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Emotion lies in the eye of the listener: Emotional arousal to novel sounds is reflected in the sympathetic contribution to the pupil dilation response and the P3

Andreas Widmann[a,*], Erich Schröger[a], Nicole Wetzel[b,c]

[a] Cognitive and Biological Psychology, Institute of Psychology, University of Leipzig, Germany
[b] CBBS Research Group Neurocognitive Development, Leibniz Institute for Neurobiology, Magdeburg, Germany
[c] Center for Behavioral Brain Sciences Magdeburg, Germany

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ABSTRACT

Novel sounds in the auditory oddball paradigm elicit a biphasic dilation of the pupil (PDR) and P3a as well as novelty P3 event-related potentials (ERPs). The biphasic PDR has been hypothesized to reflect the relaxation of the iris sphincter muscle due to parasympathetic inhibition and the constriction of the iris dilator muscle due to sympathetic activation. We measured the PDR and the P3 to neutral and to emotionally arousing negative novels in dark and moderate lighting conditions. By means of principal component analysis (PCA) of the PDR data we extracted two components: the early one was absent in darkness and, thus, presumably reflects parasympathetic inhibition, whereas the late component occurred in darkness and light and presumably reflects sympathetic activation. Importantly, only this sympathetic late component was enhanced for emotionally arousing (as compared to neutral) sounds supporting the hypothesis that emotional arousal specifically activates the sympathetic nervous system. In the ERPs we observed P3a and novelty P3 in response to novel sounds. Both components were enhanced for emotionally arousing (as compared to neutral) novels. Our results demonstrate that sympathetic and parasympathetic contributions to the PDR can be separated and link emotional arousal to sympathetic nervous system activation.

1. Introduction

The pupil diameter is controlled by both autonomic nervous systems via two muscles. The ring-shaped iris sphincter muscle is innervated by the parasympathetic nervous system while the radial iris dilator muscle is innervated by the sympathetic nervous system (Einhäuser, 2017; McDougal & Gamlin, 2008). Both nervous systems closely couple the pupil to the locus coeruleus-norepinephrine (LC-NE) system (via an inhibitory projection to the Edinger-Westphal nucleus in case of the parasympathetic system). The LC-NE system is a neuromodulatory system that is central for various functions, in particular attention, emotion, motivation, decision making, and memory (Aston-Jones & Cohen, 2005; Murphy, O'Connell, O'Sullivan, Robertson, & Balsters, 2014; Murphy, Robertson, Balsters, & O'Connell, 2011; Preuschoff, 't Hart, & Einhäuser, 2011; for review see, Laeng, Sirois, & Gredebäck, 2012; Einhäuser, 2017). The LC-NE system shows a phasic activation in response to task-relevant, salient, or arousing stimuli (for review see e.g., Sara & Bouret, 2012). Rare or novel events presented within a sequence of frequently repeated standard events (the oddball paradigm) do elicit a pupil dilation response (PDR; Friedman, Hakerem, Sutton, & Fleiss, 1973; Hochmann & Papeo, 2014; Liao, Kidani, Yoneya, Kashino, & Furukawa, 2016; Liao, Yoneya, Kidani, Kashino, & Furukawa, 2016; Murphy et al., 2014; Murphy et al., 2011; Qiyuan, Richer, Wagoner, & Beatty, 1985; Steinhauer & Hakerem, 1992; Wetzel, Buttelmann, Schieler, & Widmann, 2016).

Independently from sounds' novelty, the PDR has also been shown to be highly sensitive to emotional arousal. For example, Partala and Surakka (2003) reported enhanced PDRs in response to sounds with positive or negative valence compared to neutral sounds. Also in the visual modality, Bradley, Miccoli, Escrig, and Lang (2008) observed larger pupil dilation responses for pleasant and unpleasant emotionally arousing pictures compared to emotionally neutral pictures. In their study Bradley and colleagues observed a co-variation of the PDR and skin conductance changes but no co-variation of PDR and cardiac deceleration. Based on this indirect evidence Bradley et al. (2008) suggested that the emotion-related PDR effects are supposed to be specific for sympathetic nervous system activity. However, this has not yet been directly shown on the basis of the PDR itself. Both nervous systems

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* Corresponding author at: Institute of Psychology, University of Leipzig, Neumarkt 9-19, D-04109 Leipzig, Germany.
E-mail address: widmann@uni-leipzig.de (A. Widmann).

