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Beauty in mind: Aesthetic appreciation correlates with perceptual facilitation and attentional amplification

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ABSTRACT

Neuroaesthetic research suggests that aesthetic appreciation results from the interaction between the object perceptual features and the perceiver's sensory processing dynamics. In the present study, we investigated the relationship between aesthetic appreciation and attentional modulation at a behavioural and psychophysiological level.

In a first experiment, fifty-eight healthy participants performed a visual search task with abstract stimuli containing more or less natural spatial frequencies and subsequently were asked to give an aesthetic evaluation of the images. The results evidenced that response times were faster for more appreciated stimuli.

In a second experiment, we recorded visual evoked potentials (VEPs) during exposure to the same stimuli. The results showed, only for more appreciated images, an enhancement in C1 and N1, P3 and N4 VEP components. Moreover, we found increased attention-related occipital alpha desynchronization for more appreciated images.

We interpret these data as indicative of the existence of a correlation between aesthetic appreciation and perceptual processing enhancement, both at a behavioural and at a neurophysiological level.

1. Introduction

Results from empirical aesthetics and neuroimaging studies suggest that aesthetic appreciation emerges from the interaction between the object perceptual features and the perceiver's perceptual processing dynamics (see Consoli, 2015 for a review). Ramachandran and Hirstein (1999) proposed that visual aesthetic experiences are produced by stimuli which "optimally titillate the visual areas of the brain" (page 1). Indeed, the perception of beauty is often described as a mental state in which attention is focused on the stimulus perceptual features (Apter, 1984; Chatterjee, 2011; Chatterjee and Vartanian, 2016; Cupchik and Winston, 1990; Marković, 2012; Ramachandran and Hirstein, 1999; Shusterman, 1997). Consistently with this idea, recent fMRI studies (Calvo-Merino et al., 2008; Cupchik et al., 2009; Jacobsen et al., 2006; Koelsch et al., 2006; Munar et al., 2009; Vartanian and Goel, 2004) found enhanced sensory processing during aesthetic appreciation. As it has been proposed, these results are most likely induced by increased attentional engagement (Kirsch et al., 2016; Leder and Nadal, 2014; Nadal, 2013). Such attentional modulation might also explain the perceptual facilitation observed for more appreciated stimuli, as measured by enhanced behavioural performance (Mather et al., 2016; Spehar et al., 2015), and the subjective feeling of perceptual fluency (Carbon and Albrecht, 2016; Forster et al., 2015; Reber et al., 2004, 1998; Reber and Schwarz, 2001; Singhal et al., 2007). However, to the best of our knowledge, there is no electrophysiological evidence of a direct link between aesthetic appreciation and an increased attentional engagement, which is the object of investigation of the present study. EEG signals can efficacely capture the attentional dynamics following the presentation of a stimulus: event-related responses provide well validated objective indexes of attentional engagement both in the time domain (Mangun and Hillyard, 1991; Zani and Proverbio, 2012) - by measuring the voltage of the evoked response- and in the time-frequency domain (Klimesch, 2012; Mishra et al., 2012; Peng et al., 2012), by measuring the spectral power of the evoked responses. More specifically, C1 and N1 components of the VEP and alpha event-related desynchronization (ERD) have long been known to be modulated by attention to the stimulus (Klimesch, 2012; Mangun and Hillyard, 1991; Warbrick et al., 2014; Zani and Proverbio, 2012).

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Here we wanted to investigate the modulation of attention during aesthetic appreciation of content-free computer-generated abstract visual stimuli, containing different spatial frequencies. A number of studies show that humans tend to perceive images with spatial frequencies following the power law $1/f^{B}$, with B values approaching 2, as aesthetically more pleasing (Menzel et al., 2015; Spehar et al., 2015). Interestingly, such preferred power spectrum patterns are common both in natural environments and in visual arts (Johnson and Baker, 2004; Redies et al., 2008). The power spectrum slope B was also found to influence sensory processing efficiency: the ability of subjects to discriminate among visual stimuli peaks when the images are made more 'natural' by manipulating the slope (B) of the spatial frequencies power spectrum (Párraga et al., 2000). Altogether, these findings make the power spectrum slope a well-suited variable to investigate processing enhancements related to aesthetic appreciation.

In a first experiment, we investigated at a behavioural level the relationship between perceptual facilitation and aesthetic appreciation, as a function of image spatial frequency: we recorded response times while subjects performed a visual search task of a grey dot embedded in more or less appreciated abstract images with different power spectrum slopes (§ 2.1.2 *Stimuli*). In a second experiment, to assess the relationship between attentional engagement and aesthetic appreciation, we recorded the VEPs in response to the same more or less appreciated background images.

We expected to observe, only for more appreciated images: 1) behavioural perceptual facilitation (i.e., reduced response times) in the visual search task; 2) enhanced EEG attentional indexes, such as increased amplitude of C1 and N1 components (Mangun and Hillyard, 1991; Zani and Proverbio, 2012) and more pronounced alpha desynchronization over occipital areas (Klimesch, 2012; Peng et al., 2012; Pfurtscheller et al., 1994; Sigala et al., 2014).

2. Materials and methods

2.1. Experiment 1

2.1.1. Participants

Fifty eight right handed healthy subjects (females: 30; age: 23.8 ± 2.5; education: 15 ± 2) participated in the study. All participants had normal or corrected to normal vision. All participants gave their written informed consent to participate to the study, which conformed to the standards required by the Declaration of Helsinki and was approved by

