Attention and prepulse inhibition: the effects of task-relevant, irrelevant, and no-task conditions

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Abstract

We investigated whether attentional modulation of prepulse inhibition (PPI) is due to increased protection of processing of attended lead stimuli, decreased protection of processing of ignored lead stimuli, or a combination of both processes. Task and no-task trials, pre-cued by red and blue dots on a computer screen, were randomly intermixed. College student participants were instructed to do a tone duration judgment task on trials preceded by one color (task condition) and to do nothing on trials preceded by the other color (no-task condition). On task condition trials participants were instructed to count the number of longer duration tones of a particular pitch (attended condition) and to ignore tones of a different pitch (ignored condition). White noise startle stimuli were presented at 60 ms and 120 ms lead intervals on some trials in each condition. Additional startle stimuli were presented during the inter-trial intervals to measure baseline (unmodified) startle response. PPI in the attended condition was reliably greater than that in both the ignored and no-task conditions. PPI did not differ between the ignored and no-task conditions. The results are consistent with the conclusion that attentional modulation of PPI is due to increased protection of attended stimuli and not to decreased protection of ignored stimuli. Possible reasons for robust attentional modulation at the 60 ms lead interval as well as the usual 120 ms lead interval are discussed.

Keywords: Startle eyeblink; Prepulse inhibition; Attention; Attentional modulation

1. Introduction

A sudden and intense stimulus, such as a brief burst of white noise, elicits a startle reflex response. In humans, this response is most commonly measured by the amplitude of the eyeblink (see Berg and Balaban, 1999 for a review of startle elicitation, recording, and quantification). If the startling stimulus is preceded by a non-startling stimulus, such as a soft tone, the amplitude of the eye-blink response is modified. The non-startling stimulus is called a lead stimulus or prepulse, and the interval between the onset of the lead and startle stimuli is called the lead interval or stimulus onset asynchrony (SOA). The specific effect
of the lead stimulus on startle eyeblink depends upon the lead interval. At short lead intervals (15–400 ms), the amplitude of the startle response is decreased. This is called prepulse inhibition (PPI), which is thought to reflect a sensory gating process that protects initial processing of the lead stimulus from interference by extraneous stimuli (see Blumenthal, 1999 for a review of PPI).

The effect of the lead stimulus on startle is further modified by attention. At short lead intervals, PPI after a lead stimulus that is attended is typically greater than PPI after a lead stimulus that is not attended (Dawson et al., 1993, 2000; Filion et al., 1993, 1994; Hawk et al., 2002; Hazlett et al., 1998; Jennings et al., 1996; Schell et al., 2000). This increase in PPI is called attentional modulation.

Most of the experiments that have investigated attentional modulation of PPI have employed a tone duration judgment task (e.g., Filion et al., 1993). In this task, the lead stimuli are high and low pitch tones of short and long duration. Participants are instructed to attend to one of the two pitches (the task-relevant, or attended, stimulus) and to count the number of longer duration tones of that pitch while ignoring tones of the other pitch (the task-irrelevant, or ignored, stimulus). Startle stimuli are presented at various lead intervals during both the attended and ignored stimuli. For auditory lead and startle stimuli the typical pattern is reliably greater PPI to attended stimuli than ignored stimuli at a 120 ms lead interval and no reliable difference in PPI between attended and ignored stimuli at lead intervals of 60 and 240 ms.

Dawson et al. (1993) interpreted these findings in terms of the time course of lead stimulus processing. They proposed that pre-attentive stimulus detection and evaluation occur at lead intervals of about 60 ms, stimulus discrimination and greater allocation of attention to the attended lead stimulus occur at lead intervals of about 120 ms, and transition from stimulus evaluation to duration judgment occurs at lead intervals of about 240 ms. They proposed that greater inhibition to attended lead stimuli at the 120 ms lead interval reflects increased sensory gating, which screens out extraneous stimuli, thus protecting the processing of the task-relevant lead stimulus.

