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Nice and Easy: Mismatch Negativity Responses Reveal a Significant Correlation Between Aesthetic Appreciation and Perceptual Learning

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Neurocomputational models of cognition have framed aesthetic appreciation within the domain of knowl- edge acquisition and learning, suggesting that aesthetic appreciation might be considered as a hedonic feed- back on successful perceptual learning dynamics. Such hypothesis, however, has never been empirically demonstrated yet. In order to investigate the relationship between aesthetic appreciation and learning, we measured the EEG mismatch negativity (MMN) response to more or less appreciated musical intervals, which is considered as a reliable index of perceptual learning. To this end, we measured the MMN to fre- quency (Hz) standard and frequency deviant musical intervals (Experiment 1) while participants were asked to judge their beauty. For each single stimulus, we also computed an information-theoretic index of percep- tual learning (Bayesian surprise). We found that more appreciated musical intervals were associated with a larger MMN responses, which, in turn, correlated with trial-by-trial fluctuations in Bayesian surprise (Experiment 1). Coherently with previous results, Bayesian surprise was also found to correlate with slower RTs in a detection task of the same stimuli, evidencing that motor behavior is inhibited in presence of sur- prising sensory states triggering perceptual learning (Experiment 2). Our results provide empirical evidence of the existence of a positive correlation between aesthetic appreciation and EEG indexes of perceptual learning. We argue that the sense of beauty might have evolved to signal the nervous system new sensory knowledge acquisition and motivate the individual to search for informationally profitable stimuli.

Keywords: neuroaesthetics, perceptual learning, mismatch negativity, EEG, predictive coding

How can we learn from novel and unpredicted stimuli? Some authors suggested that intelligent systems (biological and artificial) must develop an intrinsic self-generated reward that motivates the search for learning progresses and information gains, even though this implies an initial exposure to sensory uncertainty induced by novel inputs (Friston et al., 2017; Kesner, 2014; Oudeyer et al., 2016; Schwartenbeck et al., 2019). In other words, intrinsic moti- vation toward learning is fundamental to tolerate mismatches between current and expected events, which are the driving force of memory updating (Agres et al., 2018; Krawczyk et al., 2017).

Interestingly, aesthetic emotions have been proposed to serve a central role in motivating humans to learn from the environment (Sarasso, Neppi-Modona, et al., 2020; Schoeller & Perlovsky, 2016). Recent neuroscientific accounts of aesthetic experiences defined the perception of beauty as a hedonic feedback on success- ful perceptual learning (i.e., the update of predictive representa- tions of the sensory environment; Biederman & Vessel, 2006; Cupchik et al., 2009; Kubovy, 1999; Markovi'c, 2012; Van de Cruys & Wagemans, 2011). According to this hypothesis, the brain generates an intrinsic reward (Gottlieb et al., 2013) when sensory uncertainty reduces over time and new meaningful infor- mation is acquired (Chetverikov & Kristjánsson, 2016; Muth & Carbon, 2013; Van de Cruys & Wagemans, 2011). In other words, aesthetic pleasure might be considered as a particular kind of self- generated reward, which emerges when the nervous system senses a progress in learning statistic regularities from sensory inputs, and which is correlated with the magnitude of the update of mental representations (Sarasso, Neppi-Modona, et al., 2020; Schoeller & Perlovsky, 2016).

However, this hypothesis, postulating a direct relation between perceptual learning dynamics and aesthetic emotions, still lacks solid empirical support and, to our knowledge, no physiological measures of perceptual learning has been directly related to sub- jective aesthetic appreciation.

Converging evidence from electrophysiological studies suggests that EEG signals can effectively capture perceptual learning (Lieder et al., 2013; Ostwald et al., 2012; Stefanics et al., 2018). More specifically, the auditory mismatch negativity, or MMN (Näätänen et al., 2007; Sams et al., 1985), is typically considered a neurobiological marker of perceptual learning (Chang et al., 2014; Garrido et al., 2009; Perez et al., 2017; Winkler et al., 1999). The auditory MMN is elicited by the presentation of unpredicted sounds that deviate from a pattern established by the preceding inputs (i.e., standard-repeated tones). Therefore, the emergence of MMN responses requires the automatic learning of environmental sensory regularities (Garrido et al., 2016; Näätänen et al., 2007) and is considered to reflect the magnitude of the update of the brain representation of the environment induced by surprising sen- sory inputs (Auksztulewicz & Friston, 2015; Dittmann-Balcar et al., 1999; Ostwald et al., 2012). Accordingly, MMN responses correlate with trial-by-trial fluctuations in Bayesian surprise, a well-established marker of perceptual learning (Mousavi et al., 2020). Namely, Bayesian surprise captures the degree of predic- tive model updating induced by a new event (Baldi & Itti, 2010; Itti & Baldi, 2009), that is, how much we learn from a stimulus; it quantifies the effect that novel inputs have on representations as the divergence between the encoded prior (before stimulation) and posterior probability distribution (after stimulation) of the causes of sensory input (Baldi, 2002). The Bayesian surprise, therefore, can be regarded as an index describing the “enlightenment” sur- prise, occurring after the brain has “assimilated” the new input to update its model of the world (Faraji et al., 2018).

Moreover, such an update of predictive representations has been related to a specific behavioral effect: surprising sensory states triggering perceptual learning have been associated to motor inhi- bition (Dutra et al., 2018; Ide et al., 2013). In other words, percep- tual surprise induces the activation of a frontal inhibitory network (Wessel & Aron, 2017; Wessel & Huber, 2019), reducing motor cortical excitability (Bestmann et al., 2008; Mars et al., 2008) and slowing down response times (RTs; Wessel & Huber, 2019). Such an adaptive process has been interpreted as a momentary “pause” state that allows the update of behavioral plans according to newly acquired information (Wessel & Aron, 2017). However, evidence directly supporting the presence of a correlation between RTs in a fast detection task and computational measures of surprise at the single trial level are still scarce (Bestmann et al., 2008; Mein- dertsma et al., 2018).

In the present study, we aim at: (a) confirming the presence of a correlation between trial-by-trial fluctuations in MMN responses

and perceptual Bayesian surprise (Experiment 1); (b) testing the hypothesis of a direct link between learning progresses and aes- thetic appreciation by investigating the relation between aesthetic judgements (AJs) and Bayesian perceptual learning (Experiment 1); (c) exploring the trial wise relation between motor behavior, recorded through RTs, and Bayesian perceptual learning dynamics (Experiment 2).

To this end, we exploited a classic roving task (Ostwald et al., 2012), employing more and less consonant musical intervals of varying frequency (Hz; intervals varied in both consonance level and tone frequency). Roving paradigms with frequency deviant

\standard tones are typically used to study MMN responses and represent a validated methodology to investigate learning-related mechanisms (Näätänen et al., 2007; Sams et al., 1985). Moreover, previous studies demonstrated that consonance level can effec- tively modulate subjective aesthetic appreciation of auditory stim- uli while maintaining their physical features comparable (Bowling et al., 2018; Cousineau et al., 2012; Sarasso, Ninghetto, et al., 2019; Sarasso et al., 2021).

