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Prepulse inhibition of the startle blink reflex is modulated during a memory task
requiring prepulses to be encoded for later report

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Abstract

Prepulse inhibition (PPI) of the startle blink reflex in humans can be modulated by selective attention to the prepulse. The present experiment used a memory task to determine whether the encoding of information for later report can modulate PPI. Participants were briefly presented with a display of one or three letters followed by a pattern mask and asked to make a delayed report of the letter(s) shown. Memory recall was better in the 1-letter condition than in the 3-letter condition. Prepulse inhibition was greater in the 3-letter condition than in the 1-letter condition at lead intervals of 120 and 240 ms following the onset of the letter display. Blink modulation did not differ between the letter conditions at lead intervals of 120, 240, 360, or 2600 ms following the mask, ruling out other explanations (e.g., rehearsal) for the earlier difference in PPI. The results suggest that the short-term consolidation of memory, and possibly any cognitive process that requires access to a theoretical limited capacity central processing mechanism, modulates PPI.

Keywords: prepulse inhibition, memory, startle reflex, attention

Introduction

In the prepulse inhibition (PPI) procedure, an intense blink-eliciting stimulus or pulse is preceded at lead intervals ranging from 30 to 500 ms by a less intense prepulse. Prepulse inhibition is observed as a reduction in blink magnitude during prepulse+pulse trials relative to pulse alone trials. The transient inhibition is thought to reflect automatic sensorimotor gating mechanisms that serve to maintain the integrity of the processing of the prepulse from interruption by subsequent stimuli (e.g., Graham, 1992). The amount of inhibition may index the extent to which this protective gating mechanism has been activated (Braff & Geyer, 1990). What is particularly interesting about this obligatory process is that a range of factors can modulate it. It is influenced by stimulus characteristics where, for instance, PPI tends to be maximal at shorter lead intervals for auditory prepulses when compared to visual and tactile prepulses (Neumann et al., 2004b). It tends to be reduced in special populations, most notably those with schizophrenia (see Braff & Geyer, 1990; Dawson et al., 2000). Finally, PPI can be modulated by attentional processes (for reviews see Blumenthal, 1999; Dawson et al., 1997).

The modulation of prepulse inhibition by selective attention has most commonly been observed with what has been called a differential tone-duration-judgement task (Dawson et al., 1997). Participants are presented with a random series of two tones that differ in pitch and are asked to count how many times one tone (task-relevant or attended tone) is presented for a longer-than-usual duration (7 s versus 5 s) and to ignore all presentations of the other tone (task-irrelevant or ignored tone). Blink-eliciting stimuli are presented at specific lead intervals following the onset of the prepulse tones and during the intervals between the tones. Prepulse inhibition at a 120 ms lead interval is greater during attended tones than during

ignored tones (Dawson et al., 1993; Filion & Poje, 2003; Filion et al., 1993, 1994; Hawk et al., 2002; Jennings et al., 1996; see also Steele-Laing & Hicks, 2003 for a variant of this task). The difference in PPI between attended and ignored prepulses may also be found at other lead intervals when the task is modified (e.g., 60 ms, Thorne et al., 2005) and the effect may be stronger with auditory than with visual prepulses (Böhmelt et al., 1999).

It has been noted that the differential tone-duration-judgement task requires participants to perform a series of cognitive operations. These may include (a) preattentive detection and discrimination of the attended and ignored prepulses, (b) confirmation of the prepulse identity and initiation of the duration judgement, and (c) sustained attention to the attended prepulse to determine its duration (Dawson et al., 1993). As a result, attention is initially directed to both types of prepulses, although the subsequent cognitive operations are different (Heekeren et al., 2004). On the one hand, this creates some ambiguity with regards to the exact process that modulates PPI in that it may reflect a confirmation of the preattentive evaluation of the prepulse and/or the initiation of the duration judgement. On the other hand, it seems that what is common to these processes is that they involve controlled selective attention (Dawson et al., 1997). As such, the modulation of PPI may reflect the call for or the actual allocation of controlled attentional resources from a central capacity limited processing mechanism (Filion et al., 1994).