An important question is: How does the processing of an attended lead stimulus differ from the processing of an ignored lead stimulus? Does the difference in startle inhibition between the attended and ignored conditions occur because attention increases protection of processing of the attended stimulus, decreases protection of processing of the ignored stimulus, or some combination of both processes? This issue can be operationally tested by comparing PPI following attended and ignored lead stimuli in a selective attention task with PPI following similar lead stimuli in a no-task condition. If attentional modulation reflects only enhanced protection of the attended stimulus, then PPI following the attended stimulus will be greater than that following the ignored and no-task stimuli, which will not differ. If attentional modulation reflects only suppressed protection of the ignored stimulus then PPI following the ignored stimulus will be less than PPI following the attended and no-task stimuli, which will not differ. Finally, if attentional modulation reflects both enhanced protection of the attended stimulus and suppressed protection of the ignored stimulus, then PPI following all three types of stimuli will differ.

Jennings et al. (1996), in an experiment using the tone duration judgment task in a between-subjects design with separate task and no-task groups, obtained results consistent with the conclusion that attentional modulation is due to increased protection of the attended stimulus compared to what would occur in a no-task condition. The stimulus sequence was identical for both the task and no-task groups; however, the instructions were different. Participants in the task group were told to count the number of longer duration tones of a specified pitch and to ignore tones of another pitch. As an incentive, they were paid up to US$5.00 for good performance on the task. Participants in the no-task group were not given a task and were not paid. PPI was reliably greater in the attended than the ignored condition for the task group. PPI was marginally greater in the attended condition for the task group compared to matching trials for the no-task group. There was no reliable difference in PPI between the ignored condition for the task group and matching trials for the no-task group. Greater PPI in the attended than the ignored condition for the task, but not the no-task, group, and the absence of a difference between the ignored condition for the task group and matching trials for the no-task group led Jennings et al. (1996) to
conclude that attentional modulation is due to increased protection of attended stimuli.

Filion and Poje (2003) carried out an experiment which used a tone duration judgment task with blocks of task and no-task trials in a within-subjects design. In the first of the two trial blocks, at both the 60 ms and 120 ms lead intervals, they found greater PPI in the attended and ignored conditions, which did not differ, compared to the no-task condition. In contrast, in the second of the two trial blocks, at only the 120 ms lead interval, they found greater PPI in the attended condition compared to the ignored and no-task conditions, which did not differ. Consistent with the operational criteria described above, the latter finding would indicate that attentional modulation reflects enhanced protection of attended stimuli only. However, Filion and Poje also noted that PPI at 120 ms following the ignored stimulus decreased significantly from the early to the late trial block, while PPI at 120 ms following the attended stimulus did not. They concluded that “It is unclear from this pattern alone whether selective attentional processes acted to enhance processing of the attended prepulse... or acted to reduce processing of the ignored prepulse...”

Consistent with the results of Filion and Poje (2003), Schell et al. (2000, experiment 2), in a study on the effect of habituation of the lead stimulus on PPI and attentional modulation, also obtained results consistent with decreased protection of ignored stimuli. They reported greater PPI to attended than ignored lead stimuli at a 120 ms lead interval only on the second of two trial blocks. However, the difference was due to decreased PPI in the ignored condition in the first trial block only, not to increased PPI in the attended condition. Schell et al. concluded that attentional modulation is due to reduced protection of a stimulus that can be ignored. However, since this study did not include a no-task condition, it could not be determined whether the protection for the ignored stimuli was the same as would have occurred for no-task stimuli, or whether there was active suppression of protection of ignored stimuli.

Finally, Hawk et al. (2002), in a study on the effect of payment for task performance, obtained results consistent with the conclusion that attentional modulation is due to both increased protection of attended stimuli and decreased protection of ignored stimuli. They reported reduced PPI at the 120 ms lead interval compared to the 60 ms lead interval for ignored lead stimuli and greater PPI at the 120 ms lead interval compared to the 60 ms lead interval for attended lead stimuli. Hawk et al. concluded that the attentional effect was due to both reduced protection of ignored lead stimuli and increased protection of attended lead stimuli. However, once again, the critical no-task condition was not available for comparison.

