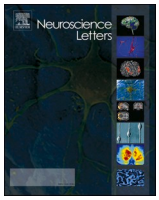
Neuroscience Letters 824 (2024) 137673

Contents lists available at ScienceDirect

Neuroscience Letters

journal homepage: www.elsevier.com/locate/neulet



Research article

Affective processing in dysphoria: Evidence from startle probe modulation of ERPs

Carola Dell'Acqua [a,*], Roza Mejza [a], Simone Messerotti Benvenuti [a,b,c]

[a] Department of General Psychology, University of Padua, Padua, Italy
[b] Padova Neuroscience Center (PNC), University of Padua, Padua, Italy
[c] Hospital Psychology Unit, Padua University Hospital, Padua, Italy

ARTICLE INFO

Keywords:
Depression
Dysphoria
Emotion
N200
P300
Startle

ABSTRACT

The hypoactivation of the appetitive and defensive motivational systems in the brain is a feature of depression and might also represent a vulnerability factor for the disorder. A measure that can be employed to investigate both motivational systems is the electroencephalographic response to an acoustic startle probe during affective processing. Particularly, the amplitude of auditory event-related potentials (ERPs) components to the startle probe is smaller when the emotional context is more arousing. Neural responses to an unattended startle probe during an emotional passive viewing task of pleasant, neutral, and unpleasant pictures was employed to assess the activation of the approach and defensive motivational systems in a sample of individuals with (n = 24, 23 females) vs. without (n = 24, 23 females) dysphoria. The group without dysphoria showed a reduced startle-elicited N200 only in the context of pleasant relative to neutral pictures, indicating that the affective processing of the appetitive context might reduce the attentional resources needed to orient attention toward unattended non-salient stimuli. Conversely, the N200 amplitude was not attenuated for pleasant relative to neutral and unpleasant contexts in the group with dysphoria. Moreover, no within- or between-group differences emerged in the P300 amplitude. Taken together, the results of this study showed that depression vulnerability is characterized by reduced attention to pleasant contexts, suggesting a blunted affective processing of appetitive emotional stimuli.

1. Introduction

Given the pervasive and debilitating nature of Major Depressive Disorder (MDD), identifying early indicators of this condition and putting forward novel prevention strategies has been set as a core priority [1]. Hence, researchers are shifting their focus to the study of vulnerable populations, namely individuals with a higher risk of developing depression but without current depressive symptoms. In this regard, the study of individuals with dysphoria (i.e., subclinical depression), characterized by the presence of depressive symptoms without meeting a formal MDD diagnosis, is particularly advantageous as it constitutes a risk for the onset of full-blown depression [2].

Individual differences in the activation of the approach and withdrawal motivational systems during emotional processing have been identified as key features of depression and represent a potential mechanism of depression vulnerability [3–10]. Over the decades, depression has been linked to distinct patterns of emotional reactivity, and three main hypotheses have been put forward [10–11]. An initial account is the negative potentiation hypothesis, which holds that pervasive negative mood states that are prevalent in depression contribute to potentiate emotional responding to negatively valenced stimuli, indicating a heightened activation of the withdrawal motivational system [12–14]. However, the literature does not fully support this view [3,9–11,15]. Moreover, there appears to be consistent support for the positive attenuation hypothesis, which suggests that depression is characterized by a reduction of approach motivation, aligning with symptoms of anhedonia and apathy [10,16]. This last hypothesis has been extended to a third one, known as Emotional Context Insensitivity (ECI), which suggests that depression might be characterized by an overall attenuated response to emotional stimuli regardless of their valence [17]. The ECI is based on evolutionary theories that describe depression as the product of environmental disengagement [9,10], which is manifested through decreased responses to both pleasant and unpleasant stimuli.

* Corresponding author at: Department of General Psychology, University of Padua, Via Venezia, 8, 35131 Padua, Italy.
E-mail address: carola.dellacqua@unipd.it (C. Dell'Acqua).

https://doi.org/10.1016/j.neulet.2024.137673
Received 11 December 2023; Received in revised form 9 January 2024; Accepted 3 February 2024
Available online 10 February 2024

A widely employed method that can be used to study affective disposition is the passive viewing of affective pictures while peripheral and central psychophysiological responses are assessed [18–20]. These studies have often relied on startle paradigms, whereby a startle-eliciting irrelevant auditory stimulus (e.g., loud white noise) is presented in a series of non-startling stimuli (i.e., emotional pictures) [19,21]. The presentation of a brief intense acoustic probe elicits the startle eyeblink reflex, which is modulated by the hedonic valence. Namely, the startle eyeblink amplitude is potentiated when participants view negatively valenced stimuli and inhibited when viewing pleasant cues [20]. Depressive symptoms have been associated with an attenuated startle reflex amplitude in response to unpleasant stimuli, indicating a potential hypoactivation of the defensive motivation system [22–25]. In addition, several studies have further shown a reduced inhibition of the startle eyeblink reflex amplitude to pleasant stimuli in depression [23,26,27], suggesting, in line with the ECI account, an overall blunted reactivity to all emotional cues.