The notion that a limited capacity central processing mechanism underlies the modulation of PPI in the differential tone-duration-judgement task is strengthened by the conclusion that the increased PPI is due to increased protection of attended prepulses and not decreased protection of ignored prepulses (Jennings et al., 1996; Thorne et al., 2005; but see Filion & Poje, 2003; Hawk et al., 2002; Schell et al.,

2000). The amount of PPI is also greater during attended prepulses than during ignored prepulses when participants are not required to discriminate between attended and ignored prepulses (Hutchinson et al., 2005; see also Heekeren et al., 2004). In addition, PPI has been modulated in other selective attention tasks. In the continuous performance task, for example, participants receive brief presentations of single digits in rapid succession and must respond whenever a target occurs after a specific digit (e.g., respond to target 7 only when it occurs after a 3; Hazlett et al., 2001). Prepulse inhibition at a 120 ms lead interval is larger following targets than following nontargets (Hazlett et al., 2001) and this effect is delayed, occurring at 240 ms, when degraded stimuli are used (Rissling et al., 2005). The cognitive processes required in the continuous performance task may include (a) stimulus detection, (b) identification as target or non-target, and (c) preparation for detection of the next stimulus (Rissling et al., 2005). Although these processes are somewhat different to those in the differential tone-duration-judgement task, the engagement of a limited capacity central processing mechanism appears to be a common feature of both tasks.

The notion of a limited capacity central processing mechanism can explain the modulation of PPI by selective attention even when the attentional outputs are diverse and task specific. By extension, it also has implications for cognitive processes other than those that follow a discrimination between attended and ignored prepulses. Any cognitive process that requires access to a central processing mechanism has the potential to modulate PPI so long as there are different levels of demand placed on the limited capacity. Jolicœur and Dell'Acquia (1998) have argued that the process of encoding information into short-term memory, which they termed short-term consolidation, requires central processing mechanisms. Importantly, short-term consolidation is thought to occur very early following the onset of the to-be-

remembered material. Taken together, PPI should be modulated in tasks requiring the short-term consolidation of memory in much the same way as it is modulated in tasks requiring selective attention.

Jolicœur and Dell'Acqua (1998) developed a task that they argued isolated the process of short-term consolidation. Their procedure avoids much of the ambiguity surrounding more complex tasks by simply requiring participants to encode information for later report. In the basic procedure, participants are presented with a display of one or three characters for a brief duration and followed by a mask. Participants must remember the characters for report at the end of the trial. Memory consolidation was examined through a secondary task requiring participants to make a reaction time response to a probe presented at various stimulus onset asynchronies (SOAs) following the onset of the character display. The slowing of reaction time was greater at short SOAs of 50 ms than at longer SOAs of 350 ms and the slowing was greater for the 3-character condition than the 1-character condition. The authors suggested that this pattern of results reflected short-term consolidation, that is, that the information generated from the sensory input was transferred into durable memory storage. Further, based on the pattern of dual task slowing across the SOAs, such as the increased slowing in the 3-character condition than in the 1-character condition, the authors argued that short-term consolidation requires a limited capacity central processing mechanism for its execution (see also Jolicœur & Dell'Acqua, 1999).

The hypothesis that PPI is modulated by cognitive processes that require access to a limited capacity central processing mechanism leads to the prediction that PPI will be modulated by the process of short-term consolidation. The main source of comparison in the present experiment was whether PPI will be greater when participants are required to encode three letters for later report in comparison to a

single letter. This prediction was tested by adapting the delayed memory task of Jolicœur and Dell'Acquia (1998). A visual display of one or three letters was briefly presented and followed by a mask. The purpose of the mask was to limit sensory encoding to the duration of the letter display (Jolicœur and Dell'Acquia, 1998). Participants were later prompted to recall the letter(s) after the mask. In the context of the PPI procedure, the letter display is the main prepulse. However, the mask display may also function as a prepulse because it results in a change of information in the visual channel. Blink modulation was thus examined across two groups of lead intervals. Prepulse inhibition assessed at 120 and 240 ms following the letter display was predicted to be greater in the 3-letter condition than in the 1-letter condition, reflecting the larger engagement of the limited capacity central processing mechanism to consolidate into memory three letters versus one letter. Blink modulation was also assessed at lead intervals of 120, 240, 360, and 2600 ms following the mask display. Blink modulation at the first three lead intervals might reflect not only the final stages of short-term consolidation, but also the effects of the mask as PPI is associated with recovery from backward masking (Wynn et al., 2004). The lead interval of 2600 ms is a "late" lead interval that does not produce PPI, but can be modulated by later controlled cognitive processes (e.g., Böhmelt et al., 1999; Neumann et al. 2004a). The assessment of blink modulation at 2600 ms will reflect the degree to which later controlled processes, such as rehearsal of the to-be-remembered letter(s), are present. Finally, if PPI reflects the extent to which a central processing mechanism has been engaged, task performance should be related to PPI. As previous research (Elden & Flaten, 2002; Norris & Blumenthal, 1996) has tended to find inconsistent results, the prediction that better task performance will be associated with greater PPI was also tested.

