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**Author(s):** Hsu, Yi-Fang; Hämäläinen, Jarmo A.

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**1 Impact statement**

2 We examined whether the reduction of precision-weighted prediction errors is jointly or  
3 separately determined by contextual regularity (as an external factor) and selective attention  
4 (as an internal factor) in hearing. The findings advance our understanding of how the reduction  
5 of prediction errors is accomplished to optimise auditory perception.

6

**Title**

Both contextual regularity and selective attention affect the reduction of precision-weighted prediction errors but in distinct manners

**Running head**

External/Internal effects on prediction errors

**Author names and affiliations**

Yi-Fang Hsu (yi-fang.hsu@cantab.net)<sup>a,b</sup>

Jarmo A. Hämäläinen (jarmo.a.hamalainen@jyu.fi)<sup>c</sup>

<sup>a</sup> Department of Educational Psychology and Counselling, National Taiwan Normal University, 10610 Taipei, Taiwan

<sup>b</sup> Institute for Research Excellence in Learning Sciences, National Taiwan Normal University, 10610 Taipei, Taiwan

<sup>c</sup> Jyväskylä Centre for Interdisciplinary Brain Research, Department of Psychology, University of Jyväskylä, 40014 Jyväskylä, Finland

Corresponding author: Yi-Fang Hsu (yi-fang.hsu@cantab.net) (+886-2-7749-3764)

**Conflict of interest**

The authors declare no competing financial interests.

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### **Author contributions**

Y-FH and JH designed the research and wrote the article. Y-FH performed the research and analysed the data.

## **Abstract**

Predictive coding model of perception postulates that the primary objective of the brain is to infer the causes of sensory inputs by reducing prediction errors (i.e., the discrepancy between expected and actual information). Moreover, prediction errors are weighted by their precision (i.e., inverse variance), which quantifies the degree of certainty about the variables. There is accumulating evidence that the reduction of precision-weighted prediction errors can be affected by contextual regularity (as an external factor) and selective attention (as an internal factor). However, it is unclear whether the two factors function together or separately. Here we used electroencephalography (EEG) to examine the putative interaction of contextual regularity and selective attention on this reduction process. Participants were presented with pairs of regular and irregular quartets in attended and unattended conditions. We found that contextual regularity and selective attention independently modulated the N1/MMN where repetition effect was absent. On the P2, the two factors respectively interacted with repetition effect without interacting with each other. The results showed that contextual regularity and selective attention more likely affect the reduction of precision-weighted prediction errors in distinct manners. While contextual regularity finetunes our efficiency at reducing precision-weighted prediction errors, selective attention seems to modulate the reduction process following the Matthew effect of accumulated advantage.

## **Keywords**

Auditory perception; predictive coding; prediction errors; precision; electroencephalography (EEG)

## 1. Introduction

Predictive coding is possibly one of the most influential frameworks for the study of perception, first conceptualised in the context of visual processing and soon tested in the field of audition (Schröger et al., 2015; Heilbron & Chait, 2017; Denham & Winkler, 2018). It argues that perception is realised within a hierarchical neural architecture, which implements a generative model describing the dynamic statistics of the environment (Rao & Ballard, 1999; Friston, 2005). Cortical processing stations send descending predictions to lower hierarchical levels to explain away ascending sensory signals. Only the differences between the descending predictions and the ascending sensory signals, conceived as prediction errors, are transmitted to higher hierarchical levels to adjust predictions. This explains many phenomena of perceptual learning in terms of the reduction of neural responses, such as repetition suppression (Baldeweg, 2006; Summerfield et al., 2008, 2011). Importantly, prediction errors are weighted by their precision (i.e., inverse variance), which quantifies the degree of certainty about the variables (Friston, 2005, 2009). The more precise the prediction errors are estimated to be, the more influence they have on the generative model.

The precision of prediction errors can be driven by contextual regularity as an external factor (Barascud et al., 2016; Southwell et al., 2017; Auksztulewicz et al., 2018). Contextual regularity refers to the statistical pattern of sensory signals, which the human brain can rapidly learn and exploit to improve perceptual inferences. Previous electroencephalography (EEG) and magnetoencephalography (MEG) studies showed that surprising stimuli elicited larger neuronal responses signalling prediction errors in high than low regularity context (N1: Hsu et al., 2015, 2018; mismatch negativity (MMN): Jacobsen & Schröger, 2001; Garrido et al., 2013; Quiroga-Martinez et al., 2019), suggesting that heightened contextual regularity increases the precision-weighting of prediction errors. Recent MEG studies further demonstrated that

