI; percent change scores) at 120 ms during attended and ignored prepulses during early and late trial blocks of startle eyeblink testing; bars indicate standard errors.



**Figure 6.** Prepulse facilitation (PPF; percent change scores) at 2,000 ms during attended and ignored prepulses during early and late trial blocks of startle eyeblink testing; bars indicate standard errors.

2.31,  $p < .03$  (two-tailed). As can be seen in Figure 6, the greater modulation of PPF in the nonhabituated group compared with the habituated group appears to be due to the greater PPF during the attended prepulse in the nonhabituated than in the habituated group,  $t(30) = 2.37$ ,  $p < .03$  (two-tailed). The difference between the groups in PPF during the ignored prepulse was not significant.

**ITI blink magnitude.** To determine whether group differences in attentional modulation of PPI and PPF could be attributable to differential responsiveness to the startle probes, a Group  $\times$  Trial Block ANOVA of startle responses to the probes presented during the ITIs was performed. This ANOVA revealed that there was a significant difference between early and late blocks,  $F(1,30) = 30.29$ ,  $p < .001$ , with startle magnitude declining over blocks, but neither the Group effect nor the Group  $\times$  Block interaction approached significance.

### Task Performance

For each participant there were nine attended stimuli that were 7 s rather than 5 s. A participant who gave a count of "nine" at the end of the experimental procedure received an error score of 0; a participant who gave a count of "eight" or "ten" received an error score of 1, and so on. The mean number of errors in the prehabituated group was .59 and the modal value was 0; the mean in the nonhabituated group was 1.13 and the modal value was 1.0. This difference in error rate is significant,  $t = 2.11$ ,  $df = 30$ ,  $p < .05$ .

## DISCUSSION

The results of Experiment 1 provided support for the hypothesis that in a passive attention task, both short lead interval PPI and long lead interval PPF are automatic processes. The successful habituation of the orienting response to the tone prepulse (measured as the magnitude of the SCOR) in the prehabituated group did not reduce the ability of the prepulse to elicit either PPI or PPF compared to that seen in a nonhabituated group. This same resistance of PPI at 60 ms to the effects of prehabilitation was also seen in Experiment 2.

The failure of habituation to reduce the PPF elicited by a prepulse casts doubt on the proposition that this facilitation is due to any sort of generalized orienting process, because this process would be expected to show habituation as did the SCOR. Thus, it is more likely that PPF is due to a nonhabituating activation effect, one of the possibilities suggested by Graham (1975). Lipp and Siddle (1998), who observed that PPF did not decrease over blocks of trials in which the prepulse and startle were paired, suggested two additional processes that may be involved in PPF. First, if the prepulse and the startle stimulus are in the same modality, PPF might be due to a localized orienting process (as opposed to a generalized orienting process) that would include changes in sensory thresholds and be slow to habituate (Sokolov, 1963). This explanation, like Graham's automatic activation effect, would account for the lack of difference between the prehabituated and nonhabituated groups in PPF during either trial block. The second process suggested by Lipp and Siddle (1998) to affect PPF might account for the increase in PPF from the early to the late trial block in Experiment 1, as seen in Figure 3. They suggested that repeated pairings of the prepulse and the startle stimulus, which may be aversive to some degree, could cause a negative valence to attach to the prepulse, resulting in the well-known potentiation of startle at long lead intervals (cf. Bradley, Cuthbert, & Lang, 1999).

Experiment 2 supported the hypothesis that attentional modulation of PPI at 120 ms and PPF in an active selective attention paradigm involves controlled processes. First, as seen in Figure 4, the course of orienting activity (SCOR magnitude) differed markedly over time in the prehabituated group compared with the nonhabituated group. In the prehabituated group, participants had received enough presentations of the high- and low-pitched tones during prehabilitation to readily make a distinction between the two, so that differential orienting was present only during prehabilitation. By the first trial block of the eyeblink testing trial series, the SCOR to both the attended and ignored tones had habituated markedly, and differential orienting was no longer present. This disappearance of differential orienting to the attended and ignored prepulses with practice is consistent with previous findings (Filion et al., 1993, 1994). Presumably making a rapid distinction between the two tones had become a practiced and largely automatic task. Habituation of the SCOR and the absence of differential orienting was associated with an absence of attentional modulation of PPI and PPF, as seen in Figures 5 and 6; neither was greater during the attended than during the ignored tone in the prehabituated group.