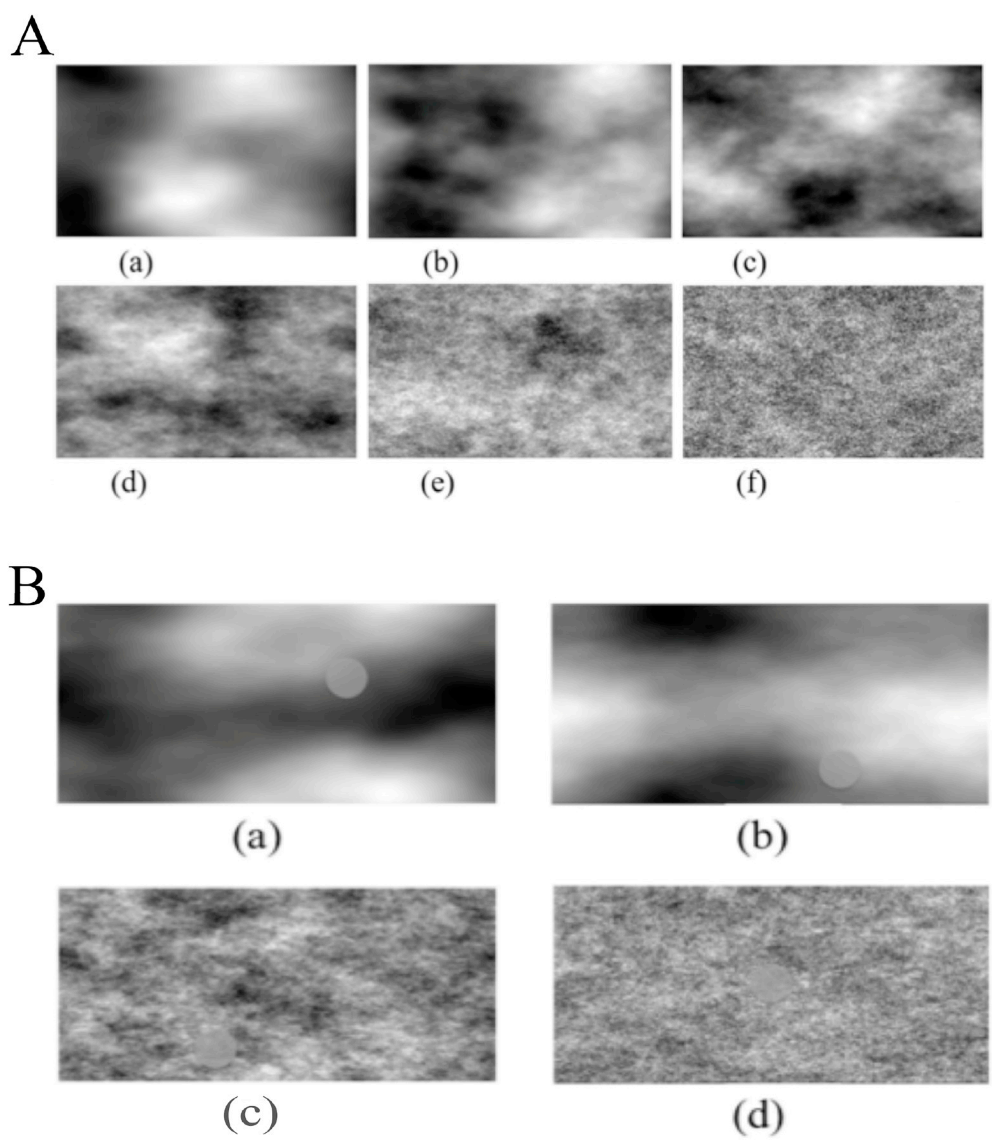

Fig. 1. Experimental stimuli. Images a)-f) in **Panel A** are extracted from the initial set of 105 images (21 categories): each image is a representative example of a stimulus category with a different B exponent value: **(a)** $B = 2.8$, **(b)** $B = 2.4$, **(c)** $B = 2$, **(d)** $B = 1.6$, **(e)** $B = 1.2$, **(f)** $B = 0.8$.

the local ethics committee (University of Turin).

2.1.2. Stimuli

We employed 2D black and white noise-images randomly created with the IDL software (Harris Geospatial Inc. USA). All images were generated according to the power law $1/f$, so that the images spectral power (P) of spatial frequencies (f) is defined by a power law $P(f) = 1/f^B$. The software allowed to specify the exponent B value (i.e., the power spectrum slope). We generated 21 different categories of stimuli with 21 different B values ranging from 0.8 to 2.8 in steps of 0.1. We knew from previous studies that aesthetic appreciation peaks for images with a power spectrum defined by a $1/f^B$ power law with B values approaching 2 (Spehar et al., 2015). Therefore, we centred the distribution of B values around B = 1.8. In Fig. 1 *(panel A)* we show six examples of representative stimuli from the initial image set.

Panel B depicts images employed in the visual search task. The target (grey circular dot) is here superimposed on 4 backgrounds pertaining to 4 representative image categories (out of the total 21 categories) characterized by $B = 2.8$ **(a)**, 2.3 **(b),** 1.3 **(c)**, 0.8 **(d)**. In order to render the grey target more visible to the reader, images in Panel B have been magnified relative to images in Panel A.

Five different images for each of the 21 B categories were generated, for a total of 105 images. During the collection of aesthetic judgments (*§2.1.4 Experimental procedures*), all 105 images (from now on *Backgrounds*) were shown once, whereas during the visual search task the same *Backgrounds* were shown twice, once with a superimposed 1 cm wide, semi-transparent, grey dot (from now on *Target*), and once without. The use of target-free images served to prevent habituation and participants' distraction during the task. To lower the probability of the occurrence of anticipatory responses, the *Target* could appear in five different positions: centrally (aligned with the subject midsagittal plane) and in four peripheral positions located at 10 degrees of visual angle from the geometrical image center along the horizontal and vertical meridians (see Fig. 1*, panel B*). The total *Background* set employed in the visual search task consisted of 210 images, 10 for each B category (5 with and 5 without the target).

2.1.3. Apparatus

The set up was identical in *Phase 1* and in *Phase 2* (§ 2.1.4 *Experimental procedures)*. Participants sat comfortably at a table in a fixed position, distant 60 cm from a 53 cm (21 inches) computer screen, with the screen center aligned with the subject's trunk vertical midline. The left arm was resting on the corresponding leg, while the right arm was placed on the desk. Subjects had their right index finger resting on the "A" keyboard button and the middle finger on the adjacent "S" button. They were asked to press "A" as fast as possible when the target was present, and "S" when the target was absent. The subjects' right hand and the response keys were aligned with the trunk vertical midline.

2.1.4. Experimental procedures

2.1.4.1. Phase 1 – Visual search task. Stimuli were presented in a random order with an inter-trial interval ranging between 2 and 2.5 s. Subjects were instructed to stay still and look at a 1 × 1cm wide white fixation cross placed in the center of the computer screen and aligned with the subjects' trunk vertical midline. The fixation cross was present on the screen for the whole duration of the inter-trial interval. *Targets* and *Backgrounds* appeared at the same time and remained visible until response (Fig. 2). Response time and accuracy data were collected.

