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Effects of Natural Scene Inversion on Visual-evoked Brain Potentials and Pupillary Responses: A Matter of Effortful Processing of Unfamiliar Configurations

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Abstract—The inversion of a picture of a face hampers the accuracy and speed at which observers can perceptually process it. Event-related potentials and pupillary responses, successfully used as biomarkers of face inversion in the past, suggest that the perception of visual features, that are organized in an unfamiliar manner, recruits demanding additional processes. However, it remains unclear whether such inversion effects generalize beyond face stimuli and whether indeed more mental effort is needed to process inverted images. Here we aimed to study the effects of *natural scene inversion* on visual evoked potentials and pupil dilations. We simultaneously measured responses of 47 human participants to presentations of images showing upright or inverted natural scenes. For inverted scenes, we observed relatively stronger occipito-temporo-parietal N1 peak amplitudes and larger pupil dilations (on top of an initial orienting response) than for upright scenes. This study revealed neural and physiological markers of natural scene inversion that are in line with inversion effects of other stimulus types and demonstrates the robustness and generalizability of the phenomenon that unfamiliar configurations of visual content require increased processing effort.© 2022 The Author(s). Published by Elsevier Ltd on behalf of IBRO. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

Key words: Pupillometry, visual-evoked potential, event-related potentials, natural scene inversion, face inversion.

INTRODUCTION

The visual world is too rich of details for it all to be fully captured and processed by the brain. To prevent overload and exuberant energy consumption, neural networks across the visual hierarchy employ several tricks, such as adaptation, sparse coding, predictive coding, and other spatiotemporal information reduction mechanisms, to aid rapid though energy-efficient subjective perception (Barlow, 1990; Huang and Rao, 2011). These mechanisms ensure that sensory information, when organized in a familiar (and predictable) manner, is processed faster and more accurately. On the other hand, observers process unfamiliar organizations of visual content slower and less accurate (e.g., Itier et al., 2006; McLaren, 1997; Yin, 1969). Here we investigate effects of image inversion, a popular method, especially in studies on face perception (Valentine, 1988; Rossion, 2009; Yovel, 2016), to substantially decrease

an observer's familiarity with the organization of visual features. While behavioral measures (e.g., recognition performance and reaction times) provide valuable insights, we will use physiological and neural measurements of the effects as these provide alternative, reliable, and objective insights in the underlying mechanisms (e.g., Frässle et al., 2014). More specifically, we will measure pupillary responses and event-related potentials (ERPs) to upright and inverted natural scenes as (neuro-) physiological markers of the degree of (additional) effort required to process (un)familiar scenes (Minnebusch and Daum, 2009; Naber and Nakayama, 2013; Strauch et al., 2022).

Face, body, and object inversion

Inverted images and their effects on visual and emotional processing have received much scientific attention, especially in the field of face perception. A human face is disproportionately more difficult to recognize or memorize when it is presented upside down (e.g., Yin, 1969). Several studies have attributed this detrimental effect to configural distortions (Bartlett and Searcy, 1993; Freire et al., 2000) that presumably lead to the inability to form a global, holistic percept (Valentine, 1988; Murray et al., 2000) based on local face features that are unaffected by inversion (Farah et al., 1995a). Conversely, others argued that face inversion (or face dis-

tortion) effects are not caused by global configural distortions (Riesenhuber et al., 2004; Konar et al., 2010) but by a reduced experience with processing local, inversed facial features for recognition (Sekuler et al., 2004).