With four different studies and three different conclusions, the question of how attended and ignored lead stimuli affect PPI is not yet clear. In addition, for each of these studies, there are methodological issues that need to be addressed. The Jennings et al. (1996) experiment used a between-subjects design with separate task and no-task groups. The conditions for the two groups were quite different. The task group had a task to perform and had the incentive of financial reward for good performance. In contrast, the no-task group had no task to perform and no prospect of financial reward. It seems probable that motivation, therefore vigilance, was higher for the task than the no-task group. The Filion and Poje (2003) experiment used a within-subjects design with blocks of task and no-task trials. However, since some of the blocks were long (up to eight trials), it is possible that overall vigilance could have declined during the long blocks of no-task trials. The Schell et al. (2000) experiment was designed to investigate the effect of habituation of the lead stimulus on attentional modulation and the Hawk et al. (2002) experiment was designed to investigate the effect of extrinsic incentive on attentional modulation. Because they were planned for these purposes, the important no-task condition was not needed and not included. Without the no-task condition, which measures PPI without experimenter-manipulated attentional modulation, it was not possible to determine whether reduced protection of the ignored compared to the attended stimuli reflects active suppression of protection below what would occur in the absence of a task.

The purpose of the present experiment was to investigate the processes involved in attentional modulation in a within-subjects design in which task and no-task trials were interspersed in a single experimental procedure. This allows the use of the no-task condition, which indexes basic PPI without attentional modulation, as a reference for comparison with the attended and ignored trials of the task.
condition. This procedure controls for between-groups differences by allowing all participants to receive the same instructions and perform the same task. Since task and no-task trials occurred randomly, it was not possible for participants to adopt a task or no-task set for entire blocks of trials. Therefore, a high level of overall vigilance was required.

2. Method

2.1. Participants

Participants were 49 volunteers (16 men and 33 women) from undergraduate psychology classes at the University of Southern California who received course credit for participation. There were no selection criteria. All participants were informed about the experiment and signed consent forms before participating. Research procedures and methods of obtaining informed consent were approved by the University of Southern California Institutional Review Board. The data for one participant were excluded from analysis due to technical problems during collection. The data for 24 additional participants were excluded because their baseline eyeblink responses to startle stimuli alone were too small (median baseline response less than 2 μV) for dependable assessment of PPI. Similar percentages of men (57%) and women (49%) were excluded. We used a 2 μV, instead of our usual 1 μV, criterion for non-responders because we have noted high variability in percentage change scores using baseline startle magnitude below this value. We have found that when baseline startle magnitude is small, normal variability occasionally produces unusual positive percentage change scores. These positive scores increase variability and skew means in a positive direction. The final sample included 24 participants with usable data.

2.2. Design, stimuli, and timing

This experiment used a variation of the tone duration judgment task in a 3 (condition: attended, ignored, no-task)×2 (lead interval: 60 ms, 120 ms) within-subjects design. Task and no-task trials, preceded by red and blue colored dots on a computer monitor, were randomly mixed. For half of the participants, red dots pre-cued task trials and blue dots pre-cued no-task trials; and for half of the participants, the meanings of the colors were reversed. Participants performed a standard tone duration judgment task on task trials and did nothing on no-task trials. On each task trial participants heard a high or low pitch tone of long or short duration. The task was to count the number of longer-than-normal duration tones of one pitch (attended condition) and to ignore tones of the other pitch (ignored condition). Participants reported the count of longer duration tones at the end of the experiment. Half of the participants performed the task upon hearing high pitch tones, and half performed the task upon hearing low pitch tones. Participants heard a middle pitch tone on no-task trials.