2.1.4.2. Phase 2 -Aesthetic judgments (AJs) collection. Following the visual search task, after a 5 min rest, participants evaluated the beauty of the 105 *Background* stimuli employed in *Phase 1.* Participants were asked to look at a 1 × 1cm wide white fixation cross placed in the center of the computer screen, against a black background, and then to pay attention

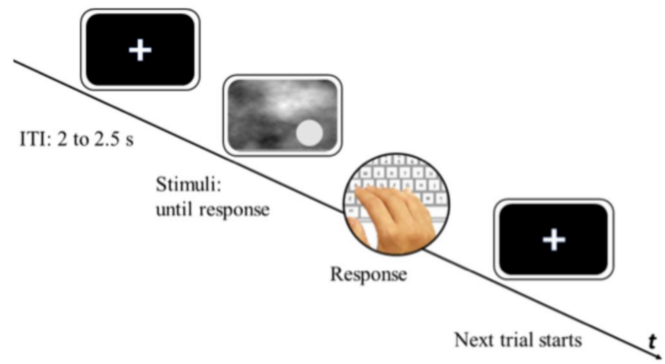

Fig. 2. Timeline of *Experiment 1*. Participant fixated on a central cross for the ITI duration. Backgrounds appeared at the center of the screen and remained until response. Participants were asked to indicate whether the target was present or not by pressing two adjacent buttons on the keyboard in front of them. As soon as they responded the fixation cross was back on the screen.

to the images appearing on screen (stimulus duration 1 s). The *Backgrounds* were presented in a random order. Participants were asked to report their aesthetic appreciation judgment on a *Likert* scale ranging from 0 ('I completely dislike it') to 9 ('I like it very much') by pressing the corresponding numerical key on the computer keyboard. Judgments were automatically recorded for each trial. Following the response, the fixation cross appeared back on the screen. Inter-trial intervals ranged between 3 and 5 s.

Both experimental procedures were programmed and administered using E-Prime 2.0 software (Psychology Software Tools, Inc. USA).

2.1.5. Data analysis

Incorrect trials were excluded from the analysis. For each participant, we computed the mean RT for each category. Every subject evaluated 5 different images for each *Background* category and mean judgments were averaged across subjects to obtain one value for each of the 21 *Background* categories. A standard two-tailed Pearson correlation analysis was then performed on all-subjects mean RTs and AJs from the 21 *Background* categories.

2.2. Experiment 2

2.2.1. Participants

Thirteen healthy right-handed subjects (females: 7; age: 25 ± 1.8; education: 16 ± 2.3) participated in the study. All subjects had normal or corrected to normal vision and gave their informed consent to participate to the study, which conformed to the standards required by the Declaration of Helsinki and was approved by the local ethics committee (University of Torino).

To determine the sample size for the EEG experiment we collected the EEG recordings of 5 participants who participated in a pilot experiment identical to *Experiment 2.* We then extracted average C1 peak amplitudes (*§3.2 Results),* corresponding to each of the 5 *Background* categories (*§2.2.2 Stimuli),* from single subject recordings (electrode O_z). *"Background* category" was considered as a within-subjects factor in a repeated measure ANOVA. The effect size and significance value for the effect of the factor "*Background* Category" ($\eta^2_{p.} = 0.239$; $p = 0.327$; $\rho = 0.326$) was subsequently used in a power analysis to determine the sample size (N = 13) required for a statistical power level set at 0.8 and an alpha significance level set at 0,05 (critical F = 1.19; actual power = 0.80004).

2.2.2. Stimuli

Stimuli were drawn from the *Background* set of images employed in *Phase 2* of *Experiment 1* (§ 2.1.2 *Stimuli* and § 2.1.3 *Apparatus*). The selected *Backgrounds* belonged to 5 different categories defined by the following *B* exponent values: 0.8, 1.3, 1.8, 2.3 and 2.8. Twenty images were shown for each *B* category, for a total of 100 images presented in two experimental blocks (50 images per block). None of the subjects had ever seen the experimental images before or was informed about their characteristics. From the results of *Experiment 1* (§3.1 and Fig. 3*)* and previous studies (Spehar et al., 2015) with large samples, we expected that images with extreme *B* values ($B = 0.8$ and 2.8) were on average less appreciated than images with intermediate *B* values ($B = 1.3$ and 2.3), while images with $B = 1.8$ were the most appreciated ones. Including *Backgrounds* with steeper or smoother *B* slopes than highly appreciated *Bs'* allowed us to discriminate between ERP modulations eventually induced by high/low spatial frequencies and those correlated to aesthetic judgements.

2.2.3. Experimental procedure

The set-up was identical to that of *Experiment 1*, except that *Targets* were absent and subjects were only asked to look at the *Backgrounds* presented on the screen while EEG data were recorded. *Backgrounds* were presented in a random order (stimulus duration 500 ms), preceded and followed by a white fixation cross (4–5 s inter-stimulus interval). The experiment was divided into two identical blocks, composed of 50 images each. In between the two experimental blocks participants were allowed to rest for about 5 min. Each block lasted approximately 6 min. To ensure that subjects were attentively performing the task, twenty catch trials were included in a random order within the experimental sequence (20% of the total number of trials), consisting of a semi-transparent red dot superimposed onto the same *Backgrounds* employed in valid trials. Subjects had to verbally report the presence of catch trials to the experimenter. Catch trials were successively excluded from statistical analyses. Subjects failing to report more than 2 catch trials were excluded from the analyses.

After the EEG session participants performed a brief aesthetic evaluation task identical to the one described in *Experiment 1 (§2.1.4)* with the only exception that they evaluated only *Backgrounds* belonging to the 5 categories selected in *Experiment 2.* In the aesthetic evaluation task, subjects evaluated 5 images for each Background category for a total of 25 stimuli.

2.2.4. Electrophysiological recordings and data analysis

EEG activity was recorded using 32 Ag–AgCl electrodes placed on the scalp of the participant according to the International 10–20 system and referenced to the nose. Electrode impedances were kept below 5 kΩ. The electro-oculogram (EOG) was recorded from two surface electrodes, one placed over the right lower eyelid and the other placed lateral to the outer canthus of the right eye. Signals were recorded and digitized by using a *HandyEGG* (Micromed, Treviso – IT) amplifier with a sampling rate of 1024 Hz.