In both experiments, consonant fifths and dissonant tritones were presented (in separate sessions) with two different frequen- cies (Hz), according to a classic roving paradigm. Within the pro- tocol, the same stimulus (i.e., fifth or tritone intervals) is repeated several times before unpredictably switching to a different stimu- lus train. Whenever a stimulus was preceded by another with a dif- ferent pitch, the former was considered as Deviant (20%), whereas the remaining stimuli were considered as Standard trials (80%). To verify our hypotheses, we computed the Bayesian surprise associated to each single trial (see Method and online supplementary materials). We expect (a) to verify the presence of the previously described correlation between trial-by-trial fluctuation in MMN (Deviant–Standard) responses and perceptual Bayesian surprise, with larger MMN responses associated with greater Bayesian sur- prise (Experiment 1); moreover, we predict that (b) AJs result posi- tively related to Bayesian perceptual learning, with greater MMN responses (signaling an enhanced perceptual learning) for more appreciated intervals (Experiment 1). Finally, we expect to find a positive trial-by-trial correlation between the computed amount of Bayesian surprise and RTs, showing that Bayesian surprise concur- rently inhibits motor behavior (Experiment 2).

Method

Participants

The same 26 right-handed healthy volunteers (females: 15; age: 25.1 61.9; education: 15.3 62.1) participated in Experiment 1 and Experiment 2. All participants gave their written informed consent to participate in the study. The study conformed to the standards required by the Declaration of Helsinki and was approved by the local ethics committee (University of Turin).

The original sample size (N = 18) was a priori determined so as to match the average number of participants involved in previous studies highlighting ERP modulations driven by aesthetic appreci- ation (Sarasso, Ninghetto, et al., 2019, N = 22; Sarasso, Ronga, et al., 2020, N = 13; average 17.5). Thirteen participants from this sample preferred perfect fifth intervals, the remaining five partici- pants preferred tritones (MMN results from the original sample are reported in the online supplementary materials). To exclude possible confounds induced by the uneven distribution of preferen- ces (i.e., to avoid that results might be mainly driven by the group preferring perfect fifths), we administered Experiment 1 and 2 to eight additional subjects preferring tritone intervals as revealed by an online version of Aesthetic Judgment task described below (N = 86). Similarly to our original sample (where 5 out of 18 par- ticipants [28%] preferred tritones over fifths), 29.1% of online par- ticipants preferred tritone intervals. Subsequent analysis and results reported below refer to the final group of 26 participants.

Stimuli and Apparatus

Intervals were created with Csound (https://csound.com/). The software made it possible to select the frequency of the two notes composing the interval, which were played simultaneously for 50 ms via headphones. Loudness of sounds was set at a comfortable level (70 dB) and was kept equal across subjects and experiments. The two types of intervals (i.e., fifth intervals and tritones) were defined by the ratio between the frequency of the two composing notes. Consonance depends on this ratio: the smaller the integer numbers that define the ratio, the more consonant will be the inter- val (Fishman et al., 2001; Plomp &

Levelt, 1965). Perfect fifth intervals (usually perceived as more consonant) have a ratio of 3:2, while tritones (frequently categorized as more dissonant) are defined by a ratio of 45:32. For each interval type (fifths or tri- tones), we employed two different pitches (i.e., high vs low). Low-pitch and high-pitch fifth intervals were composed of notes with a frequency of 150 and 100 Hz and 600 and 400 Hz, respec- tively. Low-pitch and high-pitch tritone intervals were composed of notes with a frequency of 150 and 106 Hz and 600 and 426 Hz, respectively.

During the experiments, participants sat at a table with eyes open, 53 cm (diagonal) computer screen. The screen center was aligned with the trunk midline. Participants' arms were resting on the corresponding leg during the MMN roving paradigm (Experi- ment 1). During the Aesthetic Judgment task (Experiment 1) and the Detection task (Experiment 2) participants kept their right index on a keyboard placed on a desk in front of them, ready to respond.

Experimental Procedures of Experiment 1

MMN Roving Paradigm

Participants performed four runs of a standard roving paradigm with trains of 1,152 stimuli per run, while we registered their EEG. In two runs we presented fifth (high-pitch and low-pitch) intervals only, while in the remaining two runs we presented only (high-pitch and low-pitch) tritones. The order of presentation of the four runs (total duration: approximately 80 minutes) was randomized across participants, so as to exclude any specific sequence effects on the results. In contrast to traditional oddball paradigms, where the repeated presentation of standard sounds is occasionally interrupted by the occurrence of physically different deviant sounds (Näätänen et al., 1978), in roving paradigms like this one, different stimuli (high-pitch and low-pitch intervals in our case) can represent both Deviant and Standard stimuli (Figure 1; Baldeweg et al., 2004; Ostwald et al., 2012; Rosch et al., 2019).

In our case, high-pitch and low-pitch intervals were presented in consecutive trains of alternating pitch with a constant interstimulus interval of 1 s (in accordance with previous studies on Bayesian surprise employing similar intertrials; Ostwald et al., 2012). Any time a change in the stimulation stream occurs (i.e., the passage from a high-pitch to a low-pitch stimulus train or vice versa), the first stimulus of the new train constitutes a Deviant event, since it differs (by its pitch) from the preceding train of stimuli, which are therefore considered Standard (McCleery et al., 2019). Similarly, all the intervals following the Deviant event and belonging to the same pitch category are considered Standard. The length of the trains of high-pitch and low-pitch intervals was chosen according to a pseudorandom order, so that both the number of presentation and the average value of the Bayesian surprise associated to each stimulus were equal across interval type (i.e., fifths or tritones) and pitch type (i.e., high or low; see Figure 1). Moreover, the ratio between Standard (80%), and Deviant (20%) trials was kept equal across runs. Differently from traditional oddball paradigms, in rov- ing protocols, each stimulus has exactly the same probability to occur, thus allowing to dissect genuine effects of Bayesian percep- tual learning from rarity-driven modulations.

During the experiment participants were comfortably seated, given an incidental reading task (distance from the monitor % 70 cm), and instructed to ignore the sounds.

Aesthetic Judgment Task

At the end of the experimental session, participants were asked to evaluate aesthetically the four intervals employed in Experiment

1. High-pitch and low-pitch fifth and tritone intervals were pre- sented four times each, for a total of 16 AJs. Intervals were pre- sented in a random order after a variable intertrial interval, lasting from 6 to 8 s. Participants fixated a central white cross for the whole experiment. When they heard an interval, they were asked to wait (1 s) until the cross changed into a question mark and then respond. Participants evaluated the beauty of intervals using a Lik- ert scale ranging from 1 to 9 (where 1 corresponded to The most ugly sound I can imagine and 9 corresponded to The most beauti- ful sound I can imagine; thus using the same scale employed in previous studies of our research group: Sarasso, Ninghetto, et al., 2019; Sarasso, Ronga, et al., 2020), by pressing the corresponding key on the keyboard. AJs were registered (E-Prime 2.0 software, Psychology Software Tools, Sharpsburg, PA).

Experimental Procedures of Experiment 2 (Detection Task)

On a different day, the same 26 participants performed a detec- tion task where they had to respond as fast as possible by pressing the spacebar when they heard an interval (in Experiment 2 the same intervals of Experiment 1 were employed).

Within the experiment, trains of high-pitch and low-pitch inter- vals were intermixed according to the same pseudorandom order employed in Experiment 1 (i.e., we ensured that both the number of presentation and the average value of the Bayesian surprise associated to each stimulus were equal across interval type and pitch type; see Experimental Procedures of Experiment 1 above). Participants underwent four different runs (total duration of the experiment: approximately 10 minutes), each composed of 72 stimuli, with a variable interstimulus interval ranging from 1 to 2 s. As in Experiment 1, fifth intervals were presented in two runs only, while tritones were employed in the remaining two runs. Run order were counterbalanced across subjects.