Materials and Methods

Participants

Thirty students (10 male and 20 female) from Griffith University participated for course credit. The participant ages ranged from 17 to 47 years with a mean of 24.8 years. The data from three participants was not used because equipment malfunction resulted in a loss of their data and two further participants were excluded for excessive non-responsiveness to the blink-eliciting stimulus. Participants provided informed consent prior to participating in a protocol approved by the Human Research Ethics Committee of Griffith University.

Materials

Electromyographic (EMG) recordings of the startle blink reflex were taken by placing two 4-mm diameter Ag/AgCl domed electrodes filled with Surgicon E10 electrolyte over the *orbicularis oculi* of the left eye. One electrode was positioned 1 cm below the pupil and the other approximately 1 cm lateral. A ground electrode was placed on the inside of the non-preferred arm. The raw EMG signal was sampled with an ADInstruments (Sydney, Australia) ML132 Bio Amp in conjunction with a PowerLab 10/20 data acquisition system. A sample rate of 1000 Hz was used in a time window of 100 ms prior to and 400 ms following the onset of the blink-eliciting stimulus. The raw signal was stored off-line on a Dell Optiplex Model GX270 computer for later processing. A custom-built noise generator produced the 110 dB(A) white-noise blink-eliciting stimulus. It was presented for 50 ms and with an instantaneous rise time through Sennheiser HD-25 headphones.

The stimuli for the memory task were presented via a Panasonic Model PT-L557E LCD projector onto a white screen 1.7 m in front of the participant. The stimuli were presented in white on a black background. The fixation stimulus

consisted of a hollow square that subtended 7.2° visual angle. The stimuli for the memory task were upper case letters that were selected at random on each trial, without replacement, from the set of consonants excluding S or Z (Jolicœur and Dell'Acquia, 1998). One or three letters were presented to result in two types of trials (1-letter and 3-letter trials). Each letter subtended approximately $4.3 \times 7.2^\circ$ visual angle. When three characters were presented, they were arranged horizontally with a 0.2° space between each character. Any letter combinations in the 3-letter condition that formed a word were not used. The mask consisted of superimposed 0 and \$ characters that subtended $4.3 \times 8.6^\circ$ visual angle. The mask was presented in the same location(s) as the letter display for each trial type. This resulted in one graphic of superimposed 0 and \$ characters for the 1-letter condition and three separate graphics of superimposed 0 and \$ characters for the 3-letter condition. Participants entered their responses on a computer keyboard. Stimulus presentation and recording of the participant's recall of letters were done with the DMDX program (Forster & Forster, 2003) and controlled by a second Dell Optiplex Model GX270 computer.

Procedure

The participant completed the experiment individually in an electrically shielded room, while the experiment was monitored from an adjoining room. Prior to electrode placement for the EMG recordings, the participant washed below his or her eye with soap and water. Three test presentations of the blink-eliciting stimulus were made to verify the quality of the recordings. Participants next received instructions for the task. The task consisted of a series of memory trials. The basic structure of each trial, with the placement of potential blink-eliciting stimuli is shown in Figure 1. Each trial began with a presentation of the fixation box. The participant was told to press the spacebar when the box was presented to initiate the trial. The fixation box

disappeared and after a delay of 1000 ms, a display of one or three letters was presented for 240 ms. The letter display was followed immediately by the mask for 3000 ms. Next, the text “Please enter answer” was displayed for 3000 ms to prompt the participant to enter their answer for the memory task. Participants were instructed to use the keyboard to type in the letter(s) that they were presented with on that trial only when prompted by the text message. It was stressed that the task was unspeeded and that they should be as accurate as possible. The letters could be entered in any order on trials in which three letters were shown and any errors made by mistyping letters could be corrected. After the participant entered in their response, the screen was blank during an intertrial interval delay before the next trial began. The intertrial intervals varied at random between 3000, 5000, 7000, and 9000, and 14000 ms and were selected with replacement separately for each trial and each individual participant. Thus, on average, each intertrial interval duration was equally represented for each participant. Each participant first completed 14 practice trials, consisting of a random order of 7 trials of the 1-letter condition and 7 trials of the 3-letter condition. The data obtained from the practice trials were not analysed further. There were next 112 randomized trials of the memory task in the experiment proper, with half the trials for the 1-letter condition and the remaining half for the 3-letter condition.