In the nonhabituated group, on the other hand, although orienting to the tone stimuli was strong during the habituation trial series, differential orienting to the attended and ignored tones was not present, nor was differential orienting present during the early trial block of the testing series. In the prehabituated group, many presentations of the tones occurred during the habituation series, but in the nonhabituated group, only two presentations of each tone occurred during the initial 40-trial habituation series. This procedure appears to have made the learning of and memory for the distinction between the tones more difficult for the nonhabituated group, as reflected by their poorer performance of the tone discrimination and length-judging task. Their failure to show differential orienting to the tones before the late block of test trials is consistent with difficulty in making the perceptual distinction. However, by the second trial block of testing they had begun to show differential orienting to the attended and ignored tones. In that same late trial block attentional modulation of PPI and PPF also appeared, with both being greater during the attended tone than during the ignored tone. The absence of attentional modulation of

PPI and PPF in the prehabituated group, and their simultaneous appearance with the differential SCOR in the nonhabituated group, suggests strongly that attentional modulation of PPI and PPF involves controlled processing.

An unanticipated and interesting aspect of the present results can be seen in the development of attentional modulation of PPI in the nonhabituated group in Experiment 2. As seen in Figure 5, from the early to the late trial block of testing, PPI at 120 ms during the attended prepulse increased slightly, while PPI during the ignored prepulse decreased significantly,  $t(15) = 2.78, p < .02$ , becoming significantly less than that seen in the prehabituated group and producing significantly greater PPI during the attended than during the ignored prepulse, which we have termed *attentional modulation*. We have interpreted attentional modulation previously as reflecting *enhanced* protection of processing of the attended prepulse (see Dawson et al., 1993; Schell et al., 1995), with the assumption that the attended prepulse received more protection of processing than it would have in a passive attention paradigm. This interpretation is consistent with the results of Jennings et al. (1996), who found that in a group performing the tone discrimination and length-judging task used in Experiment 2 and showing attentional modulation of PPI, PPI during the attended prepulse was marginally ( $p < .06$ ) greater than PPI during the same prepulse in a group receiving the same stimuli but not doing the task (79% vs. 51%), whereas PPI during the ignored prepulse was only slightly less than in the no-task group (44% vs. 60%).

The present results, however, suggest that attentional modulation may also reflect less protection for a stimulus that can be ignored. Support for this view comes from the observation that in passive attention paradigms, PPI is generally reported to increase from a lead interval of around 60 ms to a lead interval of around 120 ms (see Blumenthal, 1999, for a review). However, in using the selective attention task employed here in previous studies, we have observed several times that in normal subjects, although PPI during an attended prepulse increases from 60 to 120 ms, PPI

during the ignored prepulse does not (Böhmelt, Schell, & Dawson, in press; Dawson et al., 1993; Schell et al., 1995). This observation suggests that the task instructions acted to reduce the protection of the ignored stimulus, and that both facilitatory and inhibitory controlled attentional processes may affect PPI.

The present results suggest that in conceptualizing automatic and controlled influences on PPI and PPF, it is useful to bear in mind the categorization of perceptual processing acts by Kahneman and Triesman (1984, p. 42) into those that are strongly automatic (not modifiable by attention), partially automatic (normally not requiring attention but capable of being facilitated by attention), and occasionally automatic (generally requiring attention but sometimes capable of acting without it). PPI at 120 ms and PPF at long lead intervals apparently fall into the partially automatic category—capable of proceeding automatically, but also being capable of controlled attentional modulation. In this they are like many other behaviors that are mediated by subcortical mechanisms. For instance, the simple eyeblink reflex (unmodified by a prepulse) can, like PPI, be affected by selective attention (see Hackley, 1993). Hackley (1993) also argued that evoked potential components such as N100 and mismatch negativity are partially automatic, and that much of sensory processing is best described in this way. The results of Experiment 1 indicate that PPI and PPF in a passive paradigm reflect primarily automatic information processing, whereas the results of Experiment 2 indicate that PPI and PPF in an active selective attention paradigm reflect both automatic and controlled information processing.

The accumulated data from studies of startle eyeblink modification in prepulse paradigms indicate that such paradigms can be used to study both automatic and controlled attentional processes in a nonverbal, nonintrusive way in diverse populations. Such paradigms are particularly useful in the study of disorders such as schizophrenia, in which both automatic and controlled processes have been suggested to be dysfunctional, and in which the introspective and verbal abilities of the research participant may be impaired.

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