EEG data were pre-processed and analyzed with Letswave6 toolbox (Nocions, Ucl. BE) for Matlab (Mathworks, Inc. USA). Continuous EEG data were divided into epochs of 1.5 s (total duration), including 500 ms pre-stimulus and 1 s post-stimulus intervals. Epochs were band-pass filtered (1–30 Hz) using a fast Fourier transform filter and baseline corrected using the interval from −0.5 to 0 s as reference. Artifacts due to eye movements were subtracted using Independent Component Analysis (ICA – Jung et al., 2000). Epochs belonging to the same *Background* category (i.e. same *B* exponent category) were then averaged, to obtain five average waveforms (i.e. *B* equal to 0.8, 1.3, 1.8, 2.3 and 2.8) for each subject. Single subjects preprocessed epoched data are available at: Sarasso, P. (2017), "The flow of beauty", Mendeley Data, v1 https://doi.org/10.17632/rrsvt86p4x.1.

Statistical analyses in the time domain. To test for significant differences among the ERPs elicited by different image categories, we performed a one-way, repeated measures, point-by-point ANOVA, with a three levels factor corresponding to beauty rankings according to the results of *Experiment 1* (§3.1) and *Experiment 2* (§3.2). Single subjects' average waveforms corresponding to less appreciated images with $B =$ 0.8 and 2.8 were averaged together and assigned to factor level 1; waveforms corresponding to images with $B = 1.3$ and 2.3 were averaged together and assigned to factor level 2 and waveforms corresponding to highly appreciated images with $B = 1.8$ were assigned to factor level 3. As a result, we obtained one waveform per participant for each of the three factor levels, which constituted the input of the point-by-point ANOVA (Ronga et al., 2013; Bruno et al., 2019). Correction for multiple comparisons was applied via clustersize-based permutation testing (Maris and Oostenveld, 2007; 1000 permutations; alpha level = 0.05; percentile of mean cluster sum = 95). Clusters were based on temporal contiguity and spatial adjacency of a minimum of two electrodes (Novembre et al., 2018).

Furthermore, we computed the correlation between each time point from single subjects' ERPs and mean AJs of the eliciting *Background* images from *Experiment 2* (§2.2). On each time point, this analysis (Novembre et al., 2018) computed a *r*-value between the amplitudes of the waveforms corresponding to the five different *Background* categories and their mean AJs (AJs were averaged across the 13 participants). The

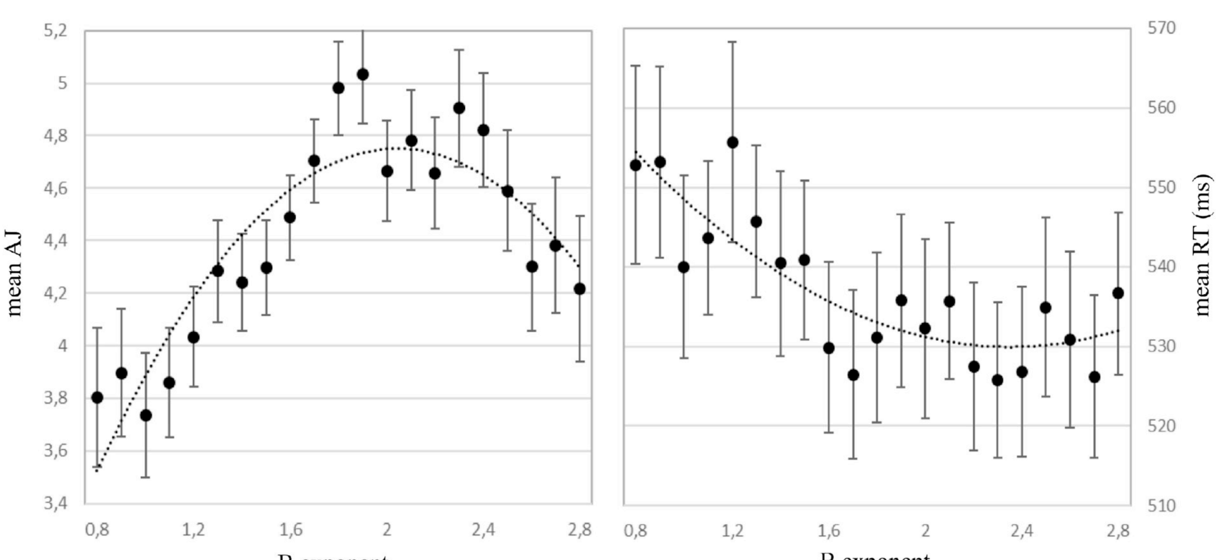

Fig. 3. Mean aesthetic ratings (left panel) and response times (right panel) ($N = 58$). Single subject RTs were normalized around the mean RT and then averaged across subjects ($N = 58$; grand-average). Error bars represent standard errors. Dotted curves represent the best-fitted second order polynomial trend lines.

outcome of the correlation analysis was a 0.5 s long time series of correlation coefficients for each channel for each subject. This constituted the input for a group-level two-tails point-by-point *t*-test with permutation-based correction for multiple comparison (Maris and Oostenveld, 2007; 1000 permutations; alpha level = 0.05; percentile of mean cluster sum = 95; minimum number of adjacent channels = 2). The test compared single subjects correlation coefficients against 0 at each time point. This allowed us to verify whether the waveform components highlighted by the ANOVA results were also significantly correlated to the AJs of the observed images and to evidence other waveform components which could possibly correlate with AJs but failed to survive cluster correction in the ANOVA.

Statistical analyses in the time-frequency domain. Time-frequency representations were computed for each single pre-processed epoch using a Short-term Fast-Fourier transform (STFFT) with a Hanning window width of 0.25 s. The STFFT expressed the amplitude as a function of time (relative to stimulus onset) and frequency. The resulting estimates were averaged across single trials belonging to the same *Background* category, to obtain one single spectrogram for each of the five *Backgrounds* per participant. For each frequency, estimates were displayed in these spectrograms as an event-related percentage (ER%) change in oscillation amplitude relative to a baseline (−0.5 to −0.1 s pre-stimulus). ER% changes constituted the input of subsequent analyses.