contextual regularity modulates not only the precision-weighting of prediction errors but also how these precision-weighted prediction errors are reduced upon stimulus repetition (Hsu et al., 2019, 2020). Participants listened to repetition of unpredictable tones embedded in high and low regularity contexts. Specifically, high regularity context consisted of organised or familiar sound pattern, whereas low regularity context consisted of random or unfamiliar sound pattern. Therefore, participants would be respectively more and less certain of the prediction they are making. It was found that repetition suppression on the event-related fields (ERFs) in high and low regularity contexts started to dissociate on early components of the auditory responses, including the N1m (when contextual regularity was manipulated via changes in the orderliness of contextual tones) and N2m (when contextual regularity was manipulated via changes in the familiarity of contextual tones). Source-level analysis suggested that the reduction of precision-weighted prediction errors involved differential activation at temporal-frontal regions, where the reduction of high-precision prediction errors was more prominent than the reduction of low-precision prediction errors.

Notably, the precision of prediction errors can be driven by selective attention as an internal factor as well, which is involved in the control of the flow of information to establish and modify mental representations. In fact, selective attention can be understood as the optimisation of the precision of prediction errors (Feldman & Friston, 2010; Jiang et al., 2013). It was proposed that attending to a feature is equal to expecting that signals with this feature will be reliable. Previous studies already revealed the neuronal consequences of selective attention on event-related potentials (ERPs) as the enhancement of the N1 (Hillyard et al., 1973; Alcaini et al., 1994; Lange et al., 2003, 2006; Lange & Röder, 2006). This is regarded as evidence for a filter mechanism which amplifies the afferent activity to task-relevant information (Lange, 2013). Supporting the role of selective attention as precision-weighting, neurocomputational

work on the MMN further showed that the engagement of attention increases the synaptic gain of inhibitory interneurons to modulate the precision of prediction errors (Aukstulewicz & Friston, 2015). Meanwhile, much like contextual regularity, selective attention also modulates how precision-weighted prediction errors are reduced upon stimulus repetition (Hsu et al., 2014a). Specifically, it was found that repetition suppression on the P2 was conspicuous only when there was a moderate level of attention.

To summarise, there is accumulating evidence that both contextual regularity (as an external factor) and selective attention (as an internal factor) can affect the reduction of precision-weighted prediction errors upon stimulus repetition. However, it remains open whether and how the two factors might interact in this reduction process. It might be that the reduction of precision-weighted prediction errors is jointly determined by all the external and internal factors online. In this case, there should be a significant interaction between contextual regularity and selective attention in the reduction process. Alternatively, the reduction of precision-weighted prediction errors might consider the effects of external and internal factors in distinct manners. This would manifest as a lack of interaction between contextual regularity and selective attention in the reduction process.

The current study used EEG to examine whether and how contextual regularity and selective attention might interact to affect the reduction of precision-weighted prediction errors. In order to observe the reduction of prediction errors, we adapted our previous paradigms (Hsu et al., 2019, 2020) which presented participants with repetitive pairs of stimulation. To manipulate contextual regularity, we presented participants with pairs of tone quartets (which contained three prime tones of either regular or irregular pattern and one probe tone). In the **regular quartets**, the frequency of the three prime tones was identical and the frequency of the probe

tone was different from that of the prime tones (e.g., B4-B4-B4-A5 B4-B4-B4-A5). Here, the unpredictable probe tones A5 embedded in high regularity context should elicit up-weighted prediction errors. In the **irregular quartets**, the frequency of the three prime tones and the probe tone was determined by a pseudo-random selection without immediate repetition (e.g., B4-C5-F4-A5 B4-C5-F4-A5). Here, the unpredictable probe tones A5 embedded in low regularity context should elicit down-weighted prediction errors. To manipulate selective attention, participants were instructed to perform either a cover task of target detection to the auditory stimulation (i.e., the **attended condition** which should up-weight the auditory prediction errors) or a cover task of demanding counting based on silent videos (i.e., the **unattended condition** which should down-weight the auditory prediction errors). Notably, in all cases, the frequency of the probe tones would turn from unpredictable (upon their 1st presentation) to predictable (upon their 2nd presentation), signalling the reduction of precision-weighted prediction errors.

## 2. Method

### 2.1. Participants

A total of 28 healthy volunteers (age: mean = 20.18,  $SD = 0.86$ ; 3 males; 27 right-handed) participated in the experiment with no history of neurological, neuropsychiatric, or visual/hearing impairments as indicated by self-report. All participants gave written informed consent and were paid for participation. The study was conducted in accordance with the Declaration of Helsinki and approved by the Research Ethics Committee at National Taiwan Normal University.