RTs in response to each interval were registered (E-Prime 2.0 software, Psychology Software Tools, Sharpsburg, PA).

Data Analyses of Experiment 1 (Roving Paradigm and Aesthetic Judgment Task)

Electrophysiological Recordings and EEG Preprocessing

EEG was collected during the four runs of the MMN roving par- adigm with 32 Ag-AgCl electrodes placed on the scalp according to the extended International 10–20 system and referenced to the nose. Electrode impedances were kept below 5 kX. The electro- oculogram (EOG) was recorded from two surface electrodes placed over the right lower eyelid and lateral to the outer canthus of the right eye. EEG activity was recorded with a HandyEGG (Micromed, Treviso, Italy) amplifier and continuously digitized by at a sampling rate of 1,024 Hz.

Off-line EEG preprocessing and analyses were conducted with Letswave6 toolbox (Nocions, Louvain, Belgium) for Matlab (Mathworks, Natick, MA). Data were segmented into epochs of 1 s, including 200 ms prestimulus and 800 ms poststimulus intervals. Epochs were band-pass filtered (.5–40 Hz) using a fast Fourier transform filter (in accordance with previous literature exploring MMN effects and Bayesian surprise; Ostwald et al., 2012).

Filtered epoched data were baseline corrected using the interval from -.2 to 0 s as reference. Ocular artefacts were eliminated using Independent Component Analysis (ICA; Jung et al., 2000).

ERPs belonging to the same interval type (i.e., fifth or tritone) and to the same condition (i.e., standard vs. deviant) were then aver- aged, to obtain four average waveforms (i.e., Fifth Standard, Fifth Deviant, Tritone Standard, Tritone Deviant) for each subject.

Bayesian Perceptual Surprise Computation

For a detailed description of the mathematical computations please refer to the online supplementary materials. Similarly to previous stud- ies (Baldi & Itti, 2010; Itti & Baldi, 2009; Ostwald et al., 2012), to relate single-trial EEG signals and detection RTs to Bayesian perceptual learning we computed Bayesian surprise for each single trial using a sequential Bayesian learning algorithm of stimulus probabilities. The model assumes that the brain implements a trial-by-trial Bayesian pa- rameter learning scheme starting from an uninformative prior and computes Bayesian surprise as the divergence between the parameter prior and posterior probability density functions at the single-trial level. Following Ostwald et al. (2012), we use a variant of this model that assumes an exponential forgetting of stimuli that are observed in the distant past (we set the forgetting parameter to s = 4, which was shown to best describe neural activity; Ostwald et al., 2012). The degree of perceptual learning at the nth trial is then defined as Bayesian surprise, that is, the Kullback–Leibler divergence between the prior and poste- rior distribution over the probability of observing a high-pitch interval on the nth trial (Kullback, 1959; Cover & Thomas, 1991).

Aesthetic Judgment Task

AJs from the AJ task were averaged across interval types to obtain two average values per participant, one for perfect fifth intervals and one for tritones. Accordingly, in subsequent analyses EEG signals from the MMN roving paradigm corresponding to the presentation of tritones and fifth intervals were either assigned to the Preferred group or to the Nonpreferred group according to sin- gle participants' subjective preferences. For example, EEG signals corresponding to perfect fifth intervals from Subject 1 were assigned to the Preferred group, since Subject 1 rated perfect fifth intervals as more beautiful than tritones on average. On the con- trary, Subject 4 preferred tritones over perfect fifth intervals. Accordingly, EEG results corresponding to tritones were assigned to the Preferred group, while those corresponding to fifth intervals were assigned to the Nonpreferred group.

Statistical Analyses

For each participant and for the two interval types separately, MMN responses were obtained by subtracting the ERP elicited by standard intervals from that elicited by the deviant intervals (Näätänen et al., 2007). Importantly, in this analysis we included only the last standard trial for each stimulus train occurring before deviant trials (N = 208 per run; Ostwald et al., 2012). In this way, in the MMN analysis, the number of standard and deviant trials was matched. Single participants' MMN registered on single channels were entered in subsequent group-level analyses. We were interested in testing for possible differences in MMN responses corresponding to more and less appreciated interval types. Therefore, we performed a point-by- point t test (Novembre et al., 2018), with clustersize-based permuta- tion correction for multiple comparisons based on temporal consecu- tivity and spatial adjacency (1,000 permutations; alpha level = .05; percentile of mean cluster sum = 95; minimum number of adjacent channels = 3) on differential MMN (Deviant–Standard). The test compared single subjects' MMN amplitudes for Preferred and Non- preferred intervals at each time point, for each channel separately. This allowed us to identify time clusters containing mismatch detection responses (Deviant–Standard) that significantly differed between Preferred and Nonpreferred intervals. Moreover, as a control analysis, the same point-by-point t test was performed on single subjects' (N = 26) MMN corresponding to tritone and perfect fifth intervals inde- pendently from subjective preferences.

Preprocessed epochs and Bayesian surprise values corresponding to single trials constituted the input of a point-by-point trial-by-trial correlation analysis (Novembre et al., 2018; Sarasso, Ninghetto, et al., 2019; Sarasso, Ronga, et al., 2020). For each participant and for Pre- ferred and Nonpreferred intervals separately, the analysis computed the correlation between Bayesian surprise and trial-by-trial (N = 2,304) fluctuations of the EEG signal registered at single channels. The outcome of the correlation analysis was two 1 s-long (from .2 s preonset to .8 s postonset) time series of r-values for each channel for each subject. This constituted the input for the subsequent group-level two-tailed point-by-point t test with permutation-based correction for multiple comparisons (1,000 permutations; alpha level = .05; percen- tile of mean cluster sum = 95; minimum number of adjacent chan- nels = 3). The test compared single subjects' (N = 26) correlation coefficients (Preferred vs. Nonpreferred) at each time point. This allowed us to identify time clusters containing r values that signifi- cantly differed between Preferred and Non-Preferred intervals.

Single subjects' EEG preprocessed data are available at Mendeley. This study was not preregistered.

Data Analysis of Experiment 2 (Detection Task)

To investigate the presence of a positive correlation between RTs and Bayesian surprise on a trial-by-trial level, RTs from sin- gle trials were entered as a dependent variable in a linear mixed- model with subjects' ID as a random-effect factor and Bayesian surprise as a covariate (fixed-effect factor). This analysis was based on 5,184 observations (288 per each of the 26 participants). Overall, 95 trials (.022%) were considered as outliers (i.e., RTs exceeded 2 standard deviations from the single subject's mean) and were excluded from subsequent analyses (Ronga et al., 2018; Sarasso, Ronga, et al., 2019). Outliers were equally distributed across interval types and participants.

Results

Experiment 1 (Roving Paradigm and Aesthetic Judgment Task)

Aesthetic Judgements (AJs)

AJs from the original smaller sample (N = 18) replicated previ- ous findings (Bowling et al., 2018): more consonant intervals were on average more appreciated (fifths = 4.056 61.091) than more dis- sonant intervals (tritones = 3.827 6 .987). Thirteen participants rated fifth intervals as more beautiful than tritones, while the

remaining five preferred tritones over fifths. Importantly, at a group level (N = 18), AJs for the two interval types were not significantly

different (t = 1.395; p = .181; 95% CI [-.117, .575]), thus indicat- ing that participants were genuinely expressing a subjective aes-

thetic preference, rather than merely judging the stimuli according to a more general, objective feature, such as consonance.

AJs from the final group of 26 subjects (see Participants) with matched preferences (50% preferred fifth intervals, 50% preferred tritones) were similar for tritone (3.6 61.157) and fifth intervals (3.61 61.221) with no significant difference between the two.