To test for the presence of significant modulations in ERD after the presentation of different backgrounds the same approach implemented in the time domain was used in the time-frequency domain (see above). Namely, we used pairwise point-by-point t-tests comparing ER% changes (Valentini et al., 2014) following the presentation of different *Backgrounds*. ER% elicited by the presentation of the five Background categories were compared against all others for a total of ten t-tests. Correction for multiple comparisons was applied via clustersize-based permutation testing (Maris and Oostenveld, 2007; 1000 permutations; alpha level = 0.05; percentile of mean cluster sum = 95).

To help visualize ER% changes following different *Backgrounds* we extracted the minimum ER% estimate for the alpha frequency band (7.5–12.5 Hz) within a time period lasting from 0.2 s to 0.6 s post-onset. Minimum ER% were then averaged across participants to obtain one single average value for each *Background*. Moreover, single subjects baseline corrected ER% were averaged across participants to obtain one single spectrogram for each *Background*.

3. Results

3.1. Experiment 1

All participants correctly performed the task [mean number of incorrect trials/subject: 6,5 out of 210 (3.1%)]. The average participants' response time was 540 ms (SD = 82 ms). Incorrect trials were equally distributed among image categories.

Mean judgment values across categories replicated the findings from previous literature, showing an inverted u-shape function with higher preferences for images with *B* values close to 2 (Fig. 3). The mean RTs for all subjects are shown in Fig. 3 (right panel) and show an opposite trend relative to AJs. The negative relationship between all-subject average RTs and AJs is evidenced by the significant Pearson correlation coefficient ($r = -0.728$; 95% CI: $-1.057 < r < -0.4$; $p < 0.001$; $N = 21$).

3.2. Experiment 2

The results of the aesthetic evaluation are depicted in Fig. 4 *(panel A)* and replicate the findings of previous studies and *Experiment 1*. *Backgrounds* with $B = 1.8$ were rated as more beautiful than *Backgrounds* with $B = 1.3$ and $B = 2.3$, while *Backgrounds* with $B = 0.8$ and $B = 2.8$ were the least preferred ones.

The point-by-point ANOVA analysis (Fig. 5) revealed differences in

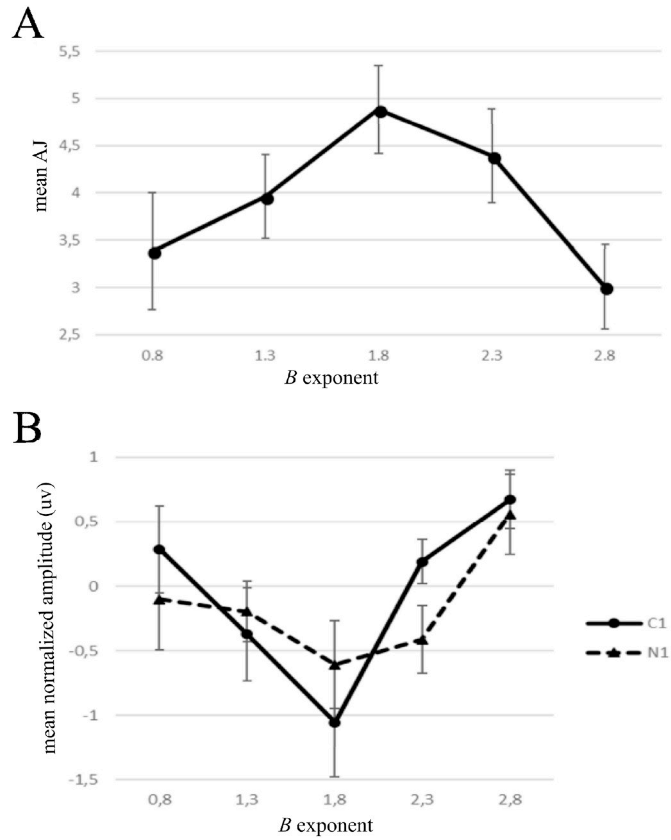

Fig. 4. Mean aesthetic ratings and mean N1 and C1 peaks (N = 5). **Panel A:** Single subjects' (N = 13) AJs were averaged to obtain a mean value for each *Background* category. The graph in **Panel B** shows the grand-average of N1 (dashed line) and C1 (solid line) peaks. C1 and N1 Peaks were normalized around their mean to display them on a common scale. Error bars represent standard errors.

two ERP time intervals between waveforms from high-, medium- and low-appreciation ranked *Background* categories: 1) the C1 early occipital-posterior component (Di Russo et al., 2001; Hillyard and Anllo-Vento, 1998) peaked around 49 ms post-stimulus; 2) the N1 posterior-central component (Johannes et al., 1995; Vogel and Luck, 2000) peaked around 122 ms post-stimulus (slightly later at 142 ms for *Backgrounds* with B = 2.8). In Fig. 5, grand-average responses for the five *Background* categories are presented, together with F-values and significant clusters from occipital (Oz) and central (Cz) electrodes.

C1 and N1 amplitudes were also significantly correlated to mean AJs as evidenced by the point-by-point correlation analysis (Fig. 6). The cluster-corrected *t*-test performed on single subjects' correlation coefficients highlighted a significant cluster ranging between 0.045 and 0.076 s post onset on the electrode O_z corresponding to C1 and another significant cluster ranging between 0.107 and 0.135 s post onset on the electrode C_z corresponding to N1. Moreover, the analysis indicated a significant correlation between mean AJs and later parieto-occipital P3 and N4 components, as revealed by a significant cluster ranging between 0.269 and 0.293 s post onset on the electrode O_z (corresponding to P3). Correlations between AJs and N4 amplitudes were indicated by a smaller significant cluster on O_z (range: 0.387–0.407 s) and a larger cluster on C_z (range: 0.386–0.428 s). Fig. 4 *(panel B)* plots the normalized grand-average of C1 and N1 single-subject peaks.