 Insert Figure 1 about here

Participants received presentations of the blink-eliciting stimulus concurrently with the memory task in the experiment proper. The blink-eliciting stimuli occurred either during the letter or mask displays during the memory task or during the interval

between the memory task trials. The blink-eliciting stimuli presented during the memory task display were presented at two groups of lead intervals (see Figure 1). The first group of lead intervals were presented at 120 and 240 ms following the onset of the letter display and are referred to as Letter 120 ms and Letter 240 ms. The second group were presented 120, 240, 360, and 2600 ms following the onset of the mask and are referred to as Mask 120 ms, Mask 240 ms, Mask 360 ms, and Mask 2600 ms respectively. The blink-eliciting stimuli were randomly assigned to a trial in the memory task with the following restrictions: (a) no more than one presentation of a blink-eliciting stimulus could occur during any one trial, (b) presentations were arranged into two blocks such that the first block were presented during the first half of the memory task and the second block were presented during the second half of the memory task, and (c) in each block, there were two presentations of each of the six lead interval combinations (Letter 120 ms, Letter 240 ms, Mask 120 ms, Mask 240 ms, Mask 360 ms, and Mask 2600 ms) at each of the two letter conditions (1-letter and 3-letter). This trial arrangement resulted in a total of 48 blink-eliciting stimuli presented during the memory task display such that they were evenly distributed across each lead interval and letter condition.

The intertrial interval presentations were used to provide a baseline measure of the participant's responsiveness to the blink-eliciting stimulus independent of the memory task display for the calculation of PPI. The intertrial interval blink-eliciting stimuli were presented only during those intervals that followed a trial for the memory task in which no blink-eliciting stimulus was presented. These intertrial interval blink-eliciting stimuli were presented 7000 ms following the participant entering a response for the memory task and the next trial for the memory task did not begin until a further 7000 ms had elapsed after the blink-eliciting stimulus presentation.

The presentations of the intertrial interval blink-eliciting stimuli were arranged in a similar manner to the blink-eliciting stimuli during the memory task display. Two blocks of intertrial interval blink-eliciting stimuli were formed such that there were four presentations in each block to result in eight intertrial interval blink eliciting stimuli in total. The presentations were distributed evenly across the 1-letter and 3-letter conditions in each block. Participants were instructed to ignore the presentations of the blink-eliciting stimuli.

Data Scoring and Statistical Analysis

Performance on the memory task was quantified for each trial by calculating the total number of letters reported correctly separately for the 1-letter and 3-letter conditions (performance was quantified without regard for the order of report for the 3-letter condition; Jolicœur & Dell'Acquia 1998). Only trials in which no blink-eliciting stimulus was presented were used to examine memory performance due to the distracting effects that the stimulus may have had (i.e., trials in which the blink-eliciting stimulus was presented during the letter display and the mask display were excluded). Preliminary data analysis using a 2 x 2 (Letter x Block) ANOVA indicated that memory performance did not significantly vary across blocks, $p > .05$, thus the data were collapsed across the entire experiment.

The scoring procedure for the startle blink responses was based on the guidelines of Blumenthal et al. (2005) and van Boxtel et al. (1998). The raw EMG signal was digitally filtered with a Butterworth filter by applying a 28-500 Hz pass band, rectified, and finally smoothed with a FIR filter (25 coefficients, low-pass cut-off frequency of 40 Hz). The resulting waveform was used for the quantification of response amplitude. Amplitude was defined as the difference between the maximum of the waveform in a window of 20 to 200 ms following blink-eliciting stimulus onset

and the onset of the response. Response onset was defined as the point after blink-eliciting stimulus onset that was greater than two standard deviations above the mean of the signal observed across the 100 ms prior to the blink-eliciting stimulus. If no response onset could be detected, amplitude was scored as zero. A trial was rejected if the signal was contaminated by noise, a spontaneous blink, or movement artefact in the 100 ms prior to the blink-eliciting stimulus (3.2% of trials). Amplitudes, including zero responses, were averaged to derive a magnitude measure separately for each of the six lead intervals and each letter condition. Similarly, mean magnitude was calculated for the blink responses elicited during the intertrial intervals. As preliminary data analysis using a repeated measures *t*-test found no differences depending on whether intertrial interval blinks were elicited after a 1-letter or 3-letter memory trial, $p > .05$, the data were collapsed across all trials. Blink magnitudes for each lead interval were expressed as a percentage change from the intertrial interval (ITI) magnitudes by using the formula of $\% \text{ change} = (\text{Lead interval} - \text{ITI}) / \text{ITI} * 100$, to reduce the impact of individual differences and to assess whether blink inhibition was found. A negative percent change indicates blink inhibition. Inhibition was deemed to be significant if zero was outside of the 95% confidence interval of the mean. An α -level of .05 was used for all statistical analyses and effect sizes are reported as partial eta squared (η_p^2), which describes the proportion of the effect + error variance that is attributable to the effect.