Whatever process changes by face inversion, researchers commonly associate such effects with the N170 electroencephalography (EEG) component, likely stemming from increases in activity from brain areas, including (right-lateralized) occipito-temporal and temporo-parietal regions, involved in object processing (Bentin et al., 1996; Aguirre et al., 1999; Haxby et al., 1999; Rossion et al., 1999; Itier and Taylor, 2004; Rousselet et al., 2004; Yovel and Kanwisher, 2005; Eimer, 2011; Jacques et al., 2019). Some researchers demonstrated even earlier inversion effects around 70–100 ms after picture onset using magnetoencephalography (Liu et al., 2002). In addition to such neural signatures, pupil size also serves as a marker of face inversion, showing stronger dilations to inverted faces than upright faces, supposedly reflecting the allocation of more mental effort to process the unfamiliar facial configuration (Conway et al., 2008; Falck-Ytter, 2008). Interestingly, it is not yet clear whether inversion effects on ERPs and pupil dilation generalize beyond face stimuli to bodies, houses, and other objects. Some studies find evidence in favor of object inversion effects on behavior and brain potentials (Eimer, 2000; Reed et al., 2003; Stekelenburg and de Gelder, 2004; Epstein et al., 2006; Righart and de Gelder, 2007; Minnebusch and Daum, 2009; Mohamed et al., 2011) while others find much weaker or no such evidence (Diamond and Carey, 1986; Bentin et al., 1996; Rossion et al., 2000; Itier et al., 2007; Rousselet et al., 2007). Besides these inconsistencies, the effects of inversion of complex images that display multiple or undistinctive objects, such as often the case in images of natural scenes (landscapes), are even less clear.

Scene inversion

Effects of scene inversion on behavior are in line with face inversion effects. The presentation of scenes, here defined as pictures of landscapes or complex objects with cluttered backgrounds, result in detrimental recognition performance and delayed reaction times for inverted pictures (Scapinello and Yarmey, 1970; Epstein et al., 2006; Walther et al., 2009). Note that scene inversion effects may be weaker than those of face inversion (Rousselet et al., 2003). Besides behavior, the peripheral nervous system is also affected by scene inversion. Inverted as compared to upright images of scenes evoke relatively weaker pupil constrictions (or stronger pupil dilations on top of an initial pupil constriction) (Naber and Nakayama, 2013; Castellotti et al., 2020), suggesting either enhanced attention for upright images (Binda et al., 2013; Mathôt et al., 2013; Naber et al., 2013; Mathôt et al., 2014; Portengen et al., 2021) or increased mental effort to process inverted images (Laeng et al., 2012; Binda and Murray, 2015; Mathôt, 2018; Joshi and Gold, 2020). Less is known about neural markers of (natural) scene inversion in the central nervous system.

Inverted versus upright *artificial* and *natural* scenes evoke distinct patterns of functional magnetic resonance imaging (fMRI)-based activity measured in mostly extrastriate areas and parahippocampal place area (Epstein et al., 2006; Walther et al., 2009; Kaiser et al., 2020a). The inversion-evoked pattern of increased activity across areas implicated in visual processing point at the possibility that inverted scenes require more effort to be processed, like the case with face inversion (Sadeh and Yovel, 2010).

However, as far as we know, no EEG studies have examined how *natural* scene inversion affects ERP components. Only few publications on (natural) scene-evoked ERPs exist (Sato et al., 1999; Rivolta et al., 2012; Bastin et al., 2013; Groen et al., 2013; Groen et al., 2016; Cichy et al., 2017) and none have reported on effects of inversion (but see Harel and Al Zoubi, 2019 for a conference abstract). So far it is only known that scene inversion starts to alter brain signals, that reflect the decoding of a scene's category (e.g., roads vs houses), around 170 ms (Kaiser et al., 2020b). Taken together, areas in extrastriate regions and further up the visual hierarchy appear to be affected by image inversion in general, but the question remains which ERP components are affected by the inversion of *natural* scenes. Natural scenes lend themselves to be exceptionally functional as stimuli to investigate inversion effects due to the diversity of features varying across stimuli and stimulus locations. If an inversion effect is found, one cannot relate it to a single image statistic, such as ordinal edges (e.g., houses) that suddenly become overrepresented in the upper image regions after inversion.

Current study

To summarize our research goals, we here aim to examine the effects of image inversion on pupil responses and ERPs. We will specifically examine (i) the timing of effects on pupil size to investigate whether additional effort is required to process inverted natural scenes and (ii) ERP amplitudes to investigate whether similar components are affected by natural scene inversion as compared with face/object inversion. Based on previous face inversion studies, we expect to confirm stronger relative pupil dilations (on top of pupil constrictions) and stronger amplitudes of early ERP components recorded from occipital, temporal, and parietal sites in response to inverted as compared with upright natural scenes.