The time-frequency analysis revealed the expected ERD in the alpha band that is usually evident over occipital areas after the presentation of a visual stimulus (Klimesch, 2012; Sigala et al., 2014). The latency and scalp distribution of alpha ERD closely matched those of previous studies (Abeles and Gomez-Ramirez, 2014; Mishra et al., 2012; Peng

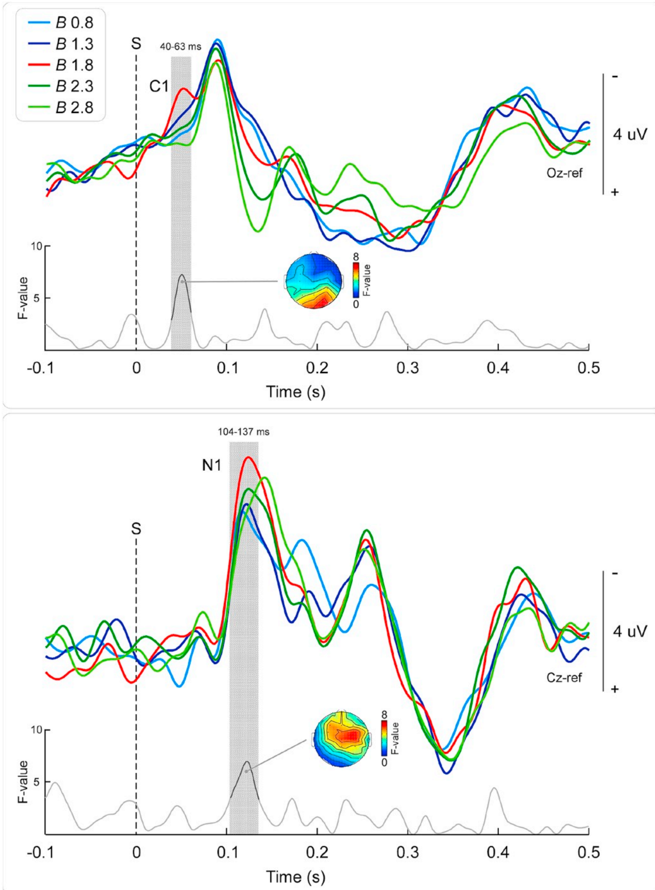

Fig. 5. Point-by-point ANOVA: waveforms represent grand-average ERPs for the 5 different image categories registered on Oz (top panel) and Cz (bottom panel). Each ERP represents the average of 20 trials per participant. Shaded areas represent the significant clusters evidenced by the cluster-based permutation analysis with 250 permutations. Maps depict the scalp distribution of F-values at 50 and 120 ms post-stimulus onsets. Point-by-point F-values for the two channels are displayed in the graph below each panel. The dotted line represents stimulus (S) onset.

et al., 2012). The analysis revealed an increase of alpha ERD after the presentation of more appreciated *Backgrounds* with $B = 1.8$, as evident in the average spectrogram and in mean ER% from Oz displayed in Fig. 7. Only the following pairwise t-tests revealed the presence of significant clusters: $B = 0.8$ vs $B = 1.8$; $B = 1.3$ vs $B = 1.8$; $B = 1.8$ vs $B = 2.3$; $B = 1.8$ vs $B = 2.8$; $B = 2.3$ vs $B = 2.8$. Significant clusters from point-by-point t-tests were mainly included in the alpha band in a time period comprised between 0.2 and 0.6 s post-onset. P values from significant clusters from Oz are displayed in Fig. 7.

4. Discussion

The results of experiment 1 and 2 confirmed our hypothesis of the presence of a correlation between aesthetic appreciation and attentional engagement: more appreciated abstract stimuli were associated to perceptual facilitation (i.e., faster RTs) and EEG indexes of enhanced attentional activation (i.e., larger C1 and N1 VEP components and increased alpha ERD).

Behavioural perceptual facilitation related to aesthetic appreciation. The results of *Experiment 1* revealed the existence of a relationship between aesthetic appreciations and RTs in a visual search task with content-free abstract stimuli. Aesthetic appreciation was found to be inversely correlated to RTs: participants were faster in detecting targets embedded in more appreciated stimuli. We propose that this effect might be caused by enhanced visual sensitivity for preferred stimuli, defined by a power law with *B* values close to 2 (Spehar et al., 2015). Such values characterize also images of natural environments, to which the human visual system has adapted both phylogenetically and ontogenetically (Graham and Field, 2010; Olshausen and Field, 1996). Interestingly, natural-like image statistics are also consistently found in visual arts (Graham and Redies, 2010) and are related to aesthetic appreciation (Spehar et al., 2015, 2003; Street et al., 2016). In sum, the results of *Experiment 1* demonstrate the existence of a positive correlation between aesthetic appreciation and behavioural indexes of attentional enhancement (Ronga et al., 2018; Sarasso et al., 2019).

Electrophysiological indexes of attentional enhancement related to aesthetic appreciation. In *Experiment 2*, the analysis of VEPs revealed a significant correlation between C1, N1, P3 and N4 amplitudes and AJs (Fig. 6). C1 and N1 amplitudes, peaking around 50 ms and 120 ms post stimulus onset, respectively, seem to be more strongly modulated by AJs than P3 and N4 amplitudes. The amplitude of attention-related C1 and N1 early components was indeed significantly different between more and less appreciated stimuli, while P3 and N4 amplitudes were not (Fig. 5). Moreover, as we expected, more appreciated stimuli induced stronger attention-related ERD in the alpha frequency over occipital areas between 200 and 600 ms post stimulus onset (Fig. 7).

Consistently with what mentioned above, C1 is considered to mainly capture neural activity from V1 (Martínez et al., 1999; Noesselt et al., 2002), reflecting early attentional processing (Kelly et al., 2008; Zani and Proverbio, 2012). Previous studies investigating exogenous cueing of involuntary attention showed enhanced C1 amplitude for validly vs invalidly cued targets (Dassanayake et al., 2016; Fu et al., 2010, 2009). Similarly, C1 responses are more pronounced after the presentation of motivationally relevant stimuli, such as threat-related images or images associated with monetary outcomes (Rossi et al., 2017; Stolarova et al., 2006). N1 is also considered an index of early attentional processing (Mangun and Hillyard, 1991), presumably reflecting the gain control or selective amplification of sensory inputs (Hillyard and Anllo-Vento, 1998). Crucially, posterior N1 was shown to index exogenous (i.e., bottom-up) object-based attentional up-weighting of sensory input (Marzecová et al., 2018 for a review). Moreover, larger N1 amplitudes are usually correlated to more efficient processing (Van Den Berg et al., 2016; Vogel and Luck, 2000). Furthermore, Van Den Berg et al. (2016) showed that response times in a visual search task could be predicted by N1 amplitudes.

