Startle Response and Prepulse Inhibition Modulation by Positive- and Negative-Induced Affect

Luis Gonzalo De la Casa, Auxiliadora Mena, and Andrea Puentes

Dpt. Experimental Psychology

Seville University (Spain)

Corresponding author:

Luis Gonzalo De la Casa

Dpt. Psicología Experimental

Facultad de Psicología

C/ Camilo José Cela, s/n

41018 Sevilla (Spain)

Tel. (34) 954557682 Fax: (34) 954551784

E-mail: delacasa@us.es

Abstract

The startle response, a set of reflex behaviours intended to prepare the organism to face a potentially threatening stimulus, can be modulated by several factors as, for example, changes in affective state, or previous presentation of a weak stimulus (a phenomenon termed Pre-Pulse Inhibition [PPI]). In this paper we analyse whether the induction of positive or negative affective states in the participants modulates the startle response and the PPI phenomenon. The results revealed a decrease of the startle response and an increase of the PPI effect when registered while the participants were exposed to pleasant images (Experiment 1), and an increase of the startle response and of the PPI effect when they were exposed to a video-clip of unpleasant content (Experiment 2). These data are interpreted considering that changes in affective states correlates with changes in the startle reflex intensity, but changes in PPI might be the result of an attentional process.

Key words: Startle, Prepulse Inhibition, Induced affect

1. Introduction

Every organism with a complex nervous system is continuously processing numerous stimuli that compose a changing world in order to get a successful adaptation to the environment. From all those stimuli, only a few are relevant to adaptation, either because they are biologically relevant for survival, or they are neutral stimuli that consistently predict relevant outcomes.

Thus, for instance, when a stimulus reaches a determined level of intensity it induces a startle reflex, a response to a possible immediate threat intended to prepare the organism to face the possible consequences of such stimulus (e.g., Dawson, Schell, Böhmelt, 1999; Eaton, 1984). Apparently, these reflex responses are fixed and appear in the same form when the intense stimulus is presented. However, a more detailed analysis reveals that startle responses change under different circumstances including repeated presentations (e.g., Geyer, & Braff, 1987; Sokolov, 1990), emotional changes (e.g., Bradley, Cuthbert, & Lang, 1999), or presentation of a weak stimulus that appears just before the more intense stimulus, a phenomenon termed Prepulse Inhibition (PPI) (e.g., Hoffman, & Searle, 1968; Graham, 1975). We will focus in this paper on the analysis of the modulation by positive and negative induced-affective states of the startle response to an intense auditory tone (see, for reviews, Bradley et al., 1999; Filion, Dawson, & Schell, 1998), and on the effect on PPI of the induction of such affective states (e.g., Hawk, & Cook, 2000).

Emotion has been often divided in two orthogonal factors, namely arousal and valence, both defined as a continuum that varies from calm to excitement and from positive to negative affect, respectively (Lang, Greenwald, Bradley, & Hamm, 1993). There is empirical evidence of a diminished startle

response to an intense stimulus when it is presented while the participants are being exposed to circumstances that favours a positive affect (e.g., Codispoti, Bradley, & Lang, 2001; Sutton, Davidson, Donzella, Irwin, & Dottl, 1997), an state associated with the presence of pleasant events that generate feelings of satisfaction and happiness (e.g., Isen, 1999). On the other hand, the startle intensity during the induction of a negative affect -an state that includes an ample variety of emotional states linked to the presence of unpleasant events that induce feelings of anxiety, fear, or anger, among others (e.g., Clark & Watson, 1988)- increased (e.g., Hawk, Stevenson, & Cook, 1992; Ehrlichman, Brown, Zhu, & Warrenburg, 1995). These effects have been observed, both in non-human animals and in humans, independently of the stimuli used to induce the emotional state (Bradley et al., 1999).

In a typical example of an experimental situation designed to modulate the startle reflex to an auditory stimuli by the induction of induced affects, Vrana, Spence & Lang (1988) programmed presentations of acoustic startle stimulus (95 db, 50-ms white noise bursts) while the participants were viewing images with positive (smiling children, sex nudes, food, etc.), negative (mutilated bodies, snakes, guns, etc.) or neutral affective value (common household objects). The results showed a significant increase of the startle response to an auditory stimulus when it was presented during the presentation of the aversive images, and an attenuation of the startle response when it was presented in presence of the positive images. When the images were neutral, the startle magnitude was of intermediate intensity. These results have been interpreted as a result of a motivational priming effect that combines the appetitive or aversive valence of the reflex, and the current affective state of the

individual (Lang, Bradley, & Cuthbert, 1990). Thus, when the reflexes related to appetitive situations (including approach, attachment or consummatory behaviours) are activated, their intensity will be increased when the organism is engaged in a positive emotional state. Similarly, those reflexes linked to aversive situations (including avoidance, escape or defensive behaviours) will tend to increase when the subject is involved in a negative emotion. The theory also proposes an interpretation of those situations in which there are no correspondence between the affective situation and the type of reflex, by considering that aversive reflexes will be attenuated with positive emotions, and appetitive reflexes will be attenuated with aversive emotions (e.g., Bradley et al., 1999).