EXPERIMENTAL PROCEDURES

Participants

Fifty-five participants from Utrecht University were recruited and received course credit or money for participating in the current study. Half of this sample size suffices to find significant inversion effects in a pupillometry study (Naber and Nakayama, 2013) but we doubled the sample to ensure that, in the light of inconsistencies of object and scene inversion effects in the EEG

literature, any null results would not be because of low statistical power. Eight subjects were excluded because they did not follow instructions (broke fixation in the majority of the trials, or did not respond during catch trials), they were tired, or because of technical issues that led to incomplete data. The remaining forty-seven participants (31 females; age: M = 22.9, SD = 2.6; 44 right-handed) were included for further analysis. All participants were healthy, had normal or corrected-to-normal vision, were naïve with respect to the purpose of the experiment, and signed the informed consent. The study conformed to the ethical principles of the Declaration of Helsinki.

Apparatus and stimuli

The experiment and stimuli were generated in MATLAB (Mathworks, Natic, MA, USA) using Psychtoolbox (Brainard, 1997). We displayed stimuli on an Asus ROG Swift PG278Q monitor (Beitou District, Taipei, Taiwan) with a resolution of 1920 × 1080 (60 Hz) against a grey background with a luminance of 58.5 cd/m^2. Hundred-twenty stimuli were grabbed from the web and consisted of images showing a natural scene (mostly landscapes with a meadow and sky). Images were transformed to grayscale and then histogram equalized to remove global luminance and contrast differences across stimuli. The adjusted images had a mean luminance of 81.8 cd/m^2 (SD = 0.4). Pictures were presented either upright or inverted (Fig. 1(A)) at the center of the screen with a resolution of 1070 × 669 pixels (corresponding to 34.9° by 22.3° in visual angle). A fixation dot with a diameter of 20 pixels (0.68°) was presented on top of each image. We randomly interleaved ten additional presentations of *colored* images of scenes (either upright or inverted) as catch trials (participants had to press a button whenever a colored scenes was observed; for details, see Procedure). A 64-channel + 8 BioSemi ActiveTwo EEG system (Amsterdam, Noord-Holland, The Netherlands) in combination with a dedicated computer running BioSemi Acti-View (version 7.05) was used to record EEG data, with a sample rate of 512 Hz and a bandwidth of 104 Hz (3 dB). An Eyelink 1000 plus (Ottawa, Ontario, Canada; version 5.09), connected to another computer for separate recordings, tracked the gaze point of the right eye at 1000 Hz.

Procedure

After equipping the EEG cap, electrodes were placed according to the 10–20 system. We placed the reference electrodes at the mastoids behind each ear and we placed additional electrodes for electrooculography (EOG) around the eyes (superior and inferior to the left eye and temporal to each eye). Participants then placed their head in the Eyelink chinrest, 55 cm from the screen and a 13-point (re-) calibration procedure was performed at the start and after every quarter of the experiment. Participants were instructed to maintain fixation on the dot in the center of the screen throughout the experiment. Trials started with the presentation of the fixation dot for a random duration chosen from the range 500–1500 ms. An image then appeared on the background for 3000 ms, with the fixation dot superimposed on top of the image. The image disappeared thereafter to automatically start a new trial, making the total presentation time of one trial 3500–4500 ms (Fig. 1(B)). Participants received the opportunity to take long breaks during the eye-trackers re-calibration and three additional self-paced breaks between calibration sessions to prevent fatigue.

The experiment consisted of 250 trials in total with the following conditions: upright (120 images), inverted (120 images), and 10 catch (color images). Participants were asked to press a keyboard button (spacebar) whenever a colored picture instead of gray-scale picture was shown on the screen. These catch trials were not analyzed but used to motivate participants to pay attention to the images. The experiment lasted approximately 45 min in total.

Analysis

We processed and analyzed both pupillometry and EEG data using a homemade pupillometry toolbox in MATLAB and the FieldTrip toolbox (Oostenveld et al., 2011), respectively.