ERP Results

ERP elicited by Preferred and Nonpreferred intervals (Method) registered from Fz are reported in Figure 2. Grand-average (N = 26) waveforms were comparable with previous studies on auditory frequency processing (Sams et al., 1985). For both Preferred and Nonpreferred intervals, MMN (Deviant minus Standard difference waveforms) showed a negative peak at approximately 225 ms postonset, coherently with previous findings (Sams et al., 1985). The point-by-point t test performed on mismatch detection responses registered on Fz (Preferred vs. Nonpreferred) revealed two significant time clusters: the first one centered on the average MMN waveform negative peak (215–260 ms; Figure 2); the sec- ond one occurring later at 680–716 ms postonset. As expected, MMN waveforms were significantly larger for more appreciated intervals. Results were comparable among fronto-central electro- des (the significant cluster corresponding to the MMN extended over Fpz, Fp1, Fp2, Fz, F4, FC2, FCz). We therefore show only results from the t test performed on Fz where differences in the mismatch detection performances are more pronounced.

Crucially, the result on MMN was independent from the more and less consonant interval type (fifth vs. tritone). Indeed, the point-by-point t test comparing MMN waveforms corresponding to the two different interval types showed no significant difference (Figure 3; see also the online supplementary materials). As shown in Figure 3, overall the amplitude of MMN negative peaks was always larger for the preferred interval.

Trial-by-Trial Correlation With Bayesian Surprise

The correlation analysis between single trial amplitudes and Bayesian Surprise indicated that r values peaked at 225 ms (cor- responding to the MMN peak latency; Figure 4) for both Pre- ferred and Nonpreferred intervals. Subsequent fluctuations in r values peaked at 300 ms and 450 ms postonset corresponding to the P3 and the N400 components (see Figure 4). These results confirmed our prediction, indicating that MMN best indexes Bayesian perceptual learning in our study. Furthermore, and in accordance with data from the literature, we also found a corre- lation between model updating following surprising stimuli and the P3 and N400 components (Bennett et al., 2015; Kolossa et al., 2015). Earlier MMN waveforms and later P3 and N400 com- ponents might be related to different levels of belief updates. More specifically, earlier MMN responses have been reported to better reflect the violation of phonetic and acoustic features (such as those occurring in our study; Friston et al., 2021). For this reason, MMN amplitude was considered the best candidate to reveal a significant difference between Preferred and Nonpre- ferred intervals.

More crucially, At Fz, results from the trial-by-trial correlation analysis performed on EEG responses following the presentation of Preferred and Nonpreferred intervals evidenced one signifi- cant cluster (i.e., r values significantly differed across Preferred and Nonpreferred intervals) corresponding to the latency of MMN (226–262 ms). The correlation between MMN amplitudes and Bayesian surprise was stronger for Preferred intervals. This result is crucial, since it shows that subjective preferences are linked to a more effective neural encoding of sensory surprise as indexed by MMN amplitudes, further confirming that the percep- tual learning of sensory regularities is enhanced for more appre- ciated intervals.

Experiment 2 (Detection Task)

As showed by the linear mixed-model analysis, RTs were found to be significantly correlated with trial-by-trial fluctuations in Bayesian surprise (p , .001; F = 47.096), indicating that Bayesian surprise can predict RTs from the Detection task. The positive estimate of the effect (estimate of the effect = 49.145; 95% CI [35.107, 63.183]; p ,

.001; t = 6.863) indicates that, as we predicted and coherently with previous studies, participants were slower to respond to more surpris- ing stimuli. The link between surprising sensory states as measured by Bayesian surprise and motor inhibition, which might subserve the update of behavioral plans according to newly acquired information (Wessel & Aron, 2017), further supports the idea that Bayesian sur- prise and MMN truly index perceptual learning in our study.

Discussion

In this study we showed that Bayesian surprise, an information- theoretic measure of perceptual learning, predicts trial-by-trial fluc- tuations of MMN (Experiment 1) and RTs (Experiment 2). Our results, thereby, demonstrated that perceptual learning induced by surprising sensory states is accompanied by specific electrophysio- logical and behavioral correlates, namely a fronto-central negativity corresponding to the MMN peak and motor inhibition.

Coherently with previous studies (Garrido et al., 2009; Näätänen et al., 2007), MMN differential waves peaked around 200 ms from stimulus onset and their (negative) amplitudes were maximal over frontal electrodes. Crucially, correlation coefficients between Bayesian Surprise and MMN amplitudes were larger for subjec- tively Preferred versus Nonpreferred intervals (i.e., subjects who preferred fifth intervals showed larger MMN and r values for fifth intervals and vice-versa). To the best of our knowledge, this is the first empirical evidence directly linking subjective aesthetic appreci- ation with perceptual learning, defined as the successful update of the brain representation of the sensory environment (Sarasso, Neppi-Modona, et al., 2020; Schoeller & Perlovsky, 2016; Van de Cruys & Wagemans, 2011). This result is independent from conso- nance level since the difference between MMN responses elicited by fifth vs tritones intervals per SE is not significant (see Figure 3). In the following paragraphs we provide a tentative interpretation of the present electrophysiological and behavioral results.

MMN Modulations Reflect Precision-Weighting of More and Less Preferred Sounds

Predictive coding theory (Friston & Kiebel, 2009; Friston, 2010) models perception as the process of computing hierarchical predic- tions of the sensory environment. Perceptual learning may be consid- ered as the implicit Bayes-optimal updating of the brain’s (predictive) representation to account for novel sensory stimuli (Fris- ton, 2003). According to predictive coding, prediction errors are pre- cision-weighted, in the sense that they are properly “weighted” by the system according to an estimate of their precision (Brown & Fris- ton, 2012), a complex measure of their reliability, varying as a func- tion of different context and stimuli-dependent parameters, such as signal-to-noise ratio. More precise prediction errors will induce larger updates of predictive models driving learning (den Ouden et al., 2012; Greve et al., 2017; Moran et al., 2013).

MMN is considered to reflect the violation of existing predic- tions on incoming sensory inputs, in case of unexpected events and to index the magnitude of the update of sensory predictions following precision-weighted stimulation (Auksztulewicz & Fris- ton, 2015; Garrido et al., 2016; Heilbron & Chait, 2018; Quiroga- Martinez et al., 2019; Stefanics et al., 2018). This hypothesis is supported by our findings showing that MMN indexed trial-by- trial fluctuations in Bayesian surprise, a measure of the update of predictions underlying Bayesian perceptual learning (Baldi & Itti, 2010; Itti & Baldi, 2009; Ostwald et al., 2012). Furthermore, hav- ing this in mind, differences in MMN across preferred and nonpre- ferred sounds suggest that precision weighting of prediction errors might be related to aesthetic preferences. Our results seem to indi- cate that MMN responses are enhanced for deviant preferred sounds, when compared to deviant less preferred ones, possibly because, in our study, the system marks as “more beautiful” the input subjectively weighted as more “precise.”