Alpha oscillation amplitude in occipital areas is generally found to be reduced (stronger alpha ERD) in presence of increased attention (Bollimunta et al., 2008; Ergenoglu et al., 2004; Klimesch, 2012; Mishra et al., 2012; Peng et al., 2012; Sigala et al., 2014) and perceptual performance (Bays et al., 2015; Nenert et al., 2012). Attention and processing enhancements are often associated with a post-stimulus decrease in alpha synchronization, since the latter is thought to reflect the release of inhibition of cortical excitability (Cebolla et al., 2016; Klimesch et al., 2007) thus regulating stimulus-related response in areas encoding sensory inputs (Abeles and Gomez-Ramirez, 2014).

What is the evolutionary meaning of the correlation between attentional enhancements and aesthetic appreciation? The results of Experiment 1 and 2 indicate that abstract stimuli with natural-like spatial frequencies are associated with higher aesthetic appreciation, increased processing fluency and enhanced early attentional engagement. Such attentional modulation, as indicated by present and previous evidence (Nadal, 2013; Spehar et al., 2015; Sarasso et al., 2019), seems to be associated with optimal perceptual processing dynamics, indexed by greater activation in early sensory areas (Calvo-Merino et al., 2008; Cupchik et al., 2009; Jacobsen et al., 2006; Koelsch et al., 2006; Munar et al., 2009; Vartanian and Goel, 2004) and, in the present study, by enhanced early electrophysiological responses. Crucially, these responses resulted to be consistently correlated also with our conscious experience of beauty (Cupchik et al., 2009; Graham and Redies, 2010; Massaro et al., 2012). To this respect, a relevant question arises: why would aesthetic

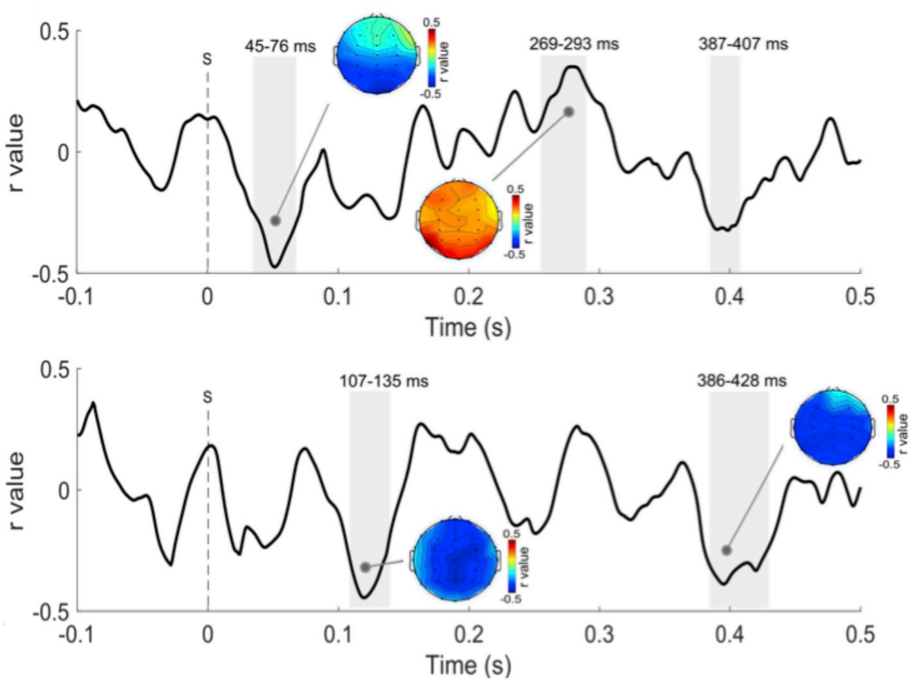

Fig. 6. Correlation between C1, N1, P3 and N4 amplitudes and AJs. The graph shows all-subjects' mean correlation coefficients (r) between AJs and the amplitudes of waveforms registered on Oz (top panel) and Cz (bottom panel). Shaded areas represent significant clusters evidenced by the point-by-point *t*-test comparing single subjects' correlation coefficients against 0. Scalpmaps depict the distribution of mean correlation coefficients across channels at peak latencies (50 ms post onset for C1; 120 ms post onset for N1; 300 ms post onset for P3; 400 ms post onset for N4).

appreciation be preceded by and correlated with attentional enhancement and greater bold and electrophysiological activations in sensory areas? Our results do not provide a definitive answer to this question, but we can speculate that aesthetic appreciation might serve as an evolutionary, hedonically marked, feedback over bottom up perceptual processing dynamics (Chetverikov and Kristjánsson, 2016; Winkielman et al., 2003), signaling the occurrence of specific stimulus features, valued as most informationally profitable by the human nervous system (e.g., because of their high signal-to-noise ratio which makes them more reliable; Consoli, 2015; Kesner, 2014; Koelsch et al., 2019; Van de Cruys and Wagemans, 2011). In line with this interpretation, previous studies also suggested that the brain generates intrinsic reward when it senses informationally profitable signals (Oudeyer et al., 2007). Informational value per se was found to attract human attention (Baldi and Itti, 2010; Itti and Baldi, 2009) and to correlate with the activation of dopamine-rich midbrain reward-related structures (Schwartenbeck et al., 2016) which were also found to underlie aesthetic appreciation (Blood and Zatorre, 2001; Cela-Conde et al., 2004; Kawabata and Zeki, 2004). Accordingly, the attentional selection of informationally valuable auditory input has been recently related with aesthetic pleasure in music (Koelsch et al., 2019).

In the case of the present study, the visual system might have "interpreted" *Background* stimuli with a more natural spatial frequency content (i.e. a power spectrum approaching natural images statistics), to which the human visual system has adapted (Párraga et al., 2000), as less noisy (i.e. more informationally valuable) and consequently might have up-weighted the incoming visual input (Ronga et al., 2017). Conversely, for stimuli diverging from natural statistics, the visual input might have been down-weighted via a reduction in the system excitability (Limanowski et al., 2018). Our electrophysiological data support this interpretation. Alpha ERD, which we found to be more evident after the presentation of more appreciated "natural" stimuli, has been shown to dynamically modulate the neural gain in sensory areas (see Sigala et al., 2014 for a review). Moreover, early components of the VEP, such as C1 and N1, have been suggested to reflect the attentional up-weighting of visual inputs according to their estimated precision via modulations of the synaptic gain of pyramidal cells (Brown and Friston, 2012). Finally, previous research (Higashi et al., 2017; Mars et al., 2008; Ostwald et al., 2012) demonstrated that measures of informational value correlate with trial by trial fluctuations of the P3 component that in our study was also found to correlate with aesthetic appreciation. Regarding the interpretation of the present results, we believe it is important to clarify that we do not hypothesize that an early aesthetic appreciation causes and precedes visual sensitivity and electrophysiological and behavioural correlates of attentional enhancement. On the contrary, we argue that aesthetic appreciation follows (i.e., is a feedback of) increased visual sensitivity and attentional enhancement for more informationally profitable stimuli.