In addition to the startle eyeblink, unattended auditory startling probes prompt a modulatory effect of emotional states during information processing of emotional cues at the neural level [28–30]. Considering that the real-world environment is typically characterized by numerous stimuli that compete for attentional resources, the degree to which the perceptual processing of emotional stimuli is prioritized (relative to unattended stimuli) is of interest in the study of affective processing [28]. In this context, given that event-related potentials (ERPs) have distinct temporal and topographic characteristics, each component is thought to reflect a different stage or aspect of information processing [19,31,32]. Hence, the assessment of ERPs can reveal the modulation in the processing of an unattended auditory startle probe while participants view emotionally valenced pictures. Intriguingly, the neural response to the startle probe is mainly modulated by the arousal elicited by the emotional stimulus, whereby the amplitude of auditory ERPs components to the startle probe is smaller when the emotional context is more arousing (both pleasant and unpleasant). In other words, the presence of emotionally arousing pictures increases the threshold for processing irrelevant auditory events in the environment, leading to having fewer resources to process the startle probe than when viewing neutral cues. Particularly, this effect has been demonstrated for both earlier (i.e., N200) and later components (i.e., P300), suggesting that it might involve both automatic detection of changes in the auditory stream and higher-level stages of attention processing [19,31–33]. To date, electroencephalographic responses to an acoustic startle probe during the viewing of emotional cues in depression have not been fully explored. Only one investigation showed that reduced startle-elicited P300 component across all emotional and non-emotional conditions significantly correlated with depressive symptoms [34].

The objective of the present study was to explore electroencephalographic responses to an unattended startle probe during an emotional passive viewing task of pleasant, neutral, and unpleasant pictures to assess the activation of the approach and defensive motivational systems in a sample of individuals with an elevated risk to develop full-blown depression, namely with dysphoria (i.e., subclinical depression). In line with the ECI account, the group with dysphoria was expected to show a hypoactivation of the approach and withdrawal motivational systems, indexed by greater amplitude of the N200 and P300 components to the acoustic startle probe, when viewing both pleasant and unpleasant relative to neutral pictures and to the group without dysphoria.

2. Methods

2.1. Participants

Based on meta-analytic evidence supporting the emotion context insensitivity hypothesis in depression [9], a priori power analysis in G*Power [35] for a repeated measures analysis of variance with one within-subject factor with three levels (picture valence: pleasant, neutral, unpleasant) and one between-subject factor with two levels (with dysphoria vs. without dysphoria) was performed to determine whether the sample size was large enough to detect a significant effect. This analysis revealed that the adequate total sample size to detect a moderate effect size (Cohen's $f = 0.26$) with a power of 0.95 was 40 participants. In the present study, a cohort of 48 Caucasian students at the University of Padua, Italy, voluntarily took part in the research project.

An *ad-hoc* anamnestic interview was employed to make sure that the included participants were medically healthy and not taking any psychotropic medication. In the sample, participants were assigned to either a group with dysphoria or without dysphoria based on specific criteria. Participants with dysphoria were identified by module A of the Structured Clinical Interview for DSM-5 (SCID 5-CV; [36,37]) assessing current and past depressive symptoms. Furthermore, the Beck Depression Inventory-II (BDI-II; [38,39]) was also employed for the assessment of depressive symptoms' severity. Participants who both scored equal to or greater than 12 on the BDI-II and had two to four current depressive symptoms, for at least two weeks, without meeting the criteria for the diagnosis of major depressive disorder, persistent depressive disorder, or bipolar disorder, were assigned to the group with dysphoria ($n = 24$, 23 females). Participants who scored equal to or lower than 8 on the BDI-II and had no depressive symptoms or history of depression, were assigned to the group without dysphoria (i.e., controls) ($n = 24$, 23 females).[1] To ensure a clear separation between the two groups, participants who scored in the range between 9 and 11 on the BDI-II or had only one depressive symptom have not been included in the study.

With respect to demographic variables, the two groups (with dysphoria, without dysphoria) did not differ in terms of sex ($x^2 = 9.5$, $p = .98$), age ($p = .83$; dysphoria group: Mean (M) = 21.9, standard deviation (SD) = 2.2; group without dysphoria: M = 22.0, SD = 1.9), and education ($p = .52$; dysphoria group: M = 16.3, SD = 1.7; group without dysphoria: M = 16.5, SD = 1.3).

2.2. Psychological measures

Participants underwent a psychological assessment composed of both the SCID-5-CV and BDI-II. The Italian version of module A (mood episode module) of the SCID-5-CV was administered by a trained clinical psychologist in order to assess the presence of dysphoria. Additionally, the diagnostic interview served as a tool to identify participants with major depressive disorder, persistent depressive disorder, or bipolar disorder and thereby exclude them from the study. All participants also completed the BDI-II, which is a reliable self-report measure used to assess the severity of the depressive symptoms present in the last two weeks. The aforementioned questionnaire is composed of 21 questions, each scored on a four-point Likert scale. The final score of the inventory ranges between 0 and 63, where more severe depressive symptoms are demonstrated with a higher score. In the Italian version of the BDI-II employed, the score of 12 was agreed to serve as a discriminant between individuals with and without depressive symptoms [39].

2.3. Experimental task

The experimental paradigm included 24 color pictures (600 × 800 pixels) from the International Affective Picture System (IAPS, [40]) each category: pleasant (e.g., erotic couples, sports), neutral (e.g., household objects, neutral faces), and unpleasant (e.g., attacking humans and animals), all of which were presented to the participants once. The pleasant and unpleasant pictures were matched for normative arousal

[1] All statistical analyses were performed after excluding two male participants from the dataset. Upon their exclusion, the observed results remained consistent and unaffected.

ratings (p =.92).[2]

The experimental paradigm was a passive viewing task of pictures, presented for 6000 ms each, in a semi-randomized manner (i.e., no more than one stimulus in the same emotional condition had to be shown consecutively). A 3000 ms interval with a white fixation cross on a grey background (baseline), preceded each picture display. Participants were instructed to focus on the fixation cross to ensure proper processing of the chosen stimuli. After each picture presentation, an intertrial interval (ITI) with a white fixation cross (like in the baseline) was presented for a time that varied between 6000 and 8000 ms. The acoustic startle probe was administered randomly at one of the four time points after picture onset: 300, 1500, 3500, or 4500 ms. However, for this investigation, only the startle probe administered at 1500 ms or later was considered in the analysis as the primary focus of the study was on affective processing, and no prior study employed startle-elicited ERPs at earlier stages of picture processing (e, g., 300 ms). Hence, a total of 18 stimuli for each emotional category were used, that is, six for each time point (1500 ms, 3500 ms, 4500 ms). The acoustic startle stimulus, used in the paradigm, was a burst of 100 dB white noise with a duration of 50 ms (instantaneous rise time), which was conveyed to both ears through Sennheiser headphones (HD 280 Pro model). Fig. 1 graphically illustrates the procedure of the employed task.