As mentioned above, another mechanism that modulates startle response intensity is the PPI effect, which induces a significant reduction of the startle response to an intense stimulus (Pulse) by prior presentation of a less intense stimulus (Prepulse) (see, for a review, Swerdlow, Caine, Braff, & Geyer, 1992). PPI has been considered as an example of sensomotory gating, a process that blocks the processing of a stimulus in order to protect the processing of the stimulus that is already in progress (Braff & Geyer, 1990). Traditionally, PPI has been analysed in the framework of sensory and cognitive processes, while less attention has been paid to the role of affective factors.

In earlier studies analysing the effect of emotional variables on PPI positive, negative or neutral images were used as prepulses, while the pulses were auditory stimuli (Bradley, Cuthbert, & Lang, 1993; Vanman, Boehmelt, Dawson, and Schell, 1996). In some of the mentioned experiments, when the images used as prepulses were of aversive nature, PPI was reduced as

compared with those trials in which the images used as prepulses were positive or neutral. However, several factors compromise an interpretation in terms of PPI of these results, since using the same stimulus for the induction of emotional states and as the prepulse makes difficult to distinguish whether the modulatory effect is due to sensorimotor gating or to a merely affective process. Moreover, the use in the mentioned experiments of lead intervals between prepulses and pulses ranging between 250 and 4450 ms makes it difficult to draw valid conclusions for the standard phenomenon of PPI with auditory stimuli in which typical lead intervals between prepulse and pulse presentations range between 30 and 240 ms (Braff, Geyer, & Swerdlow, 2001).

More recent experiments using affective pictures as prepulses and shorter lead intervals (ranging from 200 to 300 ms) did not clarify the relationship between induced-affect and PPI, because they showed either the absence of PPI effect (Stanley & Knight, 2004), significant PPI (Deuter, Schilling, Kuehl, Blumenthal, & Schachinger, 2013), or even significant PPI when the images used as prepulses were of erotic nature, but the opposite effect (startle potentiation) when the images were threat scenes (Gard, Gard, Mehta, Kring, & Patrick, 2007).

On the other hand, those experiments that have used auditory stimuli both as pulses and prepulses, and induced the affective state of participants through an independent manipulation (e.g. featuring pictures of affective content) have not led either to conclusive results because, although the expected affective modulation of the startle response has been consistently observed, PPI remained intact (Hawk & Cook, 2000; Hawk, & Kowmas, 2003). However, the use of a within-subject procedure, in which the same subjects

received sequential presentations of blocks of positive, negative and neutral images, could be inducing interferences between the different affective states that could be masking their modulatory effect on PPI.

In this paper we analyse the effect of inducing positive or negative affects on startle magnitude and PPI using a between-subject procedure to avoid the influence of possible residual emotional effects that can be affecting the results with the within-subject procedures. The standard procedure used to detect PPI combine auditory pulse-alone trials presentations, that allow detection of the startle response magnitude, while other trials consists in a low-intensity auditory stimulus (Prepulse) preceding the pulse to induce PPI.

During startle response and PPI recording, participants were exposed to stimuli selected to induce positive or negative affective states (images in Experiment 1 and video clips in Experiment 2). From the experimental results described above we anticipate that the startle response to the pulse will increase for those participants in the negative affect condition, while it will decrease when exposed to the positive affect stimulation. With respect to the effect of affective states on the PPI, the hypotheses are less clear, because attending to previous experiments using standard auditory procedures to induce PPI there was no effect of positive- or negative-induced affects (e.g., Hawk & Cook, 2000; Hawk & Kowmas, 2003). Therefore, we do not anticipate any specific interaction between affective states and PPI, but we will consider the present experiment as an exploratory study intended to check the possible effect of different emotional states on sensorimotor gating.