### 2.2. Stimuli

14 sinusoidal tones were generated using Sound Forge Pro 10.0 (Sony Creative Software Inc.). The duration of each tone was 50 ms (including 5 ms rise/fall times). The frequency of each tone was within the range of 261.626 - 987.767 Hz, matching the absolute frequency of a series of 14 natural keys on a modern piano (i.e., C4 D4 E4 F4 G4 A4 B4 C5 D5 E5 F5 G5 A5 B5) (**Table 1**).

INSERT TABLE 1 ABOUT HERE

From the pool of 14 tones, a total of 204 pairs of tone quartets (including 102 pairs of regular quartets and 102 pairs of irregular quartets) were created using a stimulus onset asynchrony (SOA) of 500 ms. Note that the inter-quartet SOA was also 500 ms so that the pair structure was solely induced by stimulus repetition. Each pair of tone quartets consisted of a one-time repetition of three prime tones and one probe tone (i.e., prime1-prime2-prime3-probe prime1-prime2-prime3-probe). In each pair of tone quartet, the frequency of the three prime tones and the probe tone were randomly selected from the pool of 14 tones with the following constraints. For the **regular quartets**, the frequency of the three prime tones was identical and the frequency of the probe tone was different from that of the prime tones (e.g., B4-B4-B4-A5 B4-B4-B4-A5). For the **irregular quartets**, the frequency of the three prime tones and the probe tone was determined by a pseudo-random selection without immediate repetition (e.g., B4-C5-F4-A5 B4-C5-F4-A5) (**Figure 1A and 1B**).

INSERT FIGURE 1 ABOUT HERE

Out of the 204 pairs of tone quartets, 24 pairs of tone quartets (including 12 pairs of regular quartets and 12 pairs of irregular quartets) served as target trials to manipulate participants'

attention, where the frequency of one of the four tones changed from the 1st to the 2nd presentation (with its frequency determined by a random selection). The change occurred on one of the four tones with equal probability (i.e., 6 trials contained a change of frequency at prime1, 6 trials contained a change of frequency at prime2, 6 trials contained a change of frequency at prime3, and 6 trials contained a change of frequency at probe). These target trials were excluded from EEG data analysis.

### 2.3. Procedures

The 204 pairs of tone quartets were presented twice, once in attended condition and once in unattended condition. Participants were presented with 2 attended blocks (including 1 regular and 1 irregular blocks presented in randomised order) followed by 2 unattended blocks (including 1 regular and 1 irregular blocks presented in randomised order). Each block was separated into 2 miniblocks of 51 pairs of tone quartets so that participants could make a self-paced pause. Auditory stimulation was delivered binaurally via headphones (Sennheiser PX200-II) with an intensity of maximum 83.3 dB (56-82.7 dBA; 65-83.3 dBC). Participants were seated in front of a cathode-ray tube (CRT) screen viewed from a distance of 120 cm. In the **attended blocks**, participants were instructed to decide whether each tone quartet changes from the 1st to the 2nd presentation. They were instructed to make a key press within the 750-ms inter-trial interval (ITI) when there was a mismatch. Response outside of this time window would not be registered. A fixation cross (shown in grey against black background) remained on the screen for the duration of each block. In the **unattended blocks**, participants were asked to ignore the auditory stimulation and count the number of shots in two silent NBA video clips (for 1 regular and 1 irregular miniblocks) and the number of characters in two silent Moomin animation clips (for 1 regular and 1 irregular miniblocks). The two NBA video clips respectively contained 23 and 30 shots and the two Moomin animation clips respectively

contained 8 and 9 characters. Each clip (lasting 4 minutes 29 seconds) started before the first auditory stimulation and ended after the last auditory stimulation. The whole experiment took around 30 minutes (i.e., 408 trials x 4300 ms). E-prime version 2.0 (Psychology Software Tools) was used for stimulus presentation.

## **2.4. Data recording and analysis**

### ***2.4.1. EEG recording and pre-processing***

EEG was recorded from 62 sintered Ag/AgCl electrodes on a Neuroscan quik-cap according to the extended 10-20 system. The ground electrode was placed at AFz and the reference electrode was placed between Cz and CPz. Eye movements were monitored by additional four electrodes placed above and below the left eye and at the outer canthi of both eyes, which were bipolarized online to yield vertical and horizontal electrooculogram (EOG), respectively. All signals were amplified and online filtered at 0.1-100 Hz with the Neuroscan Synamps 2 amplifier (Compumedics Neuroscan, USA) and sampled at 500 Hz.