The red (luminance 39.0 cd/m²) and blue (luminance 20.5 cd/m²) dot pre-cues were presented against a dark gray (luminance 3.7 cd/m²) background on a computer monitor. Dots were presented continuously during the experiment. Only the color changed. Color changes, when required, occurred at the offset of the auditory lead stimulus at the end of each trial. The new color indicated whether there was a task to perform on the next trial. This method of cuing was chosen to prevent interference between task cue discrimination and lead stimulus discrimination. This method was also chosen to minimize the possibility that the cue stimulus would act as a lead stimulus for the subsequent trial.

The auditory lead stimuli were 70 dBA, 800, 1000, and 1200 Hz tones. The 1000 Hz tones were presented on no-task trials. The 800 and 1200 Hz tones were presented on task trials. Half of the tones of each pitch were 5 s in duration and half were 7 s in duration.

Startle stimuli (50 ms bursts of 105 dBA white noise) were presented at 60 and 120 ms lead intervals following the onset of the auditory lead stimulus on some trials in each condition. The 60 ms lead interval was chosen to index preattentive stimulus detection and evaluation processes, and the 120 ms lead interval was chosen to index stimulus discrimination and allocation processes. Additional startle stimuli were presented randomly between trials to measure baseline (unmodified) response.
2.3. Measurement of dependent variables

The startle blink reflex was measured by the amplitude of the electromyographic (EMG) response of the orbicularis oculi muscle, which controls the movement of the eyelid. This response was recorded from two miniature (4 mm) silver–silver chloride (Ag–AgCl) electrodes placed on the lower eyelid of the left eye and one large (8 mm) Ag–AgCl electrode placed behind the left ear for the common connection. Skin preparation and electrode attachment followed standard procedures to obtain an impedance of not more than 10 kΩ, preferably less than 5 kΩ. The EMG signal was amplified, filtered (low pass 500 Hz, high pass 10 Hz), digitally sampled at 1000 Hz, and stored by a computer program for off-line analysis. The computer program also controlled stimulus presentation and timing.

2.4. Procedure

After participants read and signed the consent form and listened to recorded instructions, the experimenter attached the electrodes. After the electrodes were attached, participants saw a demonstration of the colored dots; heard demonstrations of the high, middle, and low pitch tones; and heard demonstrations of the long and short duration tones. After the demonstrations, participants completed eight practice trials, including two startle stimuli, followed by the actual experiment, which ran continuously until completion.

There were five blocks of 12 trials per block. Within each block, there were four trials in each of the three conditions (task-attended, task-ignored, and no-task) in random order. Within each block, one trial in each condition was randomly probed with a startle stimulus at each lead interval. Two additional startle stimuli were presented randomly between trials in each block. Thus, there were a total of 60 trials and 40 startle stimuli. The inter-trial intervals (ITI) were random in the range 10–14 s except for trials with a baseline startle stimulus. For these trials, the ITIs were random in the range 20–28 s.

As an incentive for good performance, participants were paid a US$5.00 reward for a completely correct count. For each missed longer duration tone, US$1.00 was deducted from the reward. Total deduction did not exceed US$5.00.

2.5. Data scoring, reduction, and analysis

The recorded EMG data were scored by a computer program that computed a magnitude score for trials in which blink onset occurred within 21–120 ms of startle stimulus onset and peak amplitude occurred within 150 ms of blink onset. Missing scores were replaced with the nearest score in the same condition. Five missing scores were replaced. Scores of zero were not replaced. Median ITI magnitude was computed for each participant as a measure of baseline startle response. Medians were used in these calculations because they are robust estimators of population central tendency, unaffected by the presence of extreme scores (see Wilcox, 1996 for a discussion of robust estimation). Median ITI magnitude was used to compute percentage change scores for each trial using the formula: Percentage change = ((Magnitude − Median ITI magnitude)/Median ITI magnitude) × 100.