2.4. EEG recording and data reduction

The recording of EEG data was conducted with an elastic cap containing 32 Ag/AgCl electrodes arranged in a 10–20 system (Fp1, Fpz, Fp2, F7, F3, Fz, F4, F8, FC5, FC1, FC2, FC6, T7, C3, Cz, C4, T8, CP5, CP1, CP2, CP6, P7, P3, Pz, PA, P8, POz, O1, Oz, O2, and mastoids: M1, M2) and referenced online to CPz. Eye movements and eye blinks were monitored through a bipolar montage of horizontal and vertical electrooculograms (EOG). During the EEG recording, the impedance of all electrodes was kept lower than 10 kΩ. The eego software and eego amplifier (ANT Neuro, Enschede, Netherlands) have been used for the data acquisition. Post-amplification, the EEG and EOG signals were bandpass filtered (0.3–40 Hz) and digitalized at 1000 Hz.

EEG preprocessing was conducted in EEGLAB and Brainstorm. The EEG signal was re-referenced offline to mastoids to remove the electric noise captured by the ground electrode (online reference). To reduce the computational costs the EEG signal was downsampled at 500 Hz, in accordance with the Nyquist theorem. Then, a 0.3–30 Hz bandpass filter was applied. Additionally, blink artifacts and horizontal eye movements were manually corrected using the Independent component analysis (ICA). For each trial, the EEG was epoched starting 500 ms before the startle probe and continuing for 2000 ms. Trials exceeding ±70 μV were rejected, leading to an average of ±SD acceptance of 17.8 ± 0.5 pleasant trials, 17.8 ± 0.5 neutral trials, and 17.8 ± 0.5 unpleasant trials. No significant differences between groups or among emotional conditions in the average acceptance of pleasant, neutral and unpleasant trials were observed (all $Ps > .24$). The baseline for each epoch corresponded to the 200 ms recorded 50 ms prior to the onset of the startle probe. The ERPs were computed as an average activity at all three times of startle probe administration (1500, 3500, 4500 ms) since all are part of the late processing stages where affective processing occurs. The separate grand averages ERPs were calculated for each group (with dysphoria and without dysphoria), and condition (pleasant, neutral, and unpleasant), producing a total of three different ERP averages for each group (Fig. 2).

[2] The IAPS picture numbers were 1050, 1114, 1120, 1300, 1302, 1930, 1932, 3500, 4611, 4647, 4651, 4652, 4660, 4664, 4670, 4680, 4683, 4690, 4695, 4810, 6200, 6210, 6230, 6242, 6243, 6244, 6250, 6260, 6312, 6313, 6370, 6510, 6540, 6550, 6560, 7000, 7002, 7004, 7009, 7010, 7020, 7035, 7036, 7041, 7050, 7056, 7059, 7130, 7175, 7224, 7233, 7242, 7491, 7500, 7547, 7560, 7595, 7700, 7950, 8030, 8031, 8034, 8080, 8161, 8180, 8185, 8186, 8200, 8370, 8400, 8490, 9425.

Based on visual inspection of grandaveraged ERP waveforms, the N200 was computed as the mean amplitude in the 200–300 ms time window from startle probe onset, and the P300 as the mean amplitude in the 300–500 ms time window from startle probe onset, both at Cz. In this study, the electromyography of the *orbicularis oculi* muscle to assess the startle reflex and the electrocardiogram (ECG) to assess cardiac deceleration were collected and results can be found in a previously published work [22], while neural responses to the emotional images have been reported in another published work [4].

2.5. Procedure

Prior to the experimental session, the participants were instructed to avoid the consumption of caffeine or alcohol on that day. Upon arriving in the laboratory each participant signed a written consent form and was later administered module A of the SCID-5-CV interview and the BDI-II. Subsequently, each individual was asked to sit comfortably in the assigned chair, positioned in a dimly lit and sound-attenuated room. After electrodes attachment and a three-minute resting state condition, six practice trials were presented to the participants, two of each category (pleasant, neutral, and unpleasant). Afterward, the participants underwent the passive emotional viewing task while EEG was recorded. Finally, participants completed the assessment of arousal and valence of 36 pictures (12 in each category) using the Self-Assessment Manikin (SAM) [41]. Results of the SAM have already been reported in a previous publication and showed adequate affective manipulation [22]. The entire procedure, including the final debriefing of the participants, lasted a total of 90 min.

2.6. Statistical analyses

Distributions of all ERP variables were checked on normality with QQ plots and the Shapiro-Wilk test. The three time points of the acoustic startle probe administration (1500, 3500, and 4500 ms) were averaged and collapsed into one single condition, due to the occurrence of the same underlying mechanism (i.e., affective processing). Both N200 and P300 responses to the startle probe were analyzed using a repeated measure analysis of variance (ANOVA) with Group (with dysphoria and without dysphoria) as a between-subject factor and Condition (pleasant, neutral, and unpleasant) as a within-subject factor. The ANOVAs for the N200 and P300 amplitudes and peaks were conducted separately. Significant main effects and interactions (p <.05) were reported and a Tukey post-hoc test was carried out to inspect significant effects.