Results

Performance on the memory task was high overall with a mean proportion of .94 letters correctly recalled. However, performance for trials in which one letter was presented ($M = .98$, $SD = .03$) was better than trials in which three letters were presented ($M = .89$, $SD = .11$). The difference between the 1-letter and 3-letter

conditions was highly significant, as assessed by a repeated measures t test, $t(29) = 4.46$, $p = .0001$, $\eta_p^2 = .41$.

Percent blink change of response magnitude during the memory trials is shown in Figure 2. As can be seen, PPI was observed across most of the early lead intervals. Prepulse inhibition was significant for both the 1-letter and 3-letter conditions at the Letter 120 ms lead interval and at the Mask 120 ms, Mask 240 ms, and Mask 360 ms lead intervals. Prepulse inhibition was also significant at the Letter 240 ms lead interval in the 3-letter condition. Blink modulation was not different from zero at the Mask 2600 ms lead interval in any letter condition.

 Insert Figure 2 about here

The pattern of PPI also differed between the 1-letter and 3-letter conditions at some of the lead intervals. Analyses were conducted separately for the lead intervals during the letter and mask displays. A 2 x 2 (Letter x Lead interval) ANOVA was used to examine PPI during the letter display. As can be seen in Figure 2, PPI was greater in the 3-letter condition than in the 1-letter condition, Main effect for Letter, $F(1, 24) = 10.90$, $p = .003$, $\eta_p^2 = .31$. Prepulse inhibition during the letter display was also greater at the 120 ms lead interval than at the 240 ms lead interval, Main effect for Lead Interval, $F(1, 24) = 4.52$, $p = .044$, $\eta_p^2 = .16$. The Letter x Lead Interval interaction was not significant, $F(1, 24) = 1.60$, $p = .22$, $\eta_p^2 = .06$. Blink modulation tended not to differ between the letter conditions or the lead intervals during the mask display. A 2 x 4 (Letter x Lead interval) ANOVA confirmed this impression with no main effects or interactions reaching significance, all F s < 1.74 , $p > .05$.

 Insert Table 1 about here

As task performance was generally high overall with many participants showing perfect recall, an analysis that correlated PPI with task performance or an analysis that compared PPI during trials in which recall was correct and trials in which recall was incorrect was not suitable to examine the relationship between task performance and PPI. Instead, a median split technique was used to examine task performance and PPI at the Letter 120 ms and Letter 240 ms lead intervals. The median across all participants for the number of letters correctly recalled on the 1-letter and 3-letter trials in which the blink-eliciting stimulus was not presented was first calculated. Participants who scored lower than the median were placed in the Low Performers group ($n = 12$) and those participants who scored higher than the median were placed in the High Performers group ($n = 12$). One participant who had a performance score equal to the median was not allocated to a group. The mean PPI in each group for the two lead intervals during the letter display is shown in Table 1. A $2 \times 2 \times 2$ (Group $\times$ Letter $\times$ Lead interval) ANOVA resulted in a significant three-way interaction, $F(1, 22) = 5.13$, $p = .034$, $\eta_p^2 = .19$, showing that PPI was different between the groups at some letter and lead interval combinations and not others. Post hoc analyses were conducted using t -tests that used protected α -values based on Sidak's multiplicative inequality (Games, 1977) to correct for inflated Type I error. Comparisons showed that PPI was greater in the High Performers group than in the Low Performers group at the 240 ms lead interval for the 1-letter condition, $t = 3.15$, $p < .05$, and marginally so at the 120 ms lead interval for the 3-letter condition, $t = 2.30$, $p < .1$. All other comparisons were not significant.

Discussion

The results of the present experiment showed that participants performed poorer when asked to recall three letters than when asked to recall one letter after a delay of approximately 3 s. The difference is indicative of the higher difficulty inherent in having to recall more letters. The onset of the letter display and mask produced significant PPI across most early lead intervals. The amount of PPI was larger at lead intervals of 120 and 240 ms following a 3-letter display than following a 1-letter display. This difference is consistent with the predication that PPI will be modulated by the short-term consolidation of memory. It extends prior research that has demonstrated that PPI is modulated in tasks that require selective attention to prepulses that are to be counted or responded to when comparisons are made with prepulses that are to be ignored (e.g., Dawson et al., 1993; Filion & Poje, 2003; Filion et al., 1993; 1994; Hawk et al., 2002; Hazlett et al., 2001; Jennings et al., 1996; Rissling et al., 2005; Steele-Laing & Hicks, 2003). There was no difference in blink modulation between the 1-letter and 3-letter conditions for any of the lead intervals during the mask display. Performance on the memory task showed a limited relationship with PPI. Participants who showed better performance on the memory task also showed more PPI at a lead interval of 240 ms during the 1-letter display and at a lead interval of 120 ms during the 3-letter display than participants who showed poorer performance on the memory task. However, there were no differences between the two groups of participants at the two other lead interval and letter combinations during the letter display.