2. EXPERIMENT 1

In our first experiment we used three sets of images of Positive (Pos), Negative (Neg), and Neutral (N) affective content selected from the International Affective Picture System (Lang, Ohman, & Vaitl, 1988). While the participants were exposed to the corresponding images they received the auditory stimuli intended to measure the startle response and the PPI effect. We used a between-subjects design in which each group was consistently exposed to a single category of affective stimuli (Pos, Neg, or N). In addition, in order to evaluate the subjective emotional state of the participants, we employed a scale designed for this purpose (Spanish version of PANAS, Joiner, Sandin, Chorot, Lostao, & Marquina, 1997).

2.1. Method

2.1.1. Participants

Thirty volunteers (n=10), 11 males and 19 females, participated in this experiment. Their ages ranged between 17 and 36 years. None of the participants reported any visual or hearing problem. All participants were informed of the type of stimulation used in the experiment, and provided signed informed consent before to start the experimental manipulations. Seville University's ethical committee approved the study.

2.1.2. Materials

2.1.2.1 Questionnaire

Levels of induced affect were assessed with a Spanish version of the Positive and Negative Affect Schedule (PANAS; Joiner et al., 1988). This

questionnaire is composed by 20 items, 10 each for the positive and negative scales, which can be rated on a scale from 1 (very slightly) to 5 (very much).

2.1.2.2. Affective stimuli

Three sets of 35 pictures each were selected form the IAPS to be presented for each of the induced affect condition[1]. The mean IAPS valence for the Pos, N and Neg set of pictures was 7.27, 5.14, and 2.79, respectively. Each image was presented for 5 seconds without any temporal interval between them, and the correspondent set of images was repeated three times in the same order to fit the entire duration of the experimental stage. Transition between images did not coincide with the occurrence of any auditory stimulus.

2.1.2.3. Prepulse and pulse stimuli

Acoustic stimuli were delivered binaurally using adjustable headphones (Sony model MDR-V50), connected to a MP150 control module (Biopac Systems Inc., Goleta, CA). The signal was sent with a high sampling rate of 50 kHz. The prepulse and the pulse stimulus consisted of a 75 dB (A) and 95 dB (A) broadband white noise with instantaneous rise time, lasting for 20 and 50 ms, respectively. A background noise (broadband white noise, 65 dB) was presented during the entire duration of the experiment. Sound calibration was completed prior to record data for each participant using a Sound Level Meter PCE-999.

2.1.3. Procedure

The experiment was conducted between 10:00 AM and 14:00 PM in an isolated room. Each participant was seated in front of a colour monitor (approximately 100 cm from the eyes) controlled by a PC-computer. For all auditory trials, the ITI was 30 s (+/- 5 s) and the lead interval in prepulse-pulse

trials was 100 ms. After a 120 s adaptation period to the background noise, four pulses and four prepulses were presented in order to establish the baseline response to the auditory stimuli. During this adaptation period, screens of solid colours changing every two seconds were presented in the computer's screen. Next, the test stage began consisting in 6 pulse-alone and 6 prepulse-pulse alternated trials presentation. The correspondent Pos, Neg, or N images were presented from the beginning of this stage. Immediately after the experiment ended, the earphones were removed, and each participant was instructed to answer the Spanish version of PANAS considering the affective state perceived during the experimental stage.

2.1.4. Physiological data collection

Electromyographic (EMG) activity of the orbicularis oculi muscle was recorded using three Ag/AgCl electrodes (EL250; Biopac Systems) positioned according to the guidelines recommended by Blumenthal, Cuthbert, Filion, Hackley, Lipp, and Van Boxtel (2005). Specifically, after cleaning the participant's skin, conductive gel was applied to the electrodes before placing two of them approximately 1 cm below the eye to record the electromyographic activity of the orbicularis oculi muscle. The third electrode was placed on the forehead to detect the general level of electrical activity. Raw signals were amplified (×2000) and filtered using a passband of 10–500 Hz (EMG100C amplifier; Biopac Systems). AcqKnowledge software (4.0, Biopac Systems) was used to interface a MP150 control module (Biopac Systems) via a cross-over cable and sampled at 2 kHz. Response onset latency windows include 21- 120 ms for acoustically elicited blinks.

2.2. Results.

2.2.1. Analysis of startle magnitude for pre-experimental stage

An inspection of startle response to prepulse-alone presentations during the pre-experimental stage revealed that there did not appear any measurable response. A 4 x 3 mixed ANOVA (Trials x Induced affect: Pos vs. N vs. Neg) conducted on mean startle magnitude to Pulse-alone presentations during the pre-experimental stage (prior to affective manipulations) revealed that neither the main effects nor the interaction was significant (all $ps > .27$). The lack of differences between groups in baseline startle to the Pulse is relevant because it reveals the absence of individual differences in absolute startle, differences that are common when registering blink magnitude (Blumenthal et al., 2005).