Pupillometry and event-related pupillary responses (ERPR)

The ERPRs were obtained after applying a series of processing steps per participant. We first removed
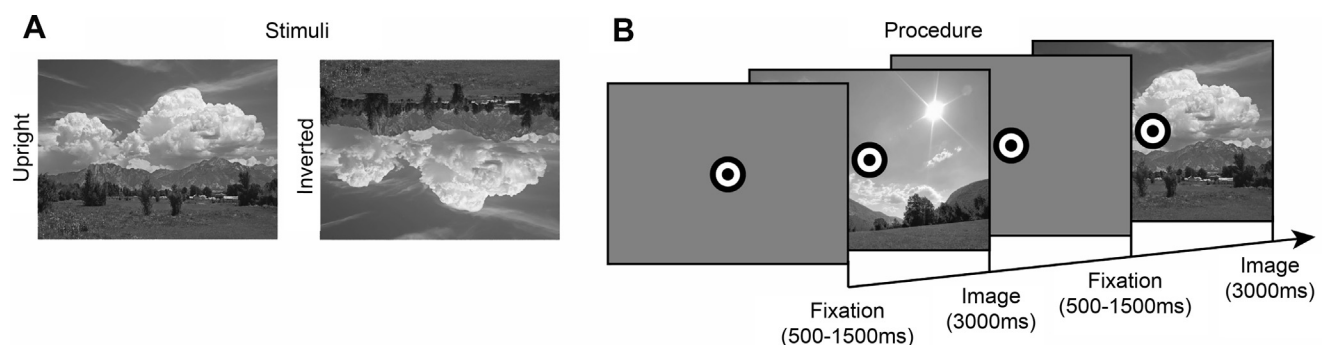
Fig. 1. Stimuli and procedure. Stimuli consisted of images displaying a landscape and could be presented either upright (top) or inverted (bottom) (**A**). Participants were instructed to focus their gaze on the fixation dot in center of the screen that was presented throughout the experiment. After a fixation period, an image appeared on the background with the fixation dot superimposed on top of the image (**B**).

blinks from the continuous recordings of pupil size by detecting sudden, extreme changes in pupil size, removing episodes starting with such a sudden decrease followed by an increase typically caused by a blink, and filling the removed episodes with simulated data with MATLAB's spline cubic interpolation algorithm. We then converted each continuous recording to an event-related data structure with segments of 0–3000 ms after image onset. This resulted in a data point matrix with 136 rows and 3000 columns. To remove baseline (steady-state) effects of individual differences, we z-normalized each pupil trace per trial (i.e., each row) by first subtracting the average pupil size in the initial 10 ms period of each trial and then dividing all matrix data points by the overall standard deviation across all matrix data points. Lastly, we extracted the amplitude of each pupil constriction per trial, which reflect the degree of visual processing of image content (Naber et al., 2018), by calculating the minimum z-normalized pupil size within a window of 400–1200 ms (i.e., during a pupil constriction episode) per trial (analyses on average pupil size in a window after pupil constriction produced similar results; data not shown). We did not compute pupil response latencies because it was not affected by image inversion in a previous study (Naber and Nakayama, 2013).

Electroencephalography and event-related potentials (ERP)

The ERPs were obtained using similar processing steps as for the ERPRs. After referencing the data to the electrodes placed at the mastoids, the FieldTrip toolbox bandpass filtered the EEG voltage recordings leaving only frequencies within a band of 0.3–30 Hz intact. We windowed the ERPs between 100 ms before and 500 ms after image onsets. We applied baseline corrections for the ERPs with a window setting of 100 ms before image onset. We removed EOG artifacts through manual inspection of the 20 first components (runica method) following the guidelines provided by FieldTrip documentation pages. We inspected variances per electrode and trial, and we removed electrodes (1 or 2 electrodes in 29 of 47 participants) and trials with outliers manually (percentage trials removed averaged across participants: M = 4%, SD = 2%). Next, we calculated relative amplitudes (i.e., the increase or decrease in potential as compared to a preceding trough or peak, respectively) per ERP component from ERPs averaged across a group of parietal electrodes (i.e., all BioSemi electrodes including the letter P, which also includes occipital and temporal electrodes). Component peaks and troughs were automatically detected using MATLAB's findpeaks function for the components N1 (60–120 ms window), P1 (90–170 ms), N2/N170 (120–200 ms), P2 (150–300 ms), N2 (200–350 ms), and P3 (250–400 ms) per participant. The manual (and subjective) detection of components (using a mouse cursor to select peaks and troughs) produced qualitatively similar results (data not shown).