3. Results

3.1. N200 component

The N200 data were normally distributed, as assessed using the Shapiro-Wilk test (all $ps > .13$). For the N200, the mixed ANOVA revealed a significant Condition main effect ($F = 4.42$, p =.02), which was further qualified by a Group × Condition interaction effect ($F = 3.95$, p =.02, Fig. 3).[3] Particularly, the N200 amplitude to the startle probe in the pleasant condition was smaller as compared to the neutral one (p <.001), while it did not differ from the unpleasant condition (p =.47). Also, the N200 amplitude to the startle probe in the neutral and unpleasant condition did not differ from each other (p =.48). On the other hand, in the group with dysphoria, the post-hoc tests did not yield to any significant difference in the N200 amplitude to the startle probe among all emotional conditions (all $Ps > .82$). The N200 response to the startle probe did not differ between the two groups in any condition (all $Ps > .70$). Finally, no significant Group effect emerged ($F = 0.55$, p

[3] The results did not change when excluding the two male participants (Group × Condition interaction effect, $F = 3.94$, p =.04).

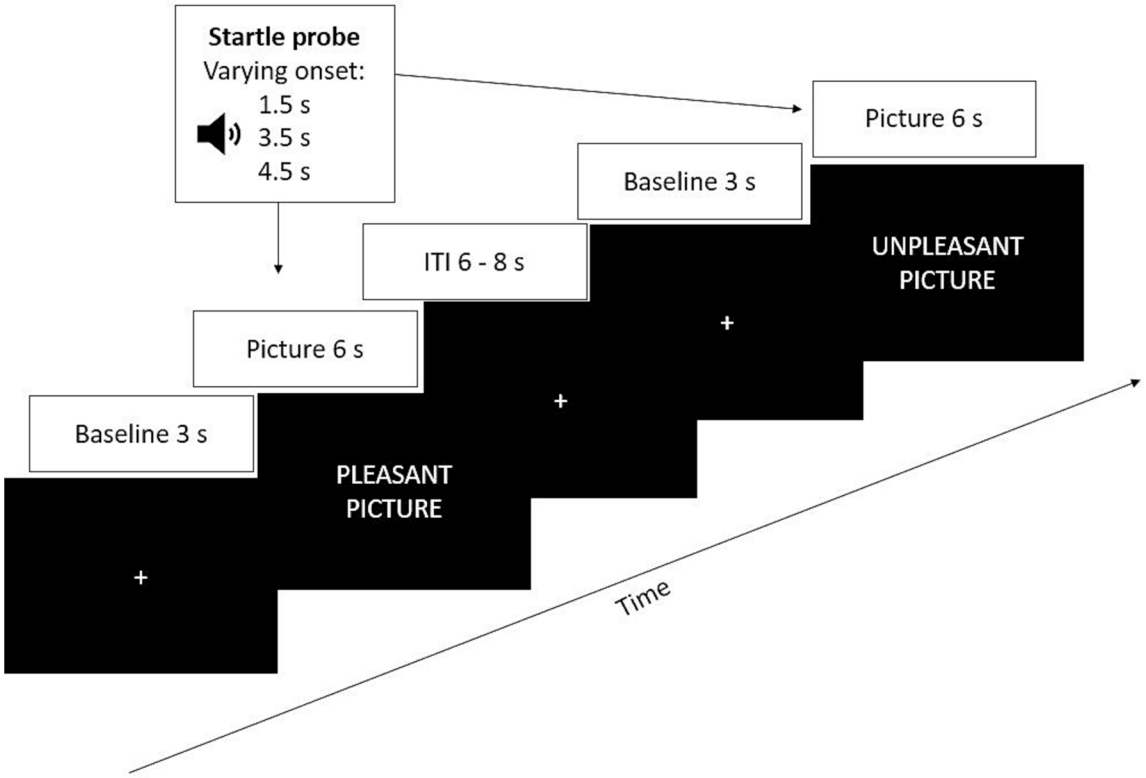


Fig. 1. Illustration of the passive viewing task with the acoustic startle probe.

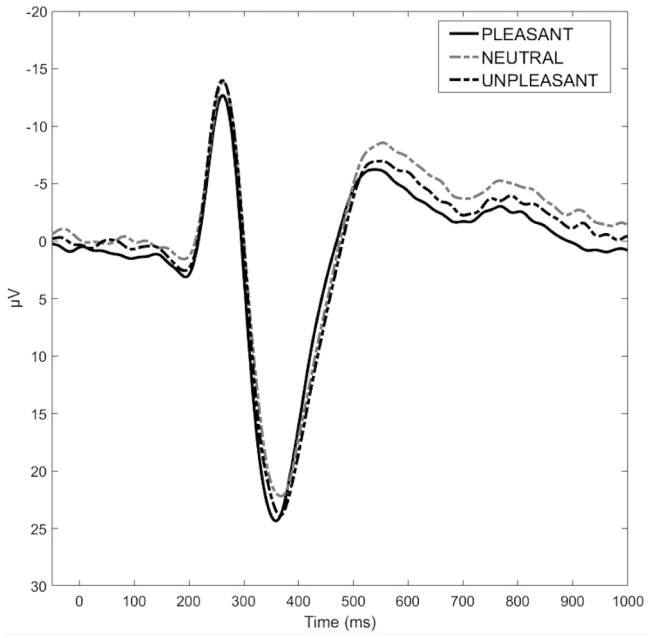


Fig. 2. Grandaverage ERP amplitude (μV) to the startle probe in the whole sample during pleasant (black solid line), neutral (grey dotted line), and unpleasant (black dotted line) picture processing.