Altogether, the present data might be considered as evidence supporting the hypothesis that aesthetic pleasure might represent an intrinsic reward allowing the system to spontaneously engage in perceptual activities maximizing informational gain. Crucially, we are not arguing that all aesthetic experiences can be explained by the attentional selection of informationally profitable low-level stimulus perceptual features. Although this might be the case for the abstract stimuli employed in our study, complex art products, such as music, literature and figurative arts can induce aesthetic appreciation via content-based or purely contextual variables (Koelsch et al., 2019) which are not considered in the present research.

Declaration of competing interest

None.

CRediT authorship contribution statement

P. Sarasso: Conceptualization, Methodology, Investigation, Data curation, Formal analysis, Investigation, Software, Visualization, Writing - original draft. **I. Ronga:** Conceptualization, Methodology, Investigation, Data curation, Formal analysis, Visualization, Writing - review & editing. **P. Kobau:** Writing - review & editing. **T. Bosso:** Data curation, Investigation, Resources. **I. Artusio:** Data curation, Investigation, Resources. **R. Ricci:** Conceptualization, Writing - review & editing. **M. Neppi-Modona:** Supervision, Conceptualization, Writing - review & editing.

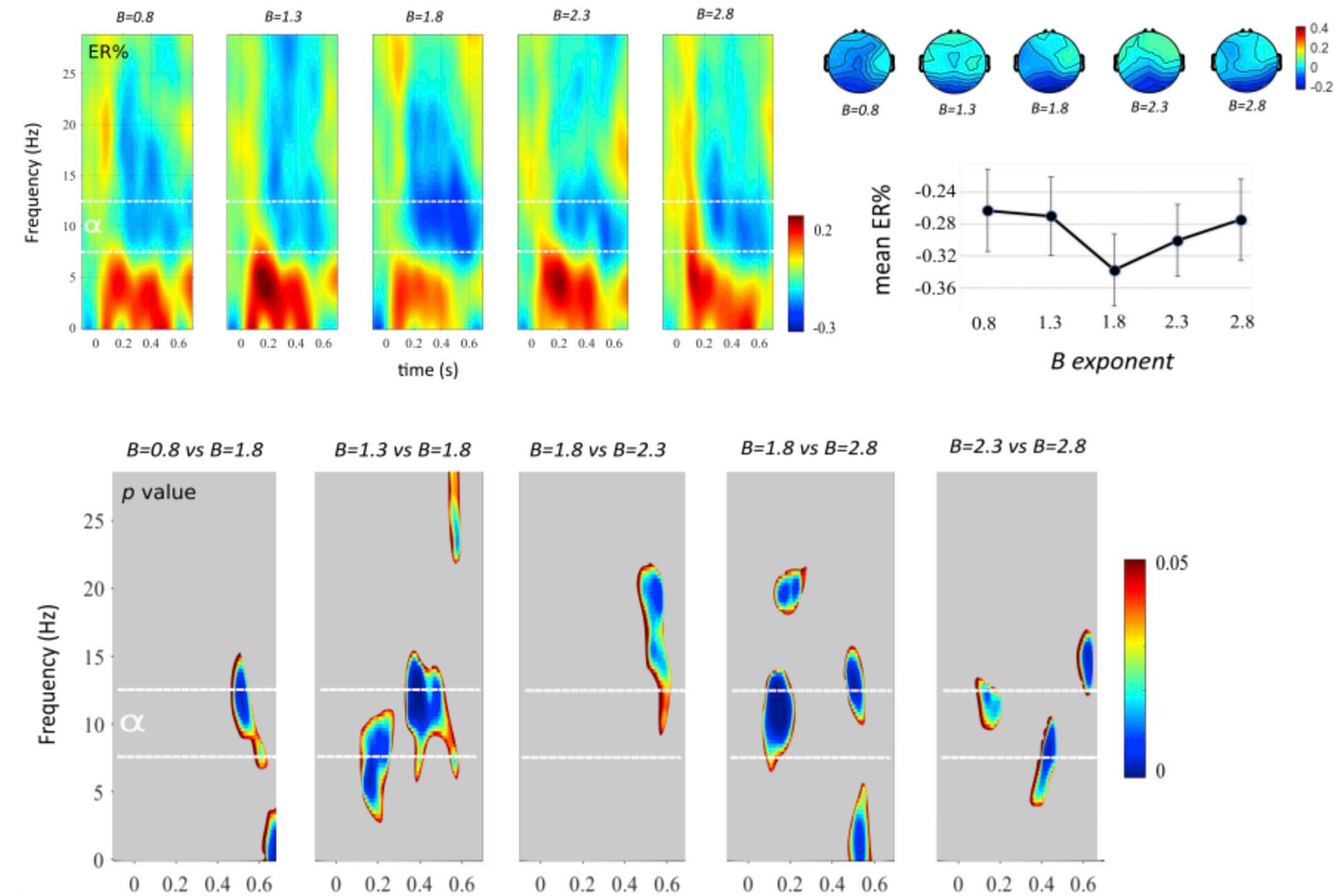

Fig. 7. Time-frequency analysis. The graph shows the grand-average spectrogram and mean alpha (7.5–12.5 Hz) ER% from Oz for each of the five Background categories (upper panel). Colors in the spectrograms represent ER% changes in oscillation amplitude relative to the baseline. Scalpmaps represent the average minimum value of ER% registered in the alpha band (7.5–12.5 Hz) between 0.2 and 0.6 s after stimulus onset. In the lower panel *p* values from single t-tests (computed on channel Oz) are displayed as a function of time and frequency. Significant clusters are colored while grey areas contain *p* values which did not survive cluster-based correction. Only t-tests which showed at least one significant cluster were reported in the figure. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuropsychologia.2019.107282.

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