The central finding of the present experiment is that PPI was modulated in a task that required participants to encode information into a durable memory storage for later recall. It was hypothesised that PPI is modulated by any cognitive process

that requires access to a capacity limited central processing mechanism, in line with Filion et al's (1994) interpretation of the PPI modulation during the differential tone-duration-judgement task. The greater PPI during the letter display in the 3-letter condition than in the 1-letter condition is consistent with this notion. Greater demands were placed on the limited capacity central processing mechanism to encode three letters than to encode one letter for later recall. It is consistent with the argument of Jolicœur and Dell'Acquia (1998) that there are significant costs associated with merely trying to remember 1 or 3 letters. These costs increase as more information must be remembered. The present findings suggest that the modulation of PPI need not be limited to tasks that compare prepulses that must be attended or responded to versus prepulses that are to be ignored.

The present task was modelled on the procedure of Jolicœur and Dell'Acquia (1998). This task is a relatively simple and unambiguous task in that it merely requires participants to encode information for later report. As such, the task can provide a different perspective on the cognitive factors that modulate PPI because it can, for instance, help to disentangle the influence of the encoding process from the matching process that are both present in the differential tone duration judgement task and the continuous performance task. All stimuli in the present task were required to be remembered, thus there was no need to discriminate between attended and ignored prepulses. In an alternative to the differential tone-duration-judgement task, Heekeren et al. (2004) required participants to discriminate between simple stimuli (e.g., prepulse alone) from composite stimuli (e.g., prepulse+pulse). Participants were prewarned prior to each trial on whether they should attend to the trial or ignore it. The method of Heekeren et al. (2004) also provides an alternative means to separate the effects of controlled cognitive processes and perceptual matching on PPI.

However, in any procedure that compares task and no task trials, one should be careful to ensure that the observed differences are due to selective attention processes and not the effects of differential arousal elicited prior to each trial (see Elden & Flaten, 2002 for a discussion). In the present task, it is clear that there was non-differential arousal to the two letter conditions because all prepulses had to be encoded for later report. It was the amount of information to be encoded that differed between the letter conditions and not whether the prepulse should be encoded or not.

Several aspects of the data appear to rule out other potential explanations for the observed differences in PPI between the letter conditions. For instance, the suggestion that the different stimulus features present in the 3-letter condition compared to the 1-letter condition (i.e., more complex display) is the reason for the differences in PPI is not supported. There were no differences between the letter conditions at the Mask 120, Mask 240, or Mask 360 ms lead intervals. As there was a single mask character following the 1-letter display and three mask characters following the 3-letter display, differences in PPI should have also been found at these lead intervals if the physical nature of the display itself influenced PPI at the Letter 120 and Letter 240 ms lead intervals. Rather, the lack of an effect of the letter conditions at the early lead intervals during the mask display may reflect a change from the short-term consolidation process to the rehearsal of the stored information in memory. The rehearsal of information in memory would require controlled attentional processes (Baddeley, 1986) and may result in a facilitation of blink reflexes. This interpretation is similar to that applied to the differential tone-duration-judgement task. In this task, Dawson et al. (1997) suggested that the lack of a difference in PPI between attended and ignored prepulses at a 240 ms lead interval reflects a change from the controlled attentional modulation of PPI at 120 ms to the

controlled sustained cognitive processes needed for judging the duration of the prepulse.

The present findings are unlikely to reflect the different response or retention requirements of the two letter conditions. Differential response requirements were not likely to influence PPI because the recall of the letter(s) were unspeeded and were prompted well after the responses to the blink-eliciting stimuli. The difference in PPI between the letter conditions is unlikely to reflect retention requirements because there was no blink facilitation or any differences in blink modulation between the 1-letter and 3-letter conditions at the Mask 2600 ms lead interval. The retention requirements thus appear to have been minimal, even in the 3-letter condition. Differential blink facilitation at the Mask 2600 ms lead interval might only be found when the rehearsal demands are increased (e.g., by requiring more letters to be recalled). Taken together, it would appear that although the memory task was minimal, as evidenced by the high level of performance and lack of differences in blink modulation between the letter conditions at the late lead interval, the process of encoding sensory information into durable memory storage was sufficient to produce significant enhancement of PPI immediately after the letter display.