2.2.2. Analyses of PANAS scores

Figure 1 depicts mean Positive Affect (PA), and Negative Affect (NA) scores from PANAS for each induced affect condition. As can be seen in the figure, the scores corresponding to the PA were higher for the Pos Group. Conversely, the highest scores for the Neg Group corresponded to the NA score. Since PA and NA are orthogonal factors (Watson, Clark and Tellegen, 1988), that is consistent with the absence of correlation between the two set of data, $r(30) = 0.25$; $p > .17$, PA and NA scores were analysed separately. A One-way ANOVA conducted on PA scores with Induced affect as main factor revealed a significant effect, $F(2,27) = 3.79$; $p < .05$. Post-hoc comparisons between groups (Tukey, $p < .05$) revealed only significant higher scores for the Pos group as compared to the Neg group. A similar ANOVA on NA scores also revealed a significant effect, $F(2,27) = 6.17$; $p < .01$. Tukey post hoc tests ($p < .05$) revealed lower scores for Neg group as compared to Pos groups.

Figure 1 about here

2.2.3. Analysis of startle to the Pulse-alone trials

In order to identify a possible effect of the induced affect on startle to the Pulse, we analysed mean startle responses to the Pulse trials. The raw startle response (measured in µv) were converted into a T score distribution (mean of 50, standard deviation of 10) to control for the inter-individual variance in startle reactivity. As can be seen in the left section of Table 1, that depicts mean standardized startle responses to the Pulse collapsed across trials as a function of induced affect condition, the startle magnitude to the Pulse-alone trials was reduced in the Pos as compare to the Neg and N Groups.

Table 1 about here

These impressions were confirmed by a oneway ANOVA with Induced-affect (Positive vs. Neutral vs. Negative) as main factor that revealed a significant main effect of Induced-Affect, $F(2,27)=5.30$; $p<.05$. Pairwise comparisons based in our hypotheses (t-tests for independent samples, one-tailed) revealed a reduced startle magnitude to the Pulse-alone trials in the Pos as compared to the N and Neg Groups, $t(18)=2.09$; $p<.05$, and $t(18)=3.4$; $p<.01$. The difference between the Neg and N conditions was non-significant, $t(18)=1.29$; $p>.11$.

2.2.4. Analyses of percent PPI

Since several studies have suggested that percent PPI is less contaminated by individual differences than raw PPI (e.g., Hawk & Cook, 2000; Schwarzkopf, McCoy, Smith, & Boutros, 1993), mean startle magnitudes for pulse and prepulse-pulse trials were converted into percent PPI, calculated as 100 x (Average startle to the pulse – Average startle to the prepulse-pulse)/ Average startle to the pulse. The left section of Table 2 shows mean PPI percent collapsed across trials as a function of Induced affect Groups. As can be seen in the Table, PPI was increased in the Pos with respect to the N and the Neg Groups, but there were not differences between the N and Neg groups. These impressions were confirmed by the statistical analyses. A one-way ANOVA with induced affect as main factor conducted on mean percent PPI revealed a significant main effect of Induced affect, $F(2,27)=3.98$; $p<.05$. Comparisons between groups (t-tests for independent samples, two tailed) revealed significant higher PPI for Pos Group as compared to Neg Group, $t(18)=2.88$; $p<.01$. The difference between the Pos and N groups was close to the standard level of significance, $t(18)=1.95$; $p<.07$. No more differences were significant.

Table 2 about here

In summary, the results indicate that, as predicted, startle magnitude was reduced when the induced affective state was positive as compared to the negative affect condition. However, and contrary to our expectations, there were no differences in startle to the Pulse-alone trials in the Neg condition when

compared to the Neutral Group. Additionally, an enhanced PPI effect was observed in the positive condition.

3. EXPERIMENT 2

The results of Experiment 1 were somehow ambiguous: By one hand, startle magnitude was modulated by the induced affect when comparing Pos with N and Neg Groups, with lower responses in the Pos condition. However, there were no significant differences on startle magnitude when comparing Neg vs. N condition. On the other hand, and regarding the effect of the induced affect on PPI (measured as percent of startle reduction to Prepulse-pulse trials as compared to Pulse-alone trials), it was observed an increase in the Pos Group as compared to both the N and the Neg Groups.