RESULTS

The result section is organized in the following manner: we first examined the image inversion effect on event-related pupillary responses (ERPR) and the associated amplitudes (Pupil$_{Amp}$). Then we investigated the same effect on event-related potentials (EPR) and the relative amplitudes of the underlying components to examine which electrodes and components marked inverted image processing best.

Effect of image inversion on ERPR

The ERPR to the images (Fig. 2(A)) followed a typical constriction pattern with a relatively fast constriction onset around 250 ms. The participants' pupils constricted most strongly in response to the presentation of upright images as compared with inverted images (i.e., an image inversion effect) with
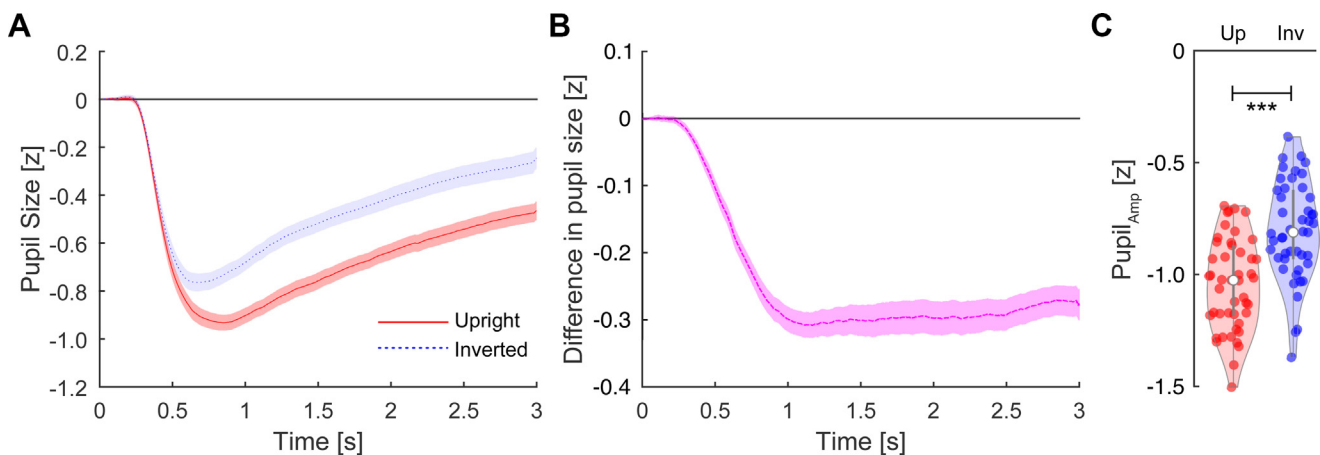
Fig. 2. Pupillometry results. Pupil responses to upright (solid red) versus inverted (dotted blue) trials as a function of time after image onset, first averaged across trials and then across participants (the half-transparent patches indicate standard errors from the mean), are shown in panel (**A**). Panel (**B**) shows the difference in pupil size between conditions (upright-inverted) across time. A violin plot of pupil response amplitudes, averaged per participant (dots) across trials, confirmed the significance of the difference between upright (Up) and inverted (Inv) conditions (**C**). Asterisks indicate the t-test significance level of difference between conditions (***$p < 0.001$).

minimum pupil size being reached around approximately 650 and 850 ms for inverted and upright images, respectively. Note that although the constriction patterns are comparable between upright and inverted conditions, the pupil traces start diverging around 300 ms (Fig. 2(**B**); for post-hoc comparisons per time point, see Fig. S1(**A**)), which is slightly later than the constriction onset. However, the maximum difference is reached around 1100 ms, that is well after the point of minimum constriction (750 ms), indicating that the effect of image inversion is likely caused by a later dilation component related to mental effort superimposed on an initial constriction component related to visual orienting. The combination of the Eyelink measuring pupil size in arbitrary units and the z-normalization procedure prevents us from making strong claims about effect sizes in millimeters, but we estimated the difference in pupil size around the order 0.1–0.3 mm. The statistical analysis of differences in response amplitudes per observer (Fig. 2(**C**)) further confirmed a strong image inversion effect on pupil size ($t(46) = 13.52$, $p < 0.001$).