Target trials (where the frequency of one of the four tones changed from the 1st to the 2nd presentation) were excluded from EEG data analysis. Epochs extended from -100 ms to 500 ms relative to probe tone onset, using a -100 ms to 0 ms pre-stimulus baseline. Ocular artefact correction was conducted with independent component analysis (ICA) in EEGLab 14\_1\_2b (Delorme & Makeig, 2004) using the runica algorithm. Independent components capturing blinks and horizontal eye movements were determined by visual inspection based on their topographical distributions and power spectrum. For each participant, two components were pruned out of the data. Bad electrodes were identified (if there were more than 25% of the epochs containing voltage deviations exceeding  $\pm 100$   $\mu$ V relative to baseline) and interpolated using spherical interpolation. The data was recomputed to average reference. Epochs

containing voltage deviations exceeding  $\pm 100 \mu\text{V}$  relative to baseline at any of the electrodes were rejected. Lastly, the data was lowpass-filtered at 20 Hz. The trial numbers after artefact rejection in each condition are listed in **Table 2**.

INSERT TABLE 2 ABOUT HERE

#### **2.4.2. ERP analysis**

ERP analysis was based on a temporal principal component analysis (PCA) in SPSS 23. Since it was first introduced (Ruchkin et al., 1964; Donchin, 1966), PCA has been considered an effective linear reduction method for multivariate ERP data (Möcks, 1988a, 1988b; Duffy et al., 1992; Chapman & McCrary, 1995; Dien, 1998; Picton et al., 2000; Dien & Frishkoff, 2005; see Kayser & Tenke, 2003, Dien, 2012 for reviews). PCA statistically decomposes the ERP waveforms into constituent building blocks, which affords data-driven ERP component measures compared with other conventional methods (Kayser et al., 1998; Beauducel et al., 2000; Kayser & Tenke, 2006). Moreover, it is not as susceptible to the influences of high-frequency noises and low-frequency drifts in the data as other conventional methods (Luck, 2005). The PCA was run across all participants, yielding outputs at the individual level. Covariance matrix and Promax rotation were used here. All components accounting for a total of 99% of the variance (maximum iterations for convergence = 500) were included in the rotation (Promax kappa = 4). The decomposition provided a set of time-variant component loadings reflecting the contribution of each temporal component to the voltage at each time point and a set of time-invariant component scores (calculated using Bartlett method) representing the contribution of each temporal component to the ERP waveforms which can be subject to inferential statistics (Van Boxtel, 1998). The principal components (PCs) corresponding to the **N1/MMN** (i.e., PC4 accounting for 6.75% of the variance) and the **P2**

(i.e., PC3 accounting for 7.84% of the variance) were identified on the basis of component score topographies and component loading latencies.

The component scores were averaged across three electrodes showing the most negative and positive responses across all conditions independent of experimental manipulation (i.e., **N1/MMN**: FC4, C3, FC3 with reversed polarity at M2, M1, O2; **P2**: FCz, Cz, FC2 with reversed polarity at F7, M1, T8). The difference between the component maxima and its reversed polarity was considered as objective representatives of the components to serve as inputs for further statistical analyses. The advantage of averaging three most negative/positive electrodes was twofold. First, it increased the signal-to-noise ratio of the components. Second, it avoided the problems inherited in the analysis of predefined areas that took an average of multiple electrodes over pre-defined regions, which might not correspond to the true topographies in the experiment.

To test how contextual regularity and selective attention might interact to affect the reduction of precision-weighted prediction errors upon stimulus repetition, a 2 (regular/irregular) x 2 (attended/unattended) x 2 (1st/2nd presentation) repeated-measures ANOVA was performed.

### **3. Results**

#### **3.1. Behavioural data**

In the attended blocks, participants were instructed to make a key press when there was a mismatch between pairs of tone quartets. In this cover task of target detection, participants' responses within the 750-ms ITI were counted as hits (if made to the target trials) and false alarms (if made to the rest of the trials). Their  $d'$  was calculated on the basis of adjusted extreme rate, where rates of 0 were replaced with  $0.5/n$  and rates of 1 were replaced with  $(n-0.5)/n$ , with