As it has previously suggested (for a detailed discussion see Sar- asso et al., 2021) contextual and cultural factors, as well as subjective experience (e.g., musical expertise) might modulate the estimated precision of consonant and dissonant sounds. It might be that differ- ent participants interpreted different sounds (fifths vs. tritones) as more and less precise. This precision-(up)weighting of incoming sen- sory inputs, electrophysiologically marked by larger MMNs (Lieder et al., 2013; Stefanics et al., 2018), induces greater updates of sensory predictive models, which in turn as predicted by our driving hypothe- sis, triggers aesthetic appreciation. As a supporting evidence for our interpretation, informational theoretic quantities of shifts in beliefs such as Bayesian surprise (a.k.a. informational value) were found to both attract attention (Baldi & Itti, 2010; Itti & Baldi, 2009) and to trigger activations of midbrain reward-related areas (Schwartenbeck et al., 2016), which are generally found to subtend aesthetic pleasure (Blood & Zatorre, 2001; Kawabata & Zeki, 2004).

Motor Inhibition as an Index of Surprising Sensory States

Previous studies suggest that the update of predictive representa- tions indexed by MMN responses co-occurs with a specific behavioral effect, that is, motor inhibition (Dutra et al., 2018; Ide et al., 2013; Wessel & Aron, 2017), related to the activation of a frontal network, directly inhibiting the excitability of the motor cortex (Bestmann et al., 2008; Mars et al., 2008; Dutra et al., 2018; Wessel & Huber, 2019). In Experiment 2, we tested the presence of such behavioral effect, by measuring the trial-by-trial correlation between RTs and Bayesian perceptual learning dynamics. In accordance with our pre- dictions and coherently with previous studies (Bestmann et al., 2008; Meindertsma et al., 2018), participants were slower to respond to more surprising stimuli. Motor inhibition in response to surprising sensory states has been proposed to serve as a functional “pause” state, crucial to reprogram behavior in accordance with the updated sensory representations (Wessel & Aron, 2017). Our findings confirm this hypothesis, evidencing the ability of RTs to effectively predict the amount of surprise conveyed by an incoming sensory input, on a trial- by-trial base. Parallelly, this evidence further testifies that Bayesian surprise actually measures perceptual learning in our study.

Aesthetic Appreciation as a Feedback of Perceptual Learning

We propose that aesthetic appreciation might be considered as a feedback signal facilitating the discrimination of informationally profitable stimuli (inducing larger prediction updates) from “unlearnable” noisy signals (Sarasso, Neppi-Modona, et al., 2020; Sarasso et al., 2021). According to this interpretation, aesthetic pleasure might motivate us to select and engage in “information- ally profitable” perceptual activities, independently from material or social reward (Chatterjee & Vartanian, 2016; Pearce et al., 2016).

Importantly, we are not arguing here that the entire range of human aesthetic experiences, as well as the pleasure we derive from the contemplation of art, can be merely explained by the dis- crimination of informationally-profitable low-level perceptual fea- tures (e.g., precision). Although this might be true in the case of

our study involving basic auditory stimulation, the “precision” of sensory inputs is only one of the aspects that might trigger the complex dynamics characterizing the perception of beauty. How- ever, it is interesting to note that often artists seem to implicitly exploit the aesthetic pleasure arising from the reduction of sensory uncertainty in their compositions. Musicians, for example, contin- uously and deliberately violate our predictions during the evolu- tion of a musical piece, thus letting us experience aesthetic pleasure whenever we are able to insightfully restore predictability and solve sensory uncertainty by updating our predictions (Huron, 2006; Kraehenbuehl & Meyer, 1957; Sarasso, Neppi-Modona, et al., 2020). Visual artists also create subtle violations of our expect- ations in the style and content of their pieces, possibly as a means to elicit the transition from prediction violations to reinstated pre- dictability (Kesner, 2014; Van de Cruys & Wagemans, 2011).

Conclusion

Our results, providing empirical evidence of a link between aes- thetic appreciation and implicit learning, seem to indicate that sometimes nice really comes with easy, as indicated by enhanced perceptual learning dynamics in correspondence to the emergence of hedonic aesthetic feedback.

The present findings might support the development of a theo- retical framework for the emerging study of the beneficial effects on learning and memory of aesthetic emotions, such as, for exam- ple, those induced by musicality (Lehmann & Seufert, 2018). On the other hand, aesthetic emotions have been already considered as a relevant factor in determining students’ engagement in learning activities (Parrish, 2009; Uhrmacher, 2009). Finally, computa- tional models of emotions subtending learning in humans could be tested in automatic machine learning research (Moerland et al., 2018), which aims at developing artificial intelligences that are intrinsically motivated to engage in efficient learning activities (Kaplan & Oudeyer, 2004).

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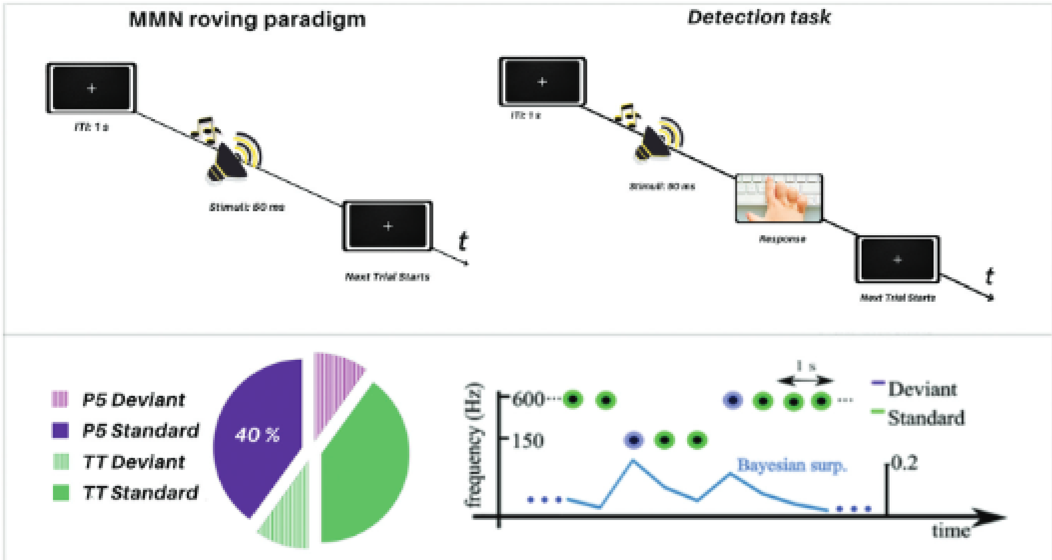


Figure 1

The Figure Represents Standard and Deviant Intervals and the Timelines of the Two Tasks

Composing Experiment 1 (Left–MMN Roving Paradigm) and Experiment 2 (Right–the Detection