Effects of image inversion on ERP

To inspect the image inversion effect on brain potentials, we first plotted the ERPs of parietal electrodes as, in line with the literature (e.g., Itier and Taylor, 2004), we expected the effects to occur in these areas. The ERPs evoked by the presentation of natural scenes, first averaged across presentation trials per participant and then averaged across participants (Fig. 3(**A**)), consisted of a complex pattern with several components with distinct latencies and amplitudes between upright and inverted images. The pattern of the timing of the components appeared to be similar to a previous ERP study that presented scenes to participants (Harel et al., 2016). The gradual evolvement of negativity before 100 ms is likely caused by a contingent negativity variation that is typically observed in preparation of stimulus presentations every couple seconds (Kononowicz and Penney, 2016). Upright images appeared to evoke an early positive peak (P80) around 80 ms, an N1 around approximately 110 ms, a P1 around 130 ms, an N2 around 150 ms, a P2 around 220 ms, an N3 around 280 ms, and a P3 around 320 ms. The components of the ERP traces evoked by inverted images showed comparable timings with the only exception that the early P80 was covered up by the relatively stronger superimposed N1 component. The ERPs showed most strongest inversion effects around the occurrence of N1 and N2 components, as confirmed by ERP difference plots (Fig. 3(**B**); for post-hoc comparisons per time point, see Fig. S1(**B**); for scalp maps per component and per condition, see Fig. S2; for difference in potentials and component amplitude between conditions, see Fig. S3) and statistical comparison of the difference in potentials (Fig. 3(**C**); N1: $t(46) = 5.77$, $p < 0.001$; P1: $t(46) = 5.16$, $p < 0.001$; N2: $t(46) = 4.35$, $p = 0.001$; P2: $t(46) = 6.45$, $p = 0.001$; latencies did not differ, data not shown). Note, however, that the relative amplitudes (i.e., the change in potential as compared to the preceding positive peak; N1 amplitude was compared to baseline as an exception due to no preceding components) only dif-

fered between the upright and inverted condition for N3 (Fig. 3(**D**); $t(46) = 5.44$, $p = 0.001$). The latter suggests that the baseline difference between upright and inverted conditions of later components (i.e., after N1; for scalp maps of potential differences per N1 and N2, see Fig. 3 (**E–F**)) was likely driven by the relative amplitude difference of N1. In sum, we found that natural scene inversion evokes an N1 component with a relatively strong amplitude, which continuously changed brain potentials up to the P2 component, followed by an additional N3 component with a relatively weaker amplitude.

DISCUSSION

The first finding reported in this paper concerns the pupillary image inversion effect. We could replicate the finding that the pupil constricts stronger to upright images as compared to inverted images (Naber and Nakayama, 2013; Castellotti et al., 2020), and a thorough examination of the time traces of pupil size suggests that scene inversion evokes an enhanced dilatory alerting response. This effort-related dilation was superimposed on an initial orienting-related constriction, which is a typical phenomenon in pupillometry (Naber et al., 2012; Mathôt, 2018; Naber and Murphy, 2020; Strauch et al., 2022).