It is possible that the selected aversive images did not were intense enough to induce strongest emotional effects that allow to discriminate from the neutral condition. Therefore, and to intensify the induced affects, in our next experiment we changed the emotion-inducing stimuli, replacing static images for video clips, a manipulation that in other areas has proven to be effective to induce strong affective states (e.g., Lazar, Kaplan, Sternberg, & Lubow, 2012).

The experimental design employed was similar to that described for Experiment 1, except for the change in the material presented to induce the different emotional states. Based on previous results and in the data obtained in our first experiment, we expected an increased startle response for the negative induced affect condition, and a reduction of the startle response in the positive condition. Regarding PPI, and attending to the results from Experiment 1, we expect an increase of the effect at least for the positive condition.

3.1. Method

3.1.1. Participants

Thirty volunteers (5 male and 25 female) participated in this experiment (n=10). All participants were students at Seville University (Spain), and their ages ranged between 17 and 21 years. None of the participants reported any visual or hearing problems. All participants were informed of the type of stimulation used in the experiment and provided signed informed consent. Seville University's ethical committee approved the research.

3.1.2. Materials

The questionnaire and the auditory stimuli were the same described for Experiment 1. However, in this experiment the material presented to induce the participants' affective states were custom designed video clips (that are available from L.G. De la Casa), instead of pictures from the IAPS. Each subject was instructed to attend to the material presented through a PC-computer controlled monitor. One third of the participants, assigned to the Positive (Pos) Group, were exposed to a selection of scenes from the "Ice age" movie, the second third, assigned to the Negative (Neg) Group, was exposed to a video clip including scenes selected from gore movies. Finally, the last third of participants, assigned to the Neutral (N) Group, was exposed to a video clip composed by screens of solid colour changing every two seconds over the entire duration of the experiment (Gross & Levenson, 1995).

3.1.3. Procedure.

The procedure was the same as described for the first experiment. Each participant was run individually, and was instructed to see a 5 min video clip, about which would be asked later. The video clip was running during the entire

duration of the experimental treatment. Finally, each subject responded to the Spanish version of the PANAS questionnaire (Joiner et al., 1977) to assess the effectiveness of the video clips in inducing the correspondent affect.

As in Experiment 1, during the first pre-experimental block of pulse- and prepulse-alone presentations all participants were exposed to screens of solid colours in order to maximize the novelty of the affective stimuli during the experimental trials.

3.1.4. Physiological data collection

Physiological data reduction and collection was similar to that described for Experiment 1.

3.2. Results

3.2.1. Analysis of startle at pre-experimental stage

An inspection of prepulse-alone presentations during the pre-experimental stage revealed that there did not elicit measurable responses. Startle responses to the Pulse during the pre-experimental trials were submitted to a 4 x 3 mixed ANOVA (Trials x Induced affect: Pos vs. N vs. Neg). Neither the main effects nor the interaction was significant (all $ps>.27$). These results suggest that there were no differences in startle reactivity between groups before the experimental manipulations.

3.2.2. Analyses of PANAS scores

Figure 2 depicts mean Positive Affect (PA), and Negative Affect (NA) scores from PANAS for each affect-induced condition. As can be seen in the Figure, there were no differences in PA scores following the positive affect video clip. However, the scores corresponding to the NA were higher following

the negative affect video clip. Since PA and NA are orthogonal factors (Watson et al., 1988), that is consistent with the absence of correlation between the two scores, $r[30]=-0.12$; $p>.54$, PA and NA were analysed separately. A One-way ANOVA conducted on PA scores with Groups as main factor revealed no significant effect of video clips, $F(2,27)=1.41$; $p>.26$. A similar ANOVA on NA scores revealed a significant effect of video clips, $F(2,27)=13.65$; $p<.001$. Tukey post hoc tests ($p<.05$) revealed a higher score for the Neg as compared to the Pos and N groups. The difference between the N and Pos groups was non-significant.

From these results we can anticipate that the video clip selected to induce the positive affect was not effective, because of the absence of differences between groups in the PA scores from PANAS.