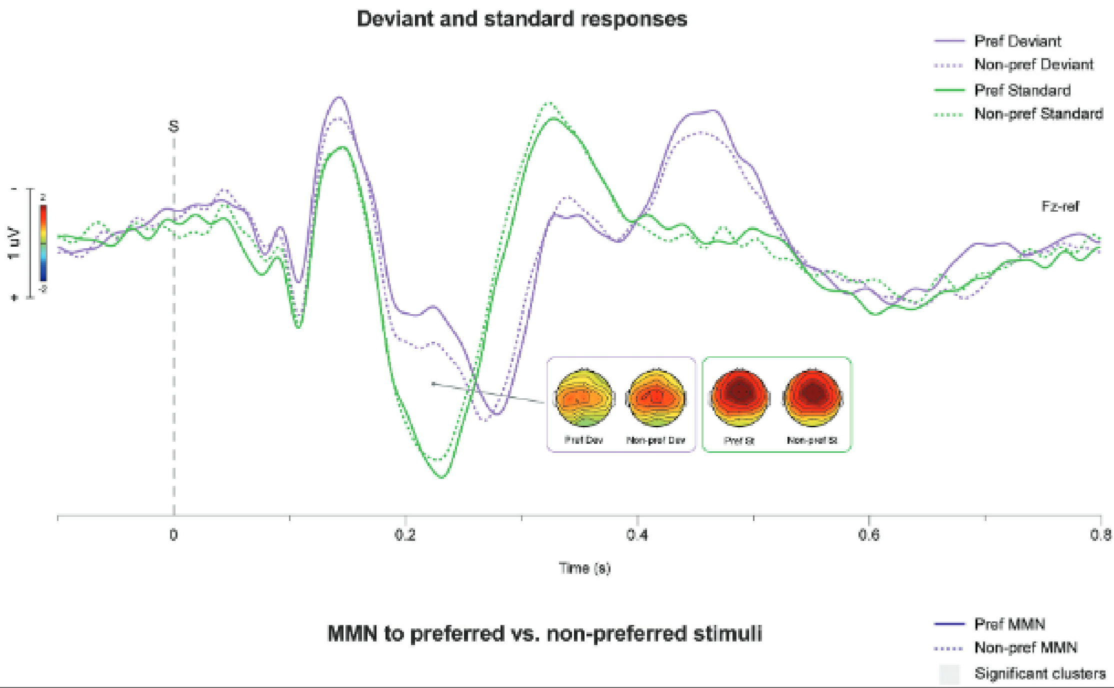
Task)

Note. In the mismatch negativity (MMN) roving paradigm participants passively listened to a train of 1,152 inter-

vals per run. The pie chart represents the percentages of Standard and Deviant fifth and tritone intervals employed in the two experiments. In both The MMN roving paradigm and the Detection task, participants performed a total of four runs. We presented fifth and tritone intervals separately, that is, two runs were composed of trains of high-pitch and low-pitch fifth intervals, whereas tritone intervals were employed in the remaining two runs. The graph

in the bottom right of the panel represents an example of a train of Standard and Deviant intervals. The frequency

(Hz) of the first note composing the interval (see Method) is represented on the y axis. Intervals which differed from the preceding one were considered as deviant. See the online article for the color version of this figure.



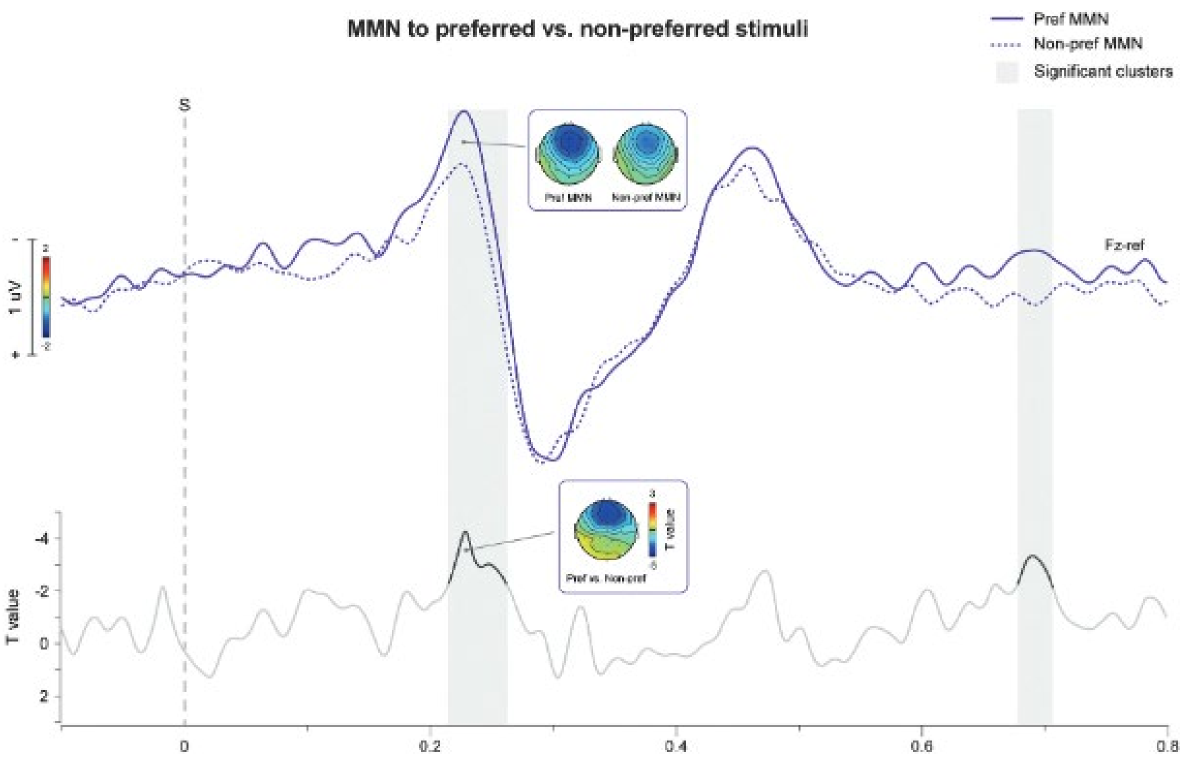


Figure 2

Preferred Versus Nonpreferred EEG Results

Note. The top panel shows the grand-average (N = 26) ERP registered from Fz for Preferred and Nonpreferred intervals (Method). Violet (dark

gray) and green (black) lines represent the average response to Deviant and Standard trials, respectively. Solid and dashed lines represent responses to

preferred and nonpreferred intervals. Scalpmaps depict amplitudes at 225 ms.The bottom panel depicts average MMN waveforms for Preferred and

Nonpreferred intervals (ERP difference between deviant and standard intervals registered on Fz). Shaded areas represent significant time-clusters high-

lighted by the point-by-by point t test comparing MMN waveforms (Preferred vs. Nonpreferred). The scalpmaps shows MMN amplitudes and t-values

across channels at 225 ms postonset; S = stimulus onset. See the online article for the color version of this figure.