Besides these pupillometric results, we also reported on the neural marker of specifically *natural scene* inversion. A considerable number of studies reported *face* inversion effects on the amplitude and latency of N170 components (Bentin et al., 1996; Rossion et al., 1999; Itier and Taylor, 2004; Stekelenburg and de Gelder, 2004; Minnebusch and Daum, 2009; Eimer, 2011). However, no study has published about whether these inversion effects generalize to images of natural scenes. During a conference, Harel and Al Zoubi (2019) did recently report interesting scene inversion results that hint at an effect of natural scene inversion on the P2 component, and we look forward to the full research report to compare the results in more detail. Another EEG decoding study suggests that the categorization accuracy of upright versus inverted natural scenes is possible after 170 ms (Kaiser et al., 2020a, b), so we had some expectations as to the timing of a potential natural scene inversion effect. Here we find that already the N1 component in occipito-tempo-parietal regions showed more pronounced troughs of activity for inverted as compared to upright natural scenes. Although we did not find any inversion effects on latency (data not shown), we do show for the first time that the previously found face inversion effects on ERP amplitudes generalize to natural scenes, although the effect occurs around 100 ms, which is earlier than the typical face inversion effect around 170 ms. Nonetheless, this means that, in general, brain potentials occurring around 100–200 ms likely reflect a process evoked by stimulus inversion.

A number of studies have related a distinct N170 face inversion component to clinical populations, including autism (for review, see Tang et al., 2015), schizophrenia (Tsunoda et al., 2012), prosopagnosia (Farah et al., 1995b), and Alzheimer's disease (Lavallée et al., 2016).
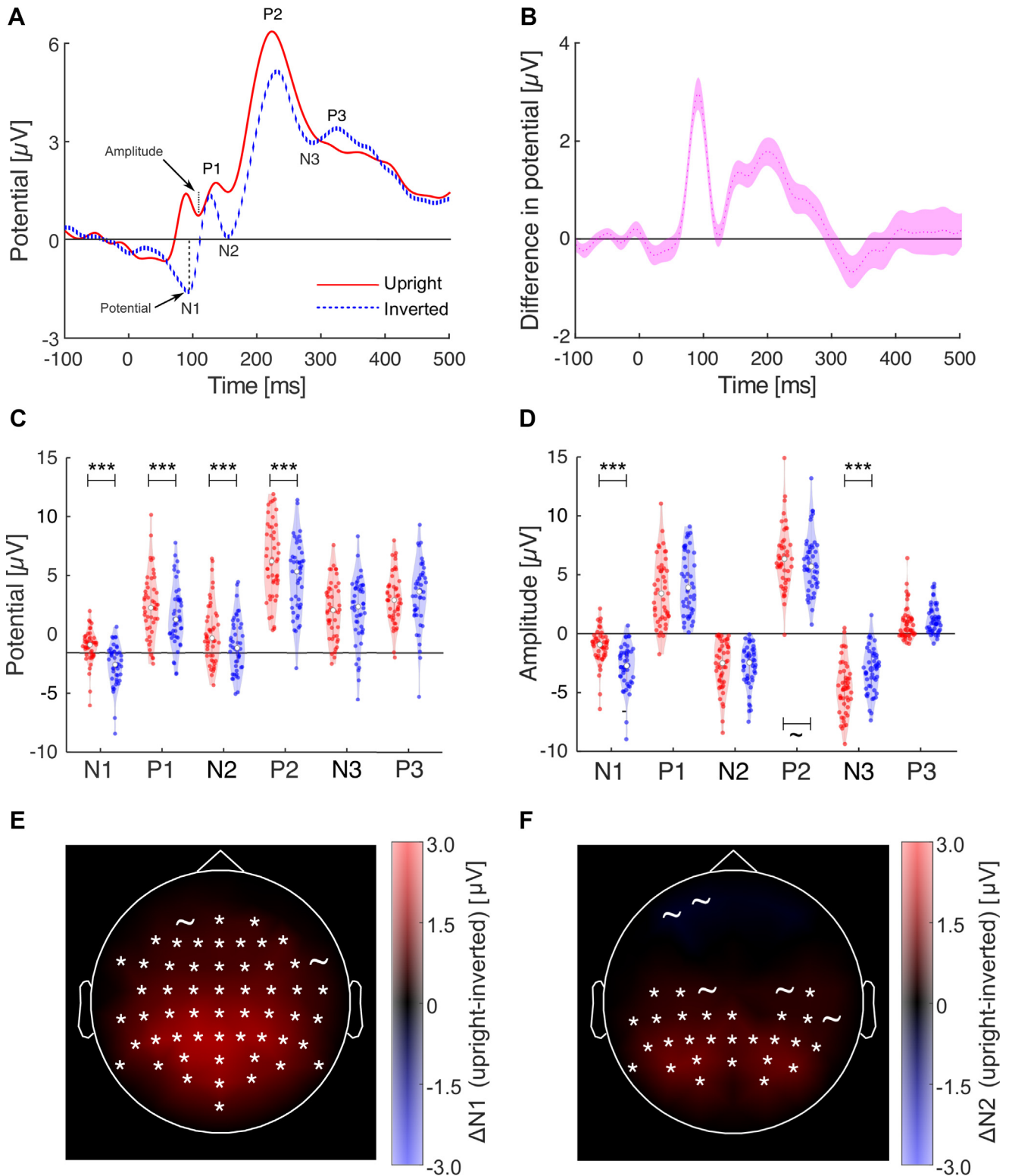
Fig. 3. ERP results. Panel (**A**) shows the ERPs averaged across trials, parietal electrodes (these electrodes most consistently showed image inversion effects in previous literature), and participants, for upright (solid red) and inverted (dotted blue) conditions. In panel (**B**) the line shows the electrode-and-participant-averaged difference of parietal ERPs across time around stimulus onset for upright minus inverted conditions. The half-transparent patches represent the standard error around the mean per time point. Panel (**C**) and (**D**) show the potentials and relative amplitudes, respectively, per component for upright (red) and inverted (blue) conditions, averaged across trials per participant (dots) and accompanying distribution (violin). Panel (**E**) and (**F**) display scalp maps of the potential difference between upright and inverted conditions, with the redder the color, the more positive the potential difference (for scalp maps of all components and amplitude differences, see Fig. S3). Asterisks and the curly signs indicate when the uncorrected *p*-values of t-test comparisons scored below significance levels ($\sim p < 0.100$; *$p < 0.050$; **$p < 0.010$; ***$p < 0.001$; most asterisks in panel (**E-F**) indicate $p < 0.001$ but only one asterisk is shown for aesthetical reasons).