Figure 2 about here

3.2.3. Analysis of startle to the Pulse-alone trials

Table 1 (right section) depicts mean standardized (*T* scores) startle response magnitude to the Pulse-alone stimulus (collapsed across trials) as a function of induced affect. As can be seen in the table, the startle magnitude to the Pulse-alone trials was higher for the Neg as compared to the Pos and N groups. These impressions were confirmed by the statistical analysis. Specifically, a oneway ANOVA with the main factor Induced-affect (Positive vs. Neutral vs. Negative) revealed a marginal effect, $F(2,27)=2.70$; $p<.09$. Pairwise comparisons (t-tests for independent samples, one-tailed) based in our hypotheses comparing startle magnitude to the Pulse-alone trials revealed an

increase in startle response when comparing the Neg vs. Pos, and the Neg vs. N conditions, $t(18)=1.77$, $p<.05$, and $t(18)=2.09$, $p<.05$, respectively. There were no differences in startle magnitude between the Pos and N conditions, $t(18)<1$.

3.2.4. Analysis of percent PPI

As in Experiment 1, in order to obtain a less contaminated index of PPI, raw startle responses were transformed into percent PPI for each pulse and prepulse-pulse trial using the formula: 100 x (Average startle to the pulse – Average startle to the prepulse-pulse)/ Average startle to the pulse. A one-way ANOVA with induced affect as main factor conducted on mean percent PPI showed a significant effect of Induced affect, $F(2,27)=4.27$; $p<.05$. As shown in the right section of Table 2, mean percent PPI increased for the Neg Group, but remained intact for the Pos Group. Accordingly, comparisons between groups (t-test for independent samples, two tailed) revealed significant differences between Neg vs. Pos, and between Neg vs. N conditions, $t(18)=3.06$; $p<.01$, and $t(18)=2.45$; $p<.05$, respectively. There were no differences between the Pos and N conditions, $t(18)<1$.

4. General Discussion.

The modulation of the startle response to the Pulse-alone trials observed in the Pos condition (Experiment 1) and Neg condition (Experiment 2) as compared to the neutral groups confirmed previous evidence indicating that the induction of a positive affect results in a decrease of the startle magnitude to a stimulus of moderate intensity, while the induction of a negative emotional state produces the opposite effect, namely an increase in the startle response (see, for reviews, Bradley et al., 1999; Filion et al, 1998). Although there were a lack

of effect when startle magnitude in the Pos and Neg conditions were compared with the N Group scores, an inspection of the startle magnitude to the Pulse-alone trials for the Pos and Neg Groups in Experiments 1 and 2 reveals that the experimental results were consistent, with mean startle magnitudes closed to 45 for the Pos groups, and to 55 for the Neg groups in both experiments (see Table 1). As mentioned in the introduction, Lang and his colleagues (e.g., Lang, 1995; Lang et al., 1990) interpreted these effects by framing them in an ample emotional theory that considers the emotions as actions dispositions that are biologically connected to reflex behaviour, with a basic dimension that goes from appetitive to aversive. In our case, the startle response was increased in the negative-induced affect condition because both the reflex and the emotional state were linked to an aversive situation and to an aversive emotion, respectively. On the other hand, the reduction of the startle reflex to the pulse-alone trials observed in the positive-induced affect condition is justified from the lack of correspondence between the reflex and the emotional state dimensions (aversive and appetitive, respectively).

Regarding the effect of the affective manipulations on PPI, the experimental results revealed that both positive-induced and negative-induced affect increased percent PPI. However, the effect of positive affect was limited to those participants exposed to the pleasant images (Experiment 1), and the negative affect to those participants exposed to the unpleasant film clip (Experiment 2). The lack of differences when analysing percent PPI between Neg and N groups for Experiment 1, and between Pos and N conditions in Experiment 2 can be interpreted in retrospect as the result of a combination of the use of a between-subject procedure, that increases the variability between

groups, and the inadequacy of the video clip selected to induce the positive affect.

The increase of percent PPI for the positive-induced affect condition (Experiment 1), and for the negative-induced affect condition (Experiment 2) contrasts with previous research on this topic using a typical auditory procedure to induce PPI, that did not reveal any effect of affective modulation on PPI (Hawk & Cook, 2000; Hawk, & Kowmas, 2003). The use of a between-subject procedure, in spite of the problems derived from the increase of variability, could have contributed to reveal the differential effects we found in the reported experiments by eliminating the interference between induced affects that is more likely to affect to the participants in experiments using within-subject designs.

The reported results represents, to our knowledge, the first demonstration of direct modulation of PPI by an emotional factor using a standard procedure with auditory stimuli to induce the PPI effect. However, and admittedly speculative since we did not manipulate explicitly attention to the stimuli, it is possible to consider an alternative interpretation to this result in terms of attentional modulation, by considering the relationships between affect and attentional modulation (e.g., Fredrickson, 2001).