Individual percentage change scores were collapsed into median attended, ignored, and no-task scores by lead interval by subject. Overall analyses were performed using a 2 × 3 analysis of variance (ANOVA) with Greenhouse–Geisser ε corrections to adjust probabilities for repeated measures F values. We report the uncorrected degrees of freedom and the ε values for these analyses. Specific comparisons were performed using repeated measures t tests. For all tests, the α level was 0.05. An estimate of effect size (d; Cohen, 1988) was also calculated for all specific comparisons.

3. Results

3.1. Task performance

Task performance was satisfactory. Among the responders 58% gave completely correct counts, 17% gave counts that were off by one, 8% gave counts that were off by two, and 17% gave counts that were off by more than two. Overall, performance indicated that participants understood and were able to perform the task.
3.2. Baseline startle

We compared the means of the ITI scores obtained prior to task trials with the means of the ITI scores obtained prior to no-task trials. The difference was not statistically reliable and the effect size was small ($t(48)=.28$, $p<0.78$, $d=0.06$). The task and no-task cues did not differentially affect baseline startle response.

3.3. Overall analysis

The pattern of mean percentage change for the attended, ignored, and no-task conditions at the 60 ms and 120 ms lead intervals is illustrated in Fig. 1. The 2 (lead interval: 60 ms, 120 ms)×3 (condition: attended, ignored, no-task) ANOVA revealed a statistically reliable main effect of condition ($F(2, 46)=4.75$, $p<0.03$, $\epsilon=0.76$), no reliable effect of lead interval ($F(1, 23)=1.05$, $p<0.32$), and no reliable lead interval by condition interaction ($F(2, 46)=.37$, $p<0.64$, $\epsilon=0.76$). In the absence of a lead×condition interaction we combined the 60 ms and 120 ms lead interval data by condition for subsequent statistical analysis.

There was a statistically reliable difference between the attended and ignored ($t(47)=2.48$, $p<0.02$, $d=0.53$) and between the attended and no-task ($t(47)=2.54$, $p<0.02$, $d=0.52$) conditions. The difference between the ignored and no-task conditions was not reliable ($t(47)=1.06$, $p<0.29$, $d=0.22$).

3.4. Block effects

Schell et al. (2000) and Filion and Poje (2003) observed attentional modulation of PPI only in the latter two trial blocks. In order to determine whether attentional modulation increased over time in the present experiment, we combined the percentage change scores for the first two of the five trial blocks into an early block and combined the percentage change scores for the last two of the five trial blocks into a late block. This procedure yielded blocks containing approximately as many startle stimuli for each lead stimulus as Filion and Poje. We then carried out a 2 (lead interval: 60 ms, 120 ms)×3 (condition: attend, ignore, no-task)×2 (trial block: early, late) ANOVA. The condition main effect was reliable ($F(2, 46)=5.11$, $p<0.04$, $\epsilon=0.54$), whereas none of the other main effects and none of the interactions was reliable (all $F<1.21$, all $p>0.29$). Thus, attentional modulation was a stable effect across early and late trial blocks. For greater stability in the measures of percentage change, the $t$ tests described above were based on data combined across all trial blocks of this experiment.

4. Discussion

Overall, the pattern of results is consistent with two conclusions. First, attentional modulation of PPI in this procedure was due to increased protection of attended lead stimuli relative to the no-task condition. This conclusion follows from the finding of greater PPI in the attended condition compared to the ignored and no-task conditions. Second, attentional modulation of PPI in this procedure was not due to decreased protection of ignored lead stimuli below that of a no-task condition. This conclusion follows from the finding of no difference in PPI between the ignored and no-task conditions.

Our results are consistent with those of Jennings et al. (1996), who also concluded that attentional modulation is due to increased protection of attended stimuli and not to actively suppressed protection of ignored stimuli. Our results extend those of Jennings et al. by showing that attentional modulation is not
due to differences in instructions, task, or extrinsic incentive since, in the present experiment, these factors were the same for all participants. Jennings et al. measured skin conductance level (SCL) as a separate measure of arousal and found that neither SCL nor baseline startle differed between task and no-task groups. Filion and Poje (2003) also reported no difference in SCL and baseline startle between task and no-task blocks. Although we did not measure SCL, we also found no difference in baseline startle response prior to task and no-task trials. Thus, the task condition did not appear to have a differential effect on arousal relevant to the no-task condition.