In light of the current findings, it would be interesting to see whether natural scenes produce similar results as with face inversion and would suggest that the visual processing deficits observed in these clinical populations extend to complex stimuli in general, rather than exclusively in response to social stimuli.

When interpreting the EEG and pupillometry results together, inversion-evoked processes are likely raised by a state of alerting (discomfort, unease, or unfamiliarity) caused by effortful processing of stimuli with unusual layouts for which the visual system is not trained to process and interpret (Conway et al., 2008; Falck-Ytter, 2008). The neural network involved in alerting and mental effort is well known (Petersen and Posner, 2012), and recent evidence from pupillometry studies suggest the involvement of noradrenergic pathways and neural loci like the locus coeruleus (for reviews, see Laeng et al., 2012; Mathôt, 2018; Joshi and Gold, 2020; Strauch et al., 2022). It will be interesting to study the exact nature of this additional process in future studies, as well as its relation to other brain potentials such as visual mismatch negativity evoked by violations of sensory regularity (Tales et al., 1999; Berti and Schröger, 2001; Horimoto et al., 2002; Heslenfeld, 2003; Pazo-Alvarez et al., 2004; Maekawa et al., 2005; Czigler et al., 2006; Kremláček et al., 2016). Stimulus inversion may evoke a whole sequence of cognitive states, including changes in processing efficiency (Sekuler et al., 2004) and a heightened state of arousal, but it may also draw more attention to the stimulus (Naber and Nakayama, 2013). Whether an increase of attention explains the stronger N1 remains to be investigated, but an ERP study by Groen and colleagues (2016) suggests that attentional effects during natural scene processing emerge only after 250 ms, meaning that the here reported N1 effect are probably not driven by changes in attentional resources.

In conclusion, we demonstrate stronger N1 peak amplitudes in the occipito-temporo-parietal area and larger pupil dilations after observing inverted natural scenes as compared with upright natural scenes, extending inversion effects beyond previously associated stimuli categories such as faces and objects. The neurophysiological markers are likely related to effortful processing of stimuli in general.

CONFLICT OF INTEREST

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APPENDIX A. SUPPLEMENTARY MATERIAL

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuroscience.2022.11.025.