It should be noted that there is at least one interpretation, other than short-term consolidation, for the modulation of PPI in the present task. In particular, the notion of perceptual load may explain why PPI was greater in the 3-letter condition than in the 1-letter condition. Perceptual load theory proposes that under certain conditions, perception has limited capacity and that this limited capacity can influence the allocation of processing resources during a selective attention task (Lavie, 1995, 2005). High levels of perceptual load will result in a greater allocation of processing resources when attending to a stimulus. Perceptual load may be varied by, for

example, changing the number of items in a display that are similar to a target or by changing the number of features of a stimulus that a response is contingent on (see Lavie, 2005 for additional examples). In the present experiment, 3-letter condition display may have induced a higher perceptual load than the 1-letter display because of the greater number of letters that had to be perceived. According to this interpretation, the increased perceptual load would have commanded more processing resources, thereby leaving fewer resources available for the processing of other concurrently present stimuli. The result was a smaller blink response (enhanced PPI) to the blink-eliciting stimulus. While it may be difficult to disentangle the effects of perceptual load and short-term consolidation of memory in the present task, it is noteworthy that both notions suggest that the PPI is modulated by the same fundamental cognitive process, that is, the allocation of controlled attentional resources from a limited capacity processing mechanism.

The difference in PPI between the 3-letter and 1-letter conditions was observed both at lead intervals of 120 ms and 240 ms during the letter display. The effect of task demands across two lead intervals is different to the outcomes of some other reports with selective attention tasks. For instance, the effects of selective attention tend to be found at a 120 ms lead interval and not at a 60 ms or 240 ms lead interval with the differential tone-duration-judgement task (e.g., Filion et al., 1994; see Dawson et al., 1997). This pattern across lead intervals is not necessarily fixed, however, as the effects of selective attention have been observed at the 60 ms and 120 ms lead intervals in a modified version of the differential tone-duration-judgement task (Thorne et al., 2005). Using a different selective attention task, Heekeren et al. (2002) reported differences between attended and ignored prepulses at a 240 ms lead interval and not a 100 ms lead interval. It is difficult to determine what factors are

relevant for whether the effects of task demands occur at one lead interval or another. The nature of stimuli used in the present task (visual, well-learned letters) are clearly different to that used in most prior research (e.g., tones of different pitch in the differential tone-duration judgement task). Stimulus features appears to be important factor in the continuous performance test where the differences in PPI between target and non-targets appear to occur at the later lead interval of 240 ms rather than 120 ms when degraded visual stimuli are used (Rissling et al., 2005). Perhaps more importantly, the requirement to encode information into durable storage in the present experiment may require a more persistent engagement of the limited capacity processing mechanism than is evident in other types of tasks. The fact that the task was unspeeded may have further facilitated the persistence of task effects across lead intervals.

A modest relationship between task performance and PPI was observed when the Letter 120 ms and Letter 240 ms lead intervals were examined at each of the 3-letter and 1-letter conditions. Analyses that compared low performers and high performers yielded a relationship showing better performance was associated with greater PPI at some of the lead intervals examined. These findings appear consistent with the mixed outcomes across previous studies. For instance, the accuracy of detecting a high or low tone prepulse has been shown to be associated with the level of PPI (Norris & Blumenthal, 1996). In contrast, there appears to be no association between the accuracy of detecting the duration of brief prepulses and the level of PPI (Elden & Flaten, 2002). It should be noted that the method of splitting the data into good and poor performers is limited in that this is a post hoc method that may not eliminate the possibility that good and poor performers differ on variables other than task performance (e.g., motivation, tiredness). A correlational analysis or one that

compared PPI on correct and incorrect trials may have been a more sensitive method to test the association between memory performance and PPI. However, such analyses were not possible due to the overall high level of performance. In addition to the differences observed between the low and high performance groups, inspection of the means shows that the effects of the letter condition were greatest at the 120 ms lead interval in the High Performers group and greatest at the 240 ms lead interval in the Low Performers group (see Table 1). This interaction may reflect that people who show good task performance have a fast and efficient mobilisation of the central processing mechanism for short-term consolidation. In contrast, the later lead interval of 240 ms at which the letter conditions differ most for the low performers suggests that their engagement of the short-term consolidation mechanism took longer.

A possible limitation of the present experiment was with the selection of the lead intervals. For instance, no lead interval earlier than 120 ms was used. Although prepulse inhibition with visual prepulses and auditory blink-eliciting stimuli tends to be maximal at around 120 to 180 ms (Neumann et al., 2004b), prepulse inhibition can occur at earlier lead intervals. Moreover, modulation of prepulse inhibition has been found at lead intervals earlier than 120 ms in a study employing the differential tone-duration-judgement task with task and not task trial types (Thorne et al., 2005) and a different type of selective attention task that also compared task versus no task conditions (Elden & Flaten, 2002). The question of whether the short-term consolidation of memory will modulate PPI at earlier lead intervals than that used in the present experiment remains for further research.