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antagonistically contribute to the observed pupil dilation: relaxation of the iris sphincter muscle by parasympathetic inhibition and constriction of the iris dilator muscle by sympathetic activation. Attempts to non-invasively dissociate their contributions have not yet been successful (Einhäuser, 2017). The possibility to separate the differential contributions of the parasympathetic and sympathetic nervous systems to the PDR is therefore of high relevance.

Frequently, the observed pupil dilation in response to rare events is biphasic and it has been suggested that the two peaks reflect the overlapping contributions of the sphincter muscle relaxation by parasympathetic inhibition and of the dilator muscle constriction by sympathetic activation (Steinhauer & Hakerem, 1992). Steinhauer and Hakerem (1992) hypothesized that overlapping sympathetic and parasympathetic contributions should be separable by means of factor analysis. A biphasic response to several environmental distractor sounds was also observed in infants and adults (Wetzel et al., 2016). Two main components were extracted using a principal component analysis (PCA), however, the attribution of components to changes in parasympathetic and sympathetic activity remained unclear. A PCA was also applied to pupillary data by Geuter, Gamer, Onat, and Büchel (2014). The components were, however, not related to pupil physiology but used to predict pain ratings by a regression based approach. Together with their original hypothesis Steinhauer and Hakerem (1992) already suggested a possible validation of this attribution by variation of lighting conditions: the parasympathetic tone, but not sympathetic tone, is minimal in darkness (Loewenfeld, 1958; and the sphincter muscle maximally relaxed). Thus, in darkness, a component related to parasympathetic inhibition should be reduced in comparison to bright lighting conditions, while a component related to sympathetic activation is not supposed to be modulated by lighting conditions. The contributions of the parasympathetic and the sympathetic pathway to pupil dilation during sustained processing have already been successfully separated by the variation of ambient lighting as well as by pharmacological manipulations (Steinhauer, Siegle, Condray, & Pless, 2004). However, for the phasic PDR observed in response to rare (sound) events the separation of the contributions of parasympathetic inhibition and sympathetic activation by means of factor analysis or PCA including a validation by lighting conditions has – to our knowledge – not yet been empirically tested.

Also the P3-family of event-related potential (ERP) responses associated with processes of attention and memory (for review see, e.g., Alho, Escera, & Schröger, 2003; Polich, 2007) has been suggested to be related to LC-NE system activity. More specifically, a current theory postulates that P3 and the autonomic component of the orienting response do reflect the co-activation of the locus coeruleus-norepinephrine (LC-NE) system and the peripheral sympathetic nervous system (SNS; Nieuwenhuis, De Geus, & Aston-Jones, 2011). The P3a subcomponent is elicited by unexpected stimuli that violate a regularity previously built up on the basis of the sensory input. Similar to the PDR, the P3a can be elicited by salient, arousing, rare, novel, or task-relevant events presented amongst regular standard stimuli in an oddball paradigm. In response to novel stimuli frequently a double peaked P3 component was observed and reported in the literature as P3a and novelty P3 (Barry, Steiner, & De Blasio, 2016; Friedman, Cycowicz, & Gaeta, 2001) or early and late P3a (Escera, Alho, Winkler, & Näätänen, 1998; Yago, Escera, Alho, Giard, & Serra-Grabulosa, 2003). P3a (early P3a) and novelty P3 (late P3a) are supposed to indicate orienting of attention and enhanced evaluation of significant or novel stimuli (Alho et al., 2003; Polich, 2007).