More specifically, and starting from a psychophysiological perspective, there is empirical evidence that shows that induction of both positive affective states (e.g., Isen, 2002) and exposure to aversive events (e.g., Young A.M., Joseph M.H., & Gray J. A. 1993) produces the release of neurotransmitters such as dopamine. Thus, for instance, Mak, Hu, Zhan, Xiao and Lee (2009) identified an increase in dopaminergic activation in the dorsolateral prefrontal

cortex as a result of the presentation of positive affective images, and Abercrombie, Keefe, DiFrischia, and Zigmond (1989) reported an increase in dopamine activity in striatum, nucleus accumbens, and medial frontal cortex when rats were exposed to intermittent tail-shock stress.

Considering that dopamine plays an important role in the regulation of attentional processing (e.g., Ashby, Isen, & Turken, 1999; Nieoullon, 2002), and that increasing attention to the prepulse increase PPI (e.g., Elden, & Flaten, 2002; Dawson, Hazlett, Filion, Nuechterlein, & Schell, 1993; Thorne, Dawson, & Schell, 2005), the observed reduction of PPI during the induction of a positive (Experiment 1) or negative (Experiment 2) affect could be interpreted as the result of an enhancement of attention to the prepulse. Such increased attention could have produced the reduction of the startle response as compared to that observed in the neutral condition. Therefore, the reported PPI increase could be related to a general attentional change induced by the affective state, or even to changes in arousal (e.g., De Oca, Villa, Cervantes, & Welbourne, 2012; McConnell & Shore, 2011), instead to an emotional-induced effect.

Finally, the reported data are also relevant because they can contribute to the understanding of startle and PPI modulation as a function of clinical pathologies. Thus, it has been reported deficits in PPI in schizophrenia patients (e.g., Braff, Swerdlow, & Geyer, 1999; Braff, Geyer, Light, Sprock, Perry, Cadenhead, & Swerdlow, 2001), in obsessive-compulsive patients (Hoenig, Hochrein, Quednow, and Wagner, 2005), in panic disorder patients (Ludewig, Geyer, Ramseier, Vollenweider, Rechsteiner, & Cattapan-Ludewig, 2005), or in bipolar disorder patients (Perry, Minassian, Feifel, and Braff, 2001). All mentioned psychopathologies are characterized for the presence of strong

affective components that, attending to our experimental results, could be affecting both to the startle magnitude and to the PPI effect. Thus, an additional source of control for the effects of affective states of the participants in the experiments, especially when such participants are affected by some kind of psychopathology, could come from getting independent measures of the participant´s affective states.

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Footnotes.

[1] IAPS picture numbers used in this study were: POSITIVE: 1019, 1111, 1112, 1274, 1280, 2095, 2692, 2694, 2710, 2717, 2730, 2751, 2900, 3000, 3069, 4621, 6242, 6244, 6311, 6555, 6561, 6562, 6831, 6940, 9120, 9340, 9409, 9417, 9423, 9426, 9428, 9570, 9594, 9429; NEGATIVE: 1340, 1463, 1603, 1722, 1750, 1920, 1999, 2071, 2165, 2209, 2224, 2303, 2311, 2344, 2345, 2352, 2530, 4532, 4601, 4614, 4624, 4640, 4641, 5270, 5450, 5480, 5721, 5760, 5833, 7220, 7230, 7270, 7330, 7430, 7508; NEUTRAL: 2580, 7000, 7009, 7025, 7055, 7059, 7100, 7150, 7175, 7180, 7185, 7187, 7190, 7192, 7211, 7224, 7235, 7236, 7247, 7248, 7490, 7491, 7545, 7546, 7547, 7550, 7705, 7950.

Correspondence concerning this article should be addressed to L. Gonzalo De la Casa, Dpt. of Experimental Psychology, Seville University, C/ Camilo Jose Cela, s/n. 41018 Sevilla (Spain). E-mail: delacasa@us.es

Table 1: Mean standardized startle magnitude and standard Deviations (between brackets) for Pulse-alone collapsed across trials as a function of induced affect condition for Experiment 1 (left section), and Experiment 2 (right section).

	EXPERIMENT 1	EXPERIMENT 2
Positive	43.49 (3.81)	47.48 (9.6)
Neutral	50.25 (9.49)	46.86 (7.41)
Negative	56.27 (11.26)	55.66 (11.02)

Table 2: Mean percent PPI and standard deviations (between brackets) collapsed across trials as a function of induced affect condition for Experiment 1 (left section), and Experiment 2 (right section).