Our results differ from those of Schell et al. (2000) and Filion and Poje (2003) in that they obtained attentional modulation only at the 120 ms lead interval. We, in contrast, obtained robust attentional modulation at the 60 ms lead interval as well. This finding of attentional modulation at 60 ms was not predicted and is inconsistent with well-replicated results using the tone duration judgment task.

What can account for these differences? Although the basic tone duration judgment task in the present experiment and that of Filion and Poje (2003) closely followed procedures used in previous experiments, there were two important differences which must be considered.

First, in the present experiment, a visual stimulus, a colored dot, pre-cued each task and no-task trial. However, the colored dots were carefully planned to minimize extraneous effects. The dots were small and the luminance values were similar. Dots were continuously visible to avoid onsets and offsets. Color changes coincided with the offset of the lead stimulus for each trial so they would have no effect on the previous trial and a minimal possibility of an effect on the next trial. Thus, it is unlikely that the dots altered the PPI results. The absence of a reliable difference in baseline startle recorded prior to task and no-task trials supports this conclusion.

Second, the average interval between task and no-task trials in the present experiment was relatively short compared to the average interval in most previous experiments. Although the mean ITI was not significantly different between the present experiment and the Filion and Poje (2003) experiment, in the latter experiment, the task and no-task trials were blocked so the actual interval between task trials when there was an intervening no-task block was much longer (up to about 160 s) in the Filion and Poje experiment. In contrast, in the present experiment there was a possibility of a task on every trial. Thus, the interval was always short (mean 14 s). For this reason, we speculate that the overall vigilance level in the present experiment was higher than in the Filion and Poje experiment.

High vigilance, we believe, accounts for attentional modulation at the 60 ms lead interval. We suggest that, in this selective attention task, prior to tone discrimination, attended and ignored lead stimuli receive similar enhanced protection, greater than what would be received in a no-task condition. This was seen at 60 ms by Filion and Poje (2003). After tone discrimination, protection of attended lead stimuli continues at the same enhanced level but protection of ignored lead stimuli simply decreases to that which is seen in a no-task condition. It is important to note that the decreased PPI following the ignored stimulus does not go below that for the no-task condition. Hence, there is no evidence of active suppression of protection of processing following the ignored stimulus. This effect was seen at 120 ms in the late trial block by Filion and Poje. We suggest that the high vigilance in the present experiment makes earlier tone discrimination possible, and can accelerate the decisions to attend to or ignore lead stimuli. Therefore, attentional modulation, which only occurred at the 120 ms lead interval in the Filion and Poje and other experiments, occurred at the earlier 60 ms lead interval in the present experiment.

Event-related potential (ERP) evidence is consistent with the conclusion that task-relevant auditory stimuli can be discriminated from other auditory stimuli at latencies as short as 60 ms. Hillyard et al. (1973) reported larger N1 component responses, which are known to be sensitive to stimulus relevance, to higher pitch (odd) tones randomly interspersed in a rapid sequence of standard tones when participants were instructed to count the number of odd tones at one ear. Onset latencies were not reported but an inspection of the figures in the paper indicates that they were in the 40–60 ms range.

It is difficult to assess how well these conclusions will generalize to other experimental procedures because the technique of trial-by-trial cuing of task and no-task trials by a visual stimulus is unique in
startle research. Nevertheless, our results demonstrate that, in this type of selective attention task, attentional modulation of the startle reflex is due to increased protection of attended stimuli, and that modulation can occur at a lead interval as early as 60 ms. To the best of our knowledge this is the first demonstration of modulation at 60 ms. Additional research is needed to examine the experimental and task factors which are necessary to elicit this early attentional modulation.

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References