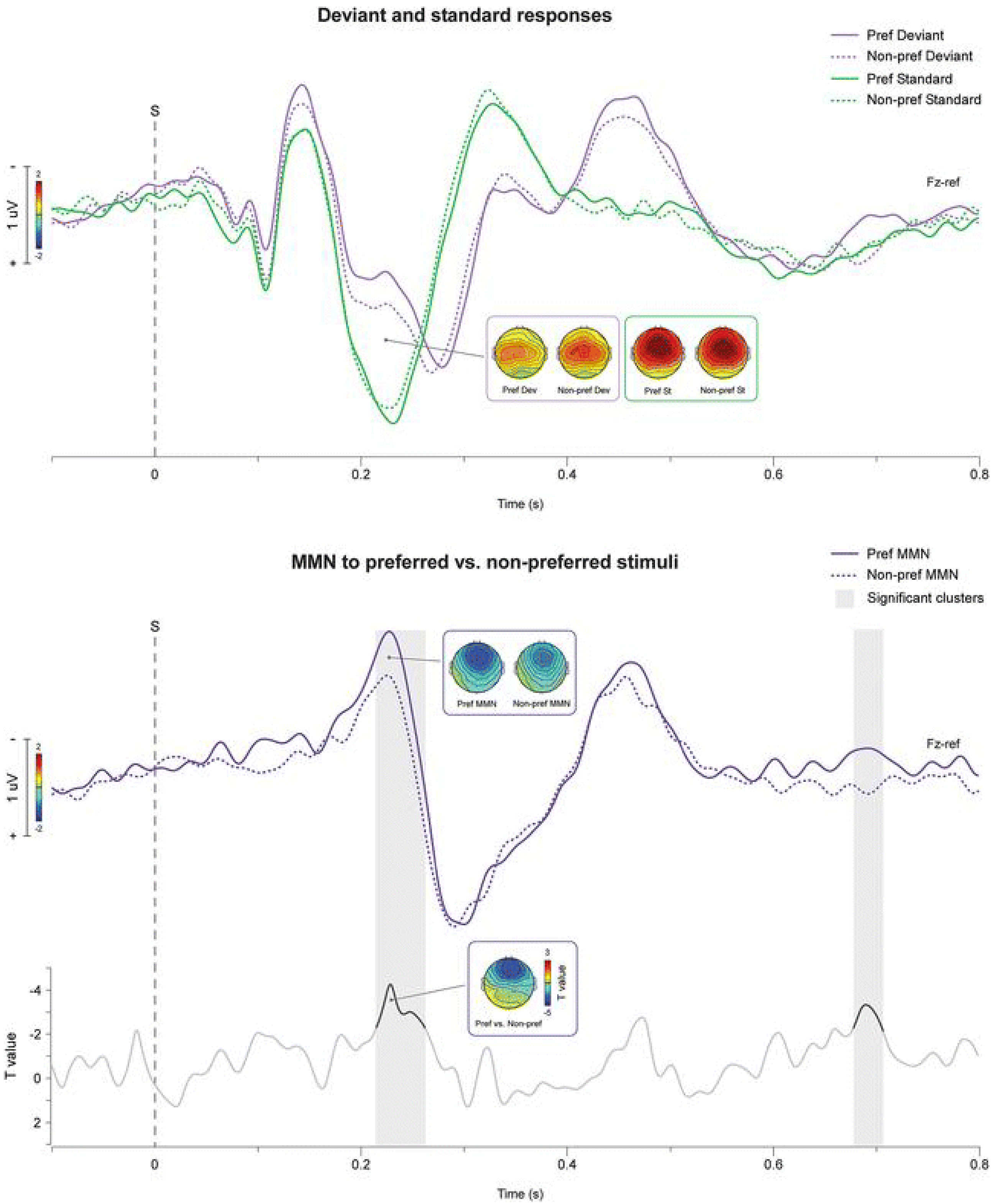


Figure 2. Note. The top panel shows the grand-average (N = 26) ERP registered from Fz for Preferred and Nonpreferred intervals (Method). Violet (dark gray) and green (black) lines represent the average response to Deviant and Standard trials, respectively. Solid and dashed lines represent responses to preferred and nonpreferred intervals. Scalpmaps depict amplitudes at 225 ms.The bottom panel depicts average MMN waveforms for Preferred and Nonpreferred intervals (ERP difference between deviant and standard intervals registered on Fz). Shaded areas represent significant time-clusters highlighted by the point-by-by point t

test comparing MMN waveforms (Preferred vs. Nonpreferred). The scalpmaps shows MMN amplitudes and t-values across channels at 225 ms postonset; S = stimulus onset. See the online article for the color version of this figure.

Crucially, the result on MMN was independent from the more and less consonant interval type (fifth vs. tritone). Indeed, the point-by-point t test comparing MMN waveforms corresponding to the two different interval types showed no significant difference (Figure 3; see also the online supplementary materials). As shown in Figure 3, overall the amplitude of MMN negative peaks was always larger for the preferred interval.

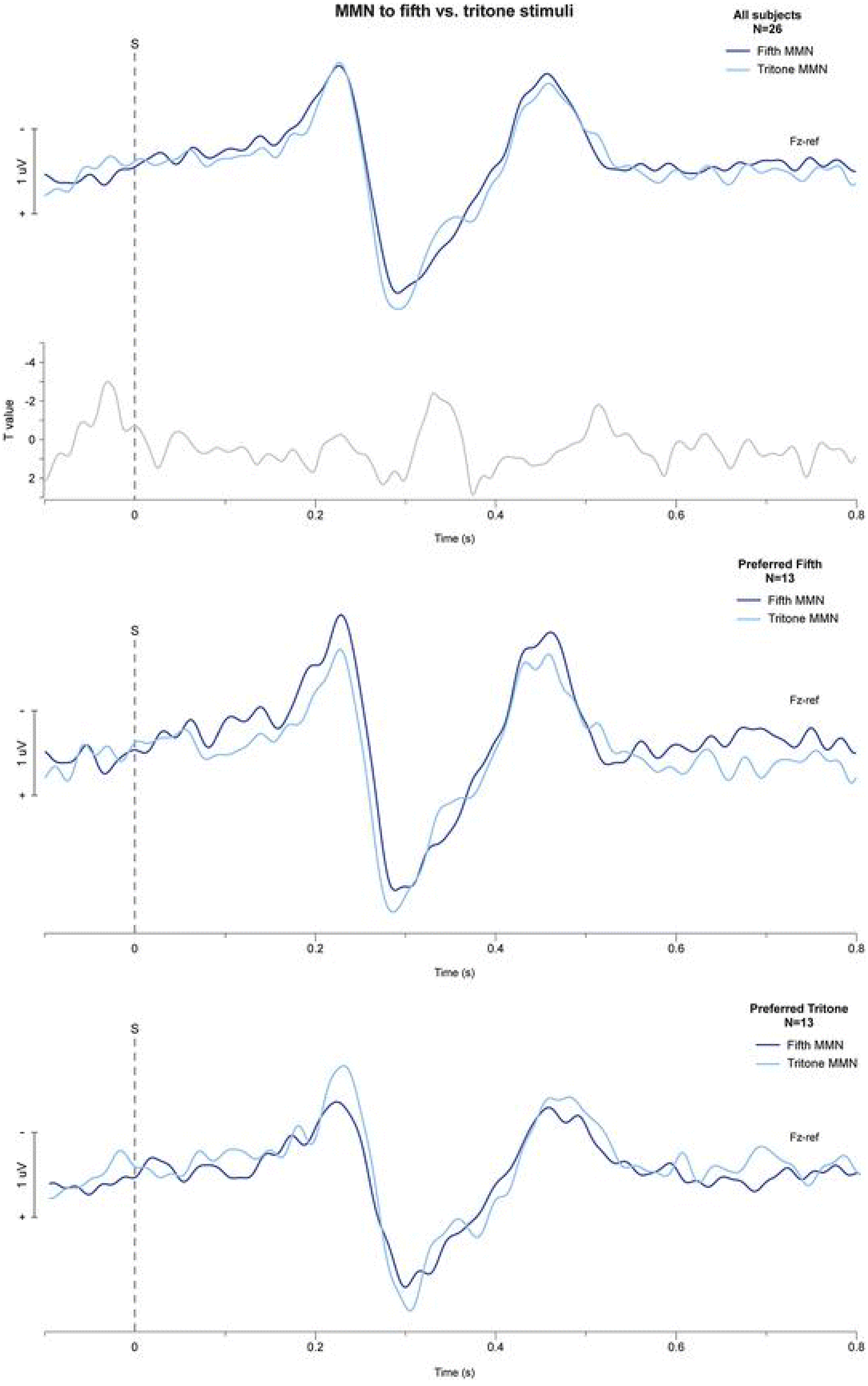
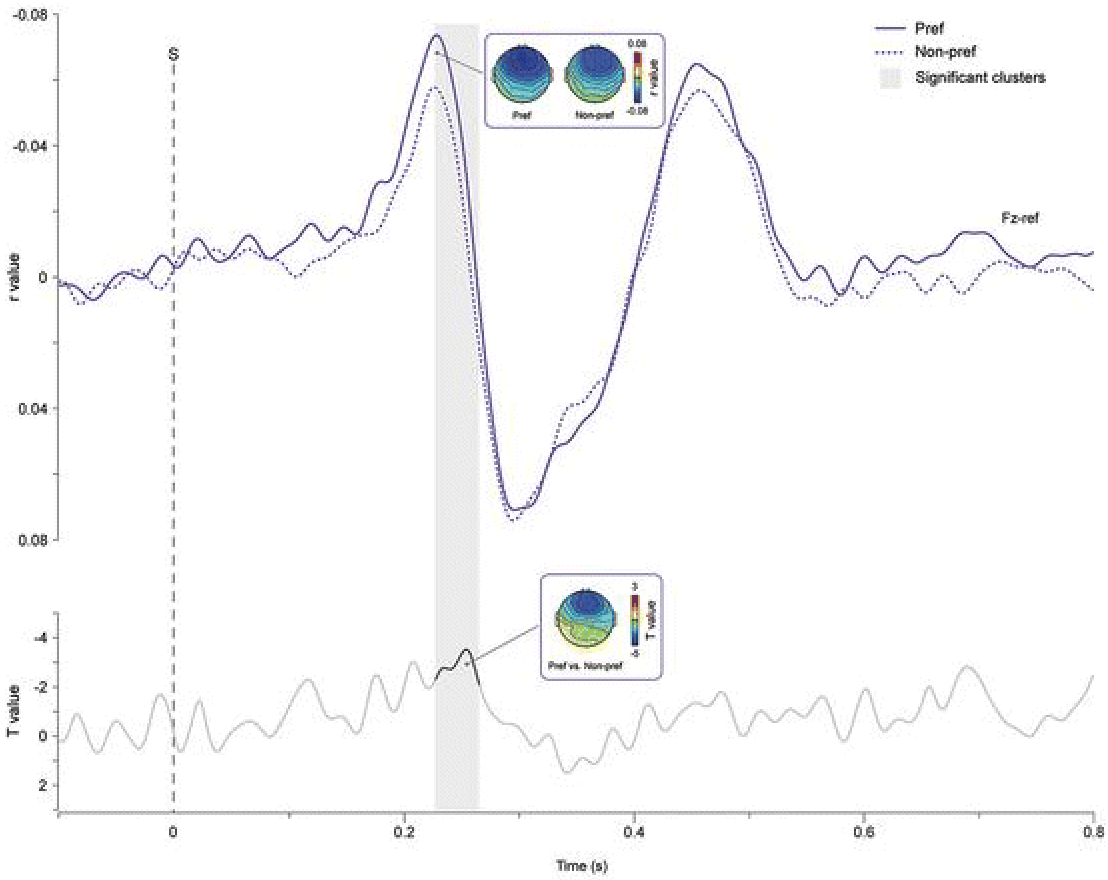