=.46).

3.2. The P300 component

The P300 data were normally distributed, as assessed using the Shapiro-Wilk test (all *ps* > .38). For the P300, the mixed ANOVA revealed a marginally significant Condition effect ($F = 3.02$, $p = .05$),[4] whereby the amplitude of the P300 in the unpleasant condition was larger than in the neutral condition. No Group effect ($F = 0.158$, $p = .70$), and no Condition × Group effect ($F = 1.21$, $p = .30$) emerged.

4. Discussion

The objective of the present study was to explore neural responses to an unattended startle probe during an emotional passive viewing task of pleasant, neutral, and unpleasant pictures to assess the activation of the approach and defensive motivational systems in a sample of individuals with dysphoria. The group with dysphoria was expected to show a hypoactivation of the approach and withdrawal motivational systems, indexed by greater amplitude of the N200 and P300 components to the acoustic startle probe, when viewing both pleasant and unpleasant relative to neutral pictures and to the group without dysphoria.

Partially in line with the hypothesis, the group without dysphoria showed a reduced startle-elicited N200 only in the context of pleasant relative to neutral pictures, indicating that the affective processing of the appetitive context might reduce the need for auditory change detection. Although the affective modulation of the startle-elicited N200 was previously documented during the viewing of both pleasant and unpleasant images, some studies have documented this effect exclusively in pleasant conditions [30,42]. These results suggest that in an arousing pleasant – but not unpleasant – condition, the automatic

[4] The results did not change when excluding the two male participants (Condition effect, $F = 2.74$, $p = .07$).

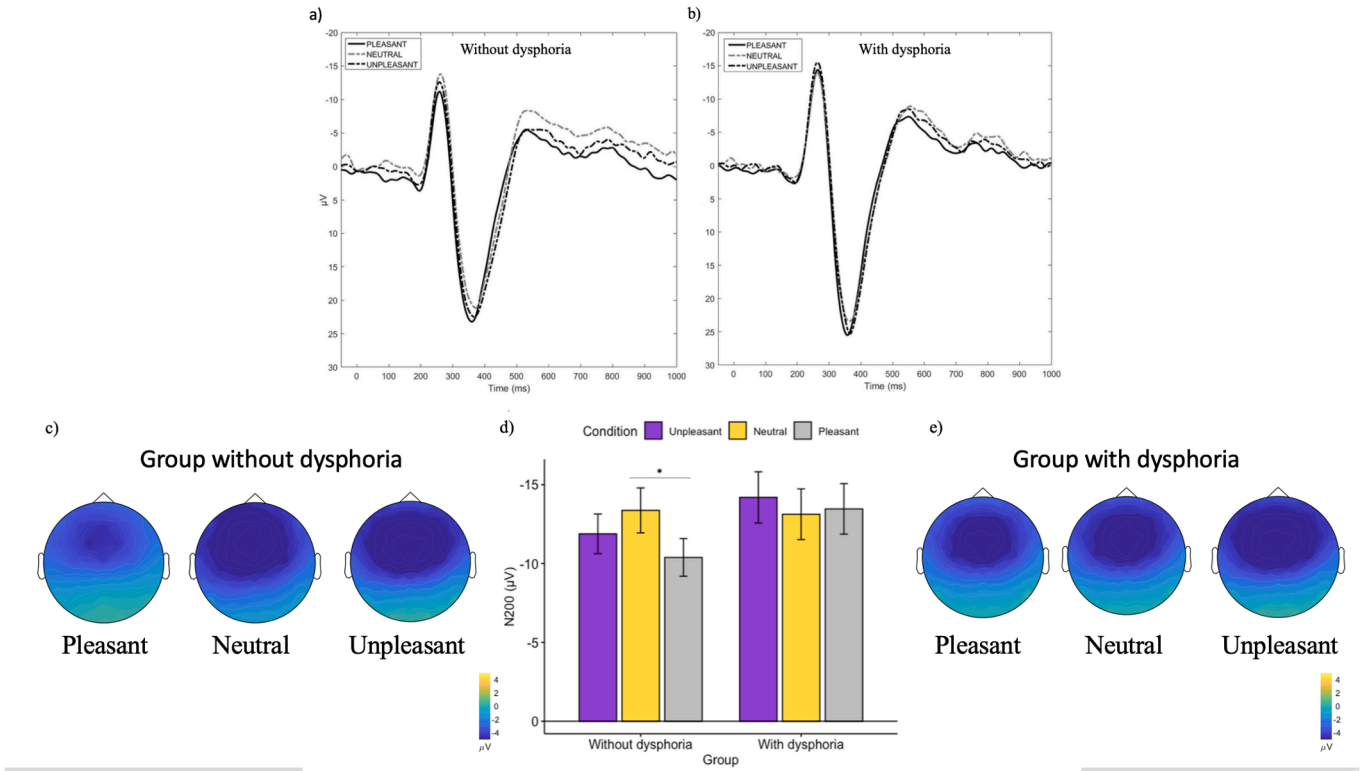


Fig. 3. Panels a) and b): Grandaverage ERP amplitude (μV) to the startle probe in the whole sample during pleasant (black solid line), neutral (grey dotted line), and unpleasant (black dotted line) picture processing in the group without dysphoria (Panel a) and the group with dysphoria (Panel b). Panels c) and e): Topography of the mean ERP amplitude (μV) of individuals without (panel c) and with dysphoria (panel e) averaged over the N200 time window (200–300 ms) for pleasant, neutral, and unpleasant conditions. Panel d): Mean amplitude (μV) of the startle-elicited N200 component during the viewing of unpleasant (purple), neutral (yellow), and pleasant (grey) pictures in the group without dysphoria (left) and with dysphoria (right). * p <.05.