The P3a component has been shown to be enhanced or modulated in response to emotional compared to neutral auditory (Pakarinen et al., 2014; Thierry & Roberts, 2007; but also see, Czigler, Cox, Gyimesi, & Horvath, 2007, not finding an effect) and visual stimuli (e.g., Keil et al., 2002) indicating stronger orienting of attention. Also the P3b and the late positive/slow wave components have been reported to be sensitive to emotionally arousing stimuli (Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000; Delplanque, Silvert, Hot, Rigoulot, & Sequeira, 2006; Delplanque, Silvert, Hot, & Sequeira, 2005; Foti, Hajcak, & Dien, 2009; Keil et al., 2002; for review see e.g., Bradley, Keil, & Lang, 2012). If emotional arousal modulates sympathetic nervous system activity a co-modulation of the sympathetic component of PDR and P3 would be expected and give some support to the suggestion that the P3-family of ERP components might reflect the co-activation of the LC-NE system and the sympathetic nervous system (even if PDR and P3 amplitude do not necessarily correlate at the single trial level; Kamp & Donchin, 2015).

Here we aimed at examining these issues in detail by the co-registration of the PDR and P3 in an auditory oddball paradigm including emotionally arousing negative and neutral novel sounds in dark and moderate lighting conditions. We hypothesized that we can replicate the decomposition of the biphasic PDR to novel sounds into two components by means of PCA (as already demonstrated by Wetzel et al., 2016), additionally confirming the parasympathetic vs. sympathetic origin of the two components by variation of lighting conditions. Further, we hypothesized that only the sympathetic contribution would be modulated by emotional arousal. Finally, following the LC-NE SNS co-activation hypothesis we expected an enhanced P3 in response to emotionally arousing novel sounds.

2. Materials and methods

2.1. Participants

A total of 22 young adults participated in the experiment, 2 of them were excluded from data analysis due to excessive blinking resulting in less than 70% of trials remaining in any condition after EEG and pupil data artifact rejection. The exclusion criterion was defined a posteriori. A total of 13 of the participants included in data analysis were female, 7 male, 16 were right-handed, and 4 left-handed. Their mean age was 23 years and 10 months (range 18;0–38;8 years;months). Participation was rewarded by money or course credit points. Participants gave written informed consent and confirmed normal hearing abilities, normal or corrected-to-normal vision, and to be not under the influence of pharmacological substances that affect the central nervous system. The project was approved by the local ethics committee of the University.

2.2. Stimuli

Novel sounds were 32 high arousing negative sounds and 32 moderately arousing neutral sounds. The standard sound was a sine wave sound with a fundamental frequency of 500 Hz including the second and third harmonic attenuated by −3 and −6 dB respectively. Sounds had a duration of 500 ms including faded ends of 5 ms. Sounds were present at a loudness level of 56.1 dB SPL measured with HMS III dummy head (HEAD Acoustics, Herzogenrath, Germany). Loudness was equalized with root mean square normalization.

The novel sounds were used and described in detail in a previous study by Max, Widmann, Kotz, Schröger, and Wetzel (2015). There, 32 high arousing emotionally negative and 32 moderately arousing emotionally neutral sounds were selected in a pilot study from a set of 210 sounds collected from the International Affective Digitized Sounds (IADS; Bradley & Lang, 2007), from a study by Hasting, Wassiliwizky, and Kotz (2010), and from other data bases as described by Max et al. (2015). Sounds were rated for valence (unpleasant – neutral – pleasant) and arousal (calm – arousing) on 9-point scales with the Self-Assessment Manikins (Bradley & Lang, 1994). Valence and arousal ratings were significantly different for emotionally negative vs. neutral sounds (Max et al., 2015).

The visual target consisted of two continuously presented, horizontally or vertically aligned grey single pixel dots (± 0.12° to the left and right or above and below the center of the screen respectively). In the dark condition, visual dots were presented on black background