	EXPERIMENT 1	**EXPERIMENT 2**
Positive	67.47% (19.28)	36.01% (21.70)
Neutral	47.06% (26.96)	33.49% (33.08)
Negative	35.86% (28.89)	62.93% (17.47)

Figure legends.

Figure 1: Mean Negative Affect scores (left panel) and Positive Affect scores (right panel) as a function of type of affect-induction set of images (Neg: Negative, N: Neutral, or Pos: Positive). Error bars represent SEMs.

Figure 2: Mean Negative Affect scores (left panel) and Positive Affect scores (right panel) as a function of type of affect-induction video clip (Neg: Negative, N: Neutral, or Pos: Positive). Error bars represent SEMs.
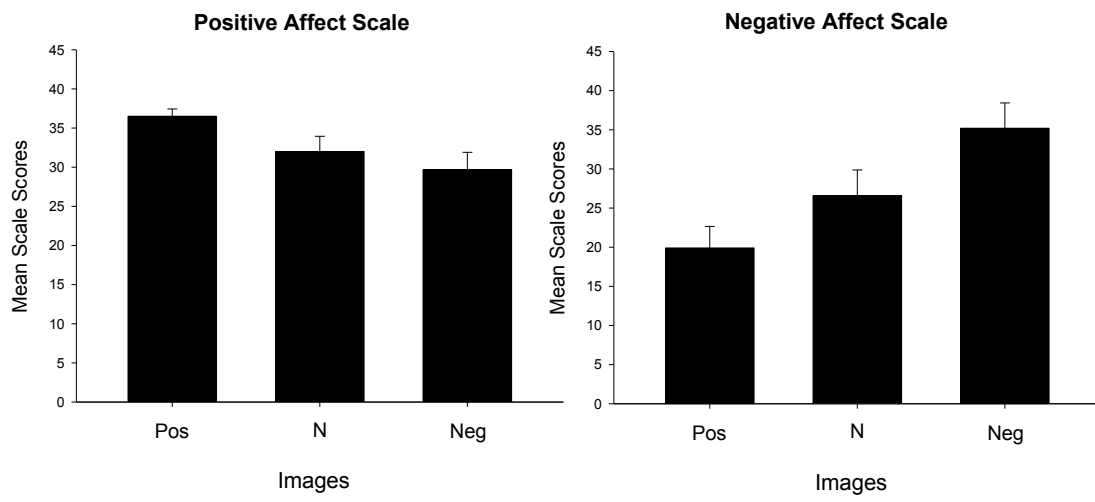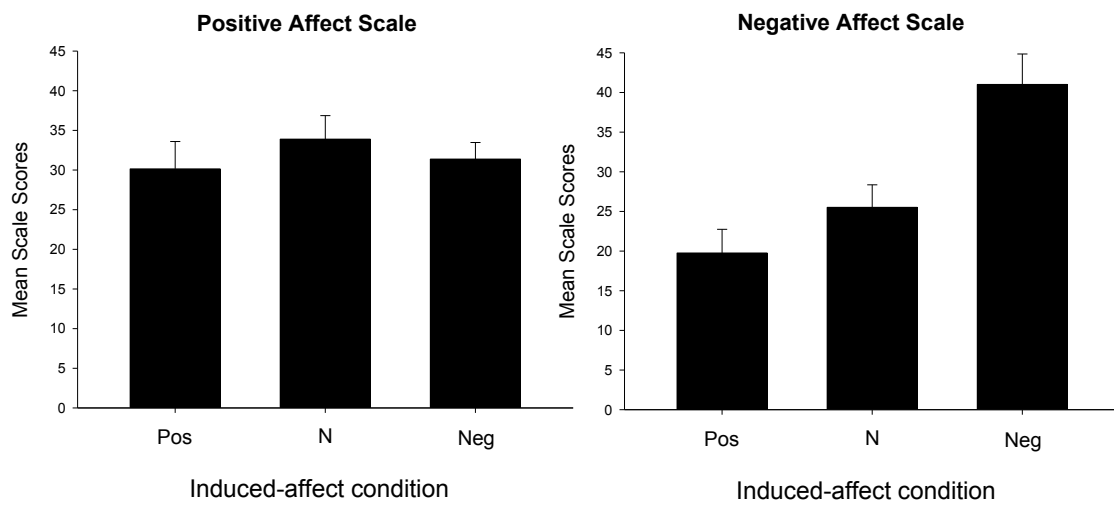
Figure 1.

Figure 2.