detection of changes in the environment might be inhibited [30,42]. Indeed, arousing pleasant stimuli serve as biological signals for a non-threatening environment, thus inhibiting automatic perceptual detection changes [30,42]. Of note, the startle-elicited N200 was not attenuated for pleasant relative to neutral and unpleasant pictures in the group with dysphoria. Hence, this at-risk group was not characterized by enhanced affective processing of the pleasant relative to neutral images, which in turn did not influence the early detection mechanism of the auditory stimulus. Taken together, these findings should be extended to longitudinal designs to determine whether a reduction in the brain's ability to process and respond to pleasant contexts in the environment can be an indicator of depression risk, as suggested by several studies in the literature [4,8–11,43,44].

Moreover, in both groups, the amplitude of the startle-elicited P300 was not attenuated in the pleasant and unpleasant relative to neutral conditions and no group difference emerged. Instead, a marginally significant larger P300 amplitude to the startle probe while viewing unpleasant pictures emerged across both groups. In line with this, a study showed that the P300 amplitude was larger, and not smaller, to an irrelevant sound when participants were watching negatively valenced videoclips, suggesting that whenever a situation is unpleasant, the automatic monitoring of the background environment for potential threats might increase [33].

From a clinical perspective, startle-elicited N200 might be integrated in the identification and prevention protocols of individuals with a higher risk of developing full-blown depression. Indeed, the significance of ERPs as potential novel screening measures was recently highlighted [45]. Besides, regarding potential therapeutic interventions to bolster startle-elicited N200, attention bias modification procedures aimed at increasing attention towards pleasant content, widely employed in clinical depression, might be used as a preventive strategy in dysphoria [46–49].

Some limitations of this study need to be acknowledged. Firstly, the sample of participants consisted entirely of university students, which might affect the generalization of these findings to the general population. Additionally, due to the higher prevalence of dysphoria in the female population [2], the great majority of the participants in this study belonged to the female sex, which further limits the generalizability of this work's findings to the male population.

Taken together, the results of this study demonstrated that individuals with dysphoria might be characterized by greater attention to an auditory startle probe presented during pleasant contexts, suggesting a blunted affective processing of pleasant emotional stimuli, in line with the positive attenuation hypothesis. The paradigm of startle modulation of ERPs may serve as a valuable measure of early identification as well as prevention of full-blown clinical depression.

Role of the funding source

The study was supported by a grant from MIUR (Dipartimenti di Eccellenza DM 11/05/2017 No 262) to the Department of General Psychology, University of Padua. Simone Messerotti Benvenuti's work was supported by the University of Padua under the 2019 STARS Grants programme (Acronym and title of the project: A-CAOS-BIRD - Asymmetries and Connectivity in Alpha OScillations: toward Biomarkers of Intergenerational Risk for Depression).

Author contributions

C.D.A. and S.M.B. conceived and designed the study; C.D.A. and S.M.B. conducted the study; C.D.A, S.M.B. and R.M. analyzed the data; C.D.A., S.M.B. and R.M. wrote the paper, and all authors reviewed the

manuscript.

CRediT authorship contribution statement

Carola Dell'Acqua: Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Data curation, Conceptualization. **Roza Mejza:** Writing – original draft, Methodology, Formal analysis. **Simone Messerotti Benvenuti:** Writing – review & editing, Writing – original draft, Supervision, Software, Resources, Project administration, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

The authors are very grateful to the participants who took part in this study.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neulet.2024.137673.