Figure 3. Note. *The top panel shows all participants' average mismatch negativity (MMN) waveforms (N = 26) for tritone and fifth intervals at channel Fz. The gray solid lines at the*

bottom of the first panel represent t-value computed by the point-by-point t-test comparing waveforms from fifth and tritone intervals (p values are reported in the online supplementary materials). In the middle panel, we included only results from the participants who preferred fifth intervals over tritone intervals. The light blue (light gray) and the dark blue (dark gray) solid lines represent average MMN waveforms (N = 13) for tritone and fifth respectively. The bottom panel shows results from the 13 participants who preferred tritone intervals over fifth intervals; S = stimulus onset. See the online article for the color version of this figure.

Trial-by-trial correlation with Bayesian Surprise for preferred vs. non-preferred stimuli



Trial-by-trial correlation with Bayesian Surprise for fifth vs. tritone stimuli

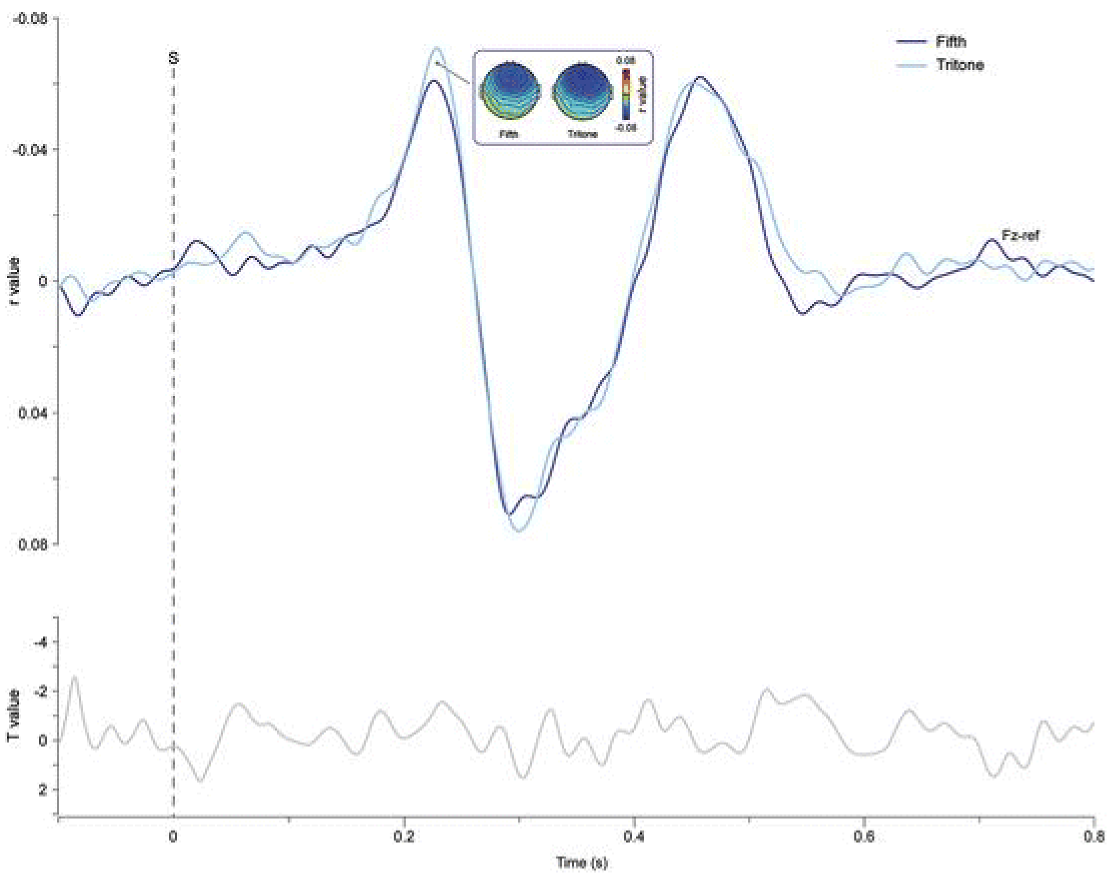


Figure 4. Note. *Waveforms represent average (N = 26) r values between trial-wise amplitude fluctuations registered at Fz and Bayesian Surprise. The top panel refers to subjectively preferred vs. Nonpreferred intervals, while the bottom panel shows the result from the same analysis comparing fifth and tritone intervals irrespectively of subjective preferences. Shaded areas represent significant clusters indicating significant differences between waveforms. Scalpmaps represent average r values and t values from the group level t-test (Trial-by-trial correlation with Bayesian surprise) at the correlation peak latency. S = stimulus onset. See the online article for the color version of this figure.*