A second limitation with the lead intervals used was that the Letter 240 ms lead interval coincided with the offset of the letter and the onset of the mask. The use of a brief letter display followed by a mask was necessary in the present experiment

because the trial structure was designed to require participants to encode information into memory storage for later recall. This necessitated a brief exposure to the letter display followed by a pattern mask. The 240 ms letter display duration was selected based on the methods used by Jolicœur and Dell'Acqua (1998). Neumann et al. (2004b) used a no task procedure in which some acoustic blink-eliciting stimuli were presented at the onset of a visual prepulse. Significant blink facilitation was observed when the onset of the blink-eliciting stimulus and prepulse coincided. This contrasts to the present experiment in which significant blink inhibition at the Letter 240 ms lead interval was found in the 3-letter condition and non-differential blink modulation was found in the 1-letter condition. Some protective process thus appears to have persisted at the Letter 240 ms lead interval, despite this lead interval coinciding with the onset of the mask. Moreover, it is possible that the size of PPI was underestimated in the present experiment because the baseline presentations of the blink eliciting stimuli were presented during the intertrial intervals, a time at which the participants selective attention was not controlled (Hutchinson et al., 2003). Nevertheless, the onset of the mask at the Letter 240 ms lead interval did not influence the effects of the letter manipulation on short-term consolidation. The enhanced PPI following the 3-letter display relative to the 1-letter display was consistent across the Letter 120 ms lead interval and the Letter 240 ms lead interval (i.e., no interaction was found). Further research that systematically varies the duration of the letter display prior to the mask and/or lead intervals used may help to clarify the effects of the mask display onset on blink modulation in the present task.

In conclusion, the results shows that PPI can be modulated during a memory task that involves brief presentations of visual prepulses showing letters that must be remembered for later report. The findings extend the generality of PPI modulation to

a range of cognitive processes or tasks that involve something other than a discrimination between a task and no task condition. The greater PPI during the 3-letter display than during the 1-letter display is consistent with the notion that PPI is modulated by the short-term consolidation of information into durable memory storage, although differences in perceptual load may provide an alternative interpretation of the results. This interpretation, together with previous studies showing that selective attention to prepulses can also modulate PPI (e.g., Filion et al., 1994), is consistent with the notion that any process that requires limited capacity central processing mechanisms is capable of modulating PPI. The present findings are not necessarily contrary to the conceptualisation of PPI as an obligatory process that serves a sensorimotor gating function that protects the processing of the prepulse (Graham, 1992) if it is assumed that the engagement of a limited capacity central processing mechanism acts by increasing the activation of the protective mechanism (Blumenthal, 1999). In the case of the present experiment, a greater amount of information (e.g., 3 letters versus 1 letter) will require greater protection of processing from subsequent stimuli in order to encode the larger amount of information into durable memory storage.

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Table 1.

Comparison of prepulse inhibition at the Letter 120 ms and Letter 240 ms lead intervals in the 1-letter and 3-letter conditions for participants classified as Low Performers (n = 12) and High Performers (n = 12) on the memory task (standard deviations are in parentheses).

Letter Condition	Group	
	Low Performers	High Performers
1-Letter Condition		
Letter 120 ms	-27.53 (34.29)	-31.86 (25.54)
Letter 240 ms	0.40 (60.80)	-26.76 (26.17)
3-Letter Condition		
Letter 120 ms	-34.25 (32.15)	-53.93 (28.16)
Letter 240 ms	-35.03 (41.52)	-38.52 (30.52)

Figures

Figure 1. Representation of the structure of the trials for the memory task. The duration of each display is indicated above (“user” indicates that the display terminated following user input). The placements of the lead intervals are indicated following the letter (Letter 120 ms, Letter 240 ms) and mask (Mask 120 ms, Mask 240 ms, Mask 360 ms, Mask 2600 ms) displays. Please note that (a) the time intervals are not drawn to scale, (b) no more than one blink-eliciting stimulus could occur during the memory display on any one trial, and (c) intertrial interval probes were presented only following trials in which no blink-eliciting stimulus had been presented during the memory display and these occurred 7000 ms after the participant entered in a response for the memory task.

Figure 2. Mean percent blink magnitude change for each lead interval relative to the letter or mask display in the 1-letter and 3-letter conditions.