References

[1] Q. Liu, H. He, J. Yang, X. Feng, F. Zhao, J. Lyu, Changes in the global burden of depression from 1990 to 2017: findings from the Global Burden of Disease study, J. Psychiatr. Res. 126 (2020) 134–140, https://doi.org/10.1016/j.jpsychires.2019.08.002.
[2] M.R. Rodríguez, R. Nuevo, S. Chatterji, J.L. Ayuso-Mateos, Definitions and factors associated with subthreshold depressive conditions: a systematic review, BMC Psychiatry 12 (2012) 1–7.
[3] S. Messerotti Benvenuti, R. Mennella, G. Buodo, D. Palomba, Dysphoria is associated with reduced cardiac vagal withdrawal during the imagery of pleasant scripts: Evidence for the positive attenuation hypothesis, Biol. Psychol. 106 (2015) 28–38, https://doi.org/10.1016/j.biopsycho.2014.11.017.
[4] S. Messerotti Benvenuti, G. Buodo, R. Mennella, E. Dal Bò, D. Palomba, Appetitive and aversive motivation in depression: The temporal dynamics of task-elicited asymmetries in alpha oscillations, Sci. Rep. 9 (2019), https://doi.org/10.1038/s41598-019-53639-8.
[5] C. Dell'Acqua, et al., Reduced electrocortical responses to pleasant pictures in depression: A brief report on time-domain and time-frequency delta analyses, Biol. Psychol. 170 (2022), https://doi.org/10.1016/j.biopsycho.2022.108302.
[6] C. Dell'Acqua, D. Palomba, E. Patron, S. Messerotti Benvenuti, Rethinking the risk for depression using the RDoC: A psychophysiological perspective, Front. Psychol. 14 (2023), https://doi.org/10.3389/fpsyg.2023.1108275.
[7] T. Moretta, S. Messerotti Benvenuti, Familial risk for depression is associated with reduced P300 and late positive potential to affective stimuli and prolonged cardiac deceleration to unpleasant stimuli, Sci. Rep. (2023), https://doi.org/10.1038/s41598-023-33534-z.
[8] C. Dell'Acqua, E. Dal Bò, T. Moretta, D. Palomba, S. Messerotti Benvenuti, EEG time–frequency analysis reveals blunted tendency to approach and increased processing of unpleasant stimuli in dysphoria, Sci. Rep. 12 (2022), https://doi.org/10.1038/s41598-022-12263-9.
[9] L.M. Bylsma, B.H. Morris, J. Rottenberg, A meta-analysis of emotional reactivity in major depressive disorder, Clin. Psychol. Rev. 28 (2008) 676–691, https://doi.org/10.1016/j.cpr.2007.10.001.
[10] L.M. Bylsma, Emotion context insensitivity in depression: Toward an integrated and contextualized approach, Psychophysiology 58 (2021), https://doi.org/10.1111/psyp.13715.
[11] J. Rottenberg, J.J. Gross, I.H. Gotlib, Emotion context insensitivity in major depressive disorder, J. Abnorm. Psychol. 114 (2005) 627–639, https://doi.org/10.1037/0021-843X.114.4.627.
[12] J.E. Beeney, K.N. Levy, L.M. Gatzke-Kopp, M.N. Hallquist, EEG asymmetry in borderline personality disorder and depression following rejection, PD:TRT 5 (2014) 178–185, https://doi.org/10.1037/per0000032.
[13] E.W. Cook III, T.L. Davis, L.W. Hawk, E.L. Spence, C.H. Gautier, Fearfulness and startle potentiation during aversive visual stimuli, Psychophysiology 29 (1992) 633–645, https://doi.org/10.1111/j.1469-8986.1992.tb02038.x.
[14] S.T. Sigmon, R.O. Nelson-Gray, Sensitivity to aversive events in depression: Antecedent, concomitant, or consequent?, J. Psychopathol. Behav. Assess. 14 (1999225–246. https://doi.org/10.1007/BF00962630.
[15] R. Mennella, S. Messerotti Benvenuti, G. Buodo, D. Palomba, Emotional modulation of alpha asymmetry in dysphoria: Results from an emotional imagery task, Int. J. Psychophysiol. 97 (2015) 113–119, https://doi.org/10.1016/j.ijpsycho.2015.05.013.
[16] K.E. Hill, S.C. South, R.P. Egan, D. Foti, Abnormal emotional reactivity in depression: Contrasting theoretical models using neurophysiological data, Biol. Psychol. 141 (2019) 35–43, https://doi.org/10.1016/j.biopsycho.2018.12.011.
[17] J. Rottenberg, Mood and emotion in major depression, Curr. Dir. Psychol. Sci. 14 (2005) 167–170, https://doi.org/10.1111/j.0963-7214.2005.00354.x.
[18] H.T. Schupp, B.N. Cuthbert, M.M. Bradley, N. Birbaumer, P.J. Lang, Probe P3 and blinks: Two measures of affective startle modulation', Psychophysiology 34 (1997) 1–6, https://doi.org/10.1111/j.1469-8986.1997.tb02409.x.
[19] B.N. Cuthbert, H.T. Schupp, M. Bradley, M. McManis, P.J. Lang, Probing affective pictures: Attended startle and tone probes, Psychophysiology 35 (1998) 344–347, https://doi.org/10.1017/S0048577298970536.
[20] M.M. Bradley, M. Codispoti, B.N. Cuthbert, P.J. Lang, Emotion and motivation I: defensive and appetitive reactions in picture processing, Emotion 1 (2001) 276–298, https://doi.org/10.1037/1528-3542.1.3.276.
[21] D.L. Filion, M.E. Dawson, A.M. Schell, The psychological significance of human startle eyeblink modification: a review, Biol. Psychol. 47 (1998) 1–43, https://doi.org/10.1016/S0301-0511(97)00020-3.
[22] S. Messerotti Benvenuti, G. Buodo, E. Dal Bò, D. Palomba, Attention and affect in dysphoria: Insights from startle reflex modulation and cardiac deceleration, Behav. Res. Ther. 131 (2020), https://doi.org/10.1016/j.brat.2020.103626.
[23] M. Mneimne, W. McDermut, A.S. Powers, Affective ratings and startle modulation in people with nonclinical depression, Emotion 8 (2008) 552–559, https://doi.org/10.1037/a0012827.
[24] H. Kaviani, J.A. Gray, S.A. Checkley, P.W. Raven, G.D. Wilson, V. Kumari, Affective modulation of the startle response in depression: influence of the severity of depression, anhedonia, and anxiety, J. Affect. Disord. 83 (2004) 21–31, https://doi.org/10.1016/j.jad.2004.04.007.
[25] N.B. Allen, J. Trinder, C. Brennan, Affective startle modulation in clinical depression: preliminary findings, Biol. Psychiatry 46 (1999) 542–550.
[26] G.S. Dichter, A.J. Tomarken, The chronometry of affective startle modulation in unipolar depression, J. Abnorm. Psychol. 117 (2008) 1–15, https://doi.org/10.1037/0021-843X.117.1.1.
[27] L. Boecker, P. Pauli, Affective startle modulation and psychopathology: Implications for appetitive and defensive brain systems, Neurosci. Biobehav. Rev. 103 (2019) 230–266, https://doi.org/10.1016/j.neubiorev.2019.05.019.
[28] H.T. Schupp, J. Stockburger, F. Bublatzky, M. Junghöfer, A.I. Weike, A.O. Hamm, The selective processing of emotional visual stimuli while detecting auditory targets: An ERP analysis, Brain Res. 1230 (2008) 168–176, https://doi.org/10.1016/j.brainres.2008.07.024.
[29] C. Herbert, J. Kissler, M. Junghöfer, P. Peyk, B. Rockstroh, Processing of emotional adjectives: Evidence from startle EMG and ERPs, Psychophysiology 43 (2006) 197–206, https://doi.org/10.1111/j.1469-8986.2006.00385.x.
[30] V. Surakka, M. Tenhunen-Eskelinen, J.K. Hietanen, M. Sams, Modulation of human auditory information processing by emotional visual stimuli', Cogn. Brain Res. 7 (1998) 159–163, https://doi.org/10.1016/S0926-6410(98)00021-4.
[31] A. Keil, M.M. Bradley, M. Junghöfer, T. Russmann, W. Lowenthal, P.J. Lang, Cross-modal attention capture by affective stimuli: evidence from event-related potentials, Cogn. Affect. Behav. Neurosci. 7 (2007) 18–24, https://doi.org/10.3758/CABN.7.1.18.
[32] H.T. Schupp, B.N. Cuthbert, M.M. Bradley, N. Birbaumer, P.J. Lang, Probe P3 and blinks: two measures of affective startle modulation, Psychophysiology 34 (1997) 1–6, https://doi.org/10.1111/j.1469-8986.1997.tb02409.x.
[33] B. Gulotta, G. Sadia, E. Sussman, Emotional processing modulates attentional capture of irrelevant sound input in adolescents, Int. J. Psychophysiol. 88 (2013) 40–46, https://doi.org/10.1016/j.ijpsycho.2013.01.003.
[34] P.J. Lang, et al., The startle-evoked potential: negative affect and severity of pathology in anxiety/mood disorders, Biol. Psychiatry Cogn. Neurosci. Neuroimaging 3 (2018) 626–634, https://doi.org/10.1016/J.BPSC.2017.07.006.
[35] E. Erdfelder, A. Buchner, GPOWER: A general power analysis program, Behav. Res Methods 28 (1996) 1–11, https://doi.org/10.3758/BF03203630.
[36] M. B. First, J. B. W. Williams, R. S. Karg, R. L. Spitzer, SCID-5-CV Intervista Clinica Strutturata per i Disturbi del DSM-5 In Versione Per Il Clinico, Italiana a cura Di Andrea Fossati e Serena Borroni Raffaello Cortina Editore Milano, 2017.
[37] M.B. First, J.B.W. Williams, R.S. Karg, R.L. Spitzer, User's guide for the SCID-5-CV Structured Clinical Interview for DSM-5® disorders: Clinical version, American Psychiatric Publishing Inc, Arlington, VA, US, 2016.
[38] A.T. Beck, R.A. Steer, G.K. Brown, Beck depression inventory, Harcourt Brace Jovanovich New York, 1987.
[39] C. Sica, M. Ghisi, The Italian versions of the Beck Anxiety Inventory and the Beck Depression Inventory-II: Psychometric properties and discriminant power, in: Leading-Edge Psychological Tests and Testing Research, Nova Science Publishers, Hauppauge, NY, US, 2007, pp. 27–50.
[40] P.J. Lang, et al., International Affective Picture System (IAPS), Technical Manual and Affective Ratings (1997).

[41] M.M. Bradley, P.J. Lang, Measuring emotion: The self-assessment manikin and the semantic differential, J. Behav. Ther. Exp. Psychiatry 25 (1994) 49–59, https://doi.org/10.1016/0005-7916(94)90063-9.
[42] S. Sugimoto, H. Nittono, T. Hori, Visual emotional context modulates brain potentials elicited by unattended tones, Int. J. Psychophysiol. 66 (2007) 1–9, https://doi.org/10.1016/j.ijpsycho.2007.05.007.
[43] J.N. Bress, D. Foti, R. Kotov, D.N. Klein, G. Hajcak, Blunted neural response to rewards prospectively predicts depression in adolescent girls, Psychophysiology 50 (2013) 74–81, https://doi.org/10.1111/j.1469-8986.2012.01485.x.
[44] P. Ethridge, C. Freeman, A. Sandre, I. Banica, M.A. Dirks, A. Weinberg, Intergenerational transmission of depression risk: Mothers' neural response to reward and history of depression are associated with daughters' neural response to reward across adolescence, J. Abnorm. Psychol. 131 (2021) 598–610, https://doi.org/10.1037/abn0000662.
[45] G. Hajcak, J. Klawohn, A. Meyer, The utility of event-related potentials in clinical psychology, Annu. Rev. Clin. Psychol. 15 (2019) 71–95, https://doi.org/10.1146/annurev-clinpsy-050718-095457.
[46] R. Jonassen, et al., Effects of attentional bias modification on residual symptoms in depression: a randomized controlled trial, BMC Psychiatry 19 (2019) 1–8, https://doi.org/10.1186/s12888-019-2105-8.
[47] Q. Dai, L. Hu, Z. Feng, Attentional bias modification reduces clinical depression and enhances attention toward happiness, J. Psychiatr. Res. 109 (2019) 145–155, https://doi.org/10.1016/j.jpsychires.2018.11.024.
[48] E.L. De Voogd, et al., Online attentional bias modification training targeting anxiety and depression in unselected adolescents: Short-and long-term effects of a randomized controlled trial, Behav. Res. Ther. 87 (2016) 11–22, https://doi.org/10.1016/j.brat.2016.08.018.
[49] T.T. Wells, C.G. Beevers, Biased attention and dysphoria: Manipulating selective attention reduces subsequent depressive symptoms, Cogn. Emot. 24 (2010) 719–728, https://doi.org/10.1080/02699930802652388.