n being the number of signal or noise trials (Stanislaw & Todorov, 1999). **Table 3** shows that their hit rate was moderate and their false alarm rate was low. Paired-samples t-test revealed significant difference between regular and irregular blocks in  $d'$  ( $t(27) = 3.46, p < .01$ ). We further calculated the hit rate separately for prime1, prime2, prime3, and probe in regular and irregular blocks (**Table 4**), where there were 3 target trials per condition. The results were submitted to a 2 (regular/irregular) x 4 (prime1/prime2/prime3/probe) repeated-measures ANOVA. There was a significant regularity x order interaction ( $F(2.31, 62.40) = 7.25, p \leq .001, \eta_p^2 = 0.21$ ). Posthoc comparisons with Bonferroni correction ( $p = .05/4$ ) showed that hit rate was higher in regular than irregular blocks on prime1 ( $t(27) = 3.97, p < .001$ ) and prime3 ( $t(27) = 4.50, p < .001$ ) but not on prime2 ( $t(27) = 0.88, p = .39$ ) and probe ( $t(27) = 2.47, p = .02$ ). Overall, the pattern suggested that participants didn't necessarily attend to regular and irregular stimuli in the same manner.

INSERT TABLE 3 ABOUT HERE

INSERT TABLE 4 ABOUT HERE

In the unattended blocks, participants were asked to ignore the auditory stimulation and count the number of shots in the NBA video clips and the number of characters in the Moomin animation clips. We calculated how much participants' reported numbers deviated from the actual numbers (i.e., the smaller the discrepancy, the better the performance). Participants' performance was at ceiling (NBA video clips: mean = 0.82,  $SD = 1.04$ ; Moomin animation clips: mean = 0.29,  $SD = 0.52$ ), suggesting that they followed the instruction to focus on this cover task of demanding counting. Paired-samples t-test showed no significant difference

between regular and irregular blocks in the NBA video clips ( $t(27) = 0.53, p = .60$ ) and the Moomin animation clips ( $t(27) = 0.64, p = .53$ ).

### 3.2. ERP data

**Figure 2** shows the grand average ERPs on three representative electrodes at midline (i.e., Fz, Cz, Pz) and M1, where N1/MMN with a frontocentral distribution and P2 with a central distribution are evident. **Figure 3** shows the results of the temporal PCA yielding 24 PCs. PC4 and PC3 are respectively identified as components corresponding to the N1/MMN and the P2.

INSERT FIGURE 2 ABOUT HERE

INSERT FIGURE 3 ABOUT HERE

A 2 (regular/irregular) x 2 (attended/unattended) x 2 (1st/2nd presentation) repeated-measures ANOVA was performed on the difference between the component maxima and its reversed polarity for the N1/MMN and P2 (**Figure 4**).

INSERT FIGURE 4 ABOUT HERE

#### 3.2.1. N1/MMN component

There was no regularity x attention x repetition interaction ( $F(1,27) = 0.11, p = .74, \eta_p^2 < 0.01$ ) nor any two-way interaction (regularity x attention:  $F(1,27) = 3.01, p = .09, \eta_p^2 = 0.10$ ; regularity x repetition:  $F(1,27) = 1.87, p = .18, \eta_p^2 = 0.07$ ; attention x repetition:  $F(1,27) = 0.04, p = .84, \eta_p^2 < 0.01$ ). However, there was a significant main effect of **regularity** ( $F(1,27) = 70.24, p < .001, \eta_p^2 = 0.72$ ) where regularity enhanced the N1/MMN and a significant main

effect of **attention** ( $F(1,27) = 15.99, p < .001, \eta_p^2 = 0.37$ ) where attention enhanced the N1/MMN (**Figure 4B** left). The main effect of repetition did not reach significance ( $F(1,27) = 1.04, p = .32, \eta_p^2 = 0.04$ ).

### 3.2.2. P2 component

There was no regularity x attention x repetition interaction ( $F(1,27) = 0.09, p = .76, \eta_p^2 < 0.01$ ). However, there was a significant regularity x repetition interaction ( $F(1,27) = 13.00, p \leq .001, \eta_p^2 = 0.33$ ) and a significant attention x repetition interaction ( $F(1,27) = 32.65, p < .001, \eta_p^2 = 0.55$ ) (**Figure 4B** right). For the **regularity x repetition** interaction, post hoc comparisons showed that repetition effect was significant in the regular condition ( $t(27) = -5.03, p < .001$ ) but not irregular condition ( $t(27) = 0.15, p = .89$ ). Moreover, it manifested as repetition enhancement rather than repetition suppression. For the **attention x repetition** interaction, post hoc comparisons showed that repetition effect was significant in both attended condition ( $t(27) = -5.84, p < .001$ ) and unattended condition ( $t(27) = 3.09, p < .01$ ). Specifically, there was a repetition enhancement in attended condition but a repetition suppression in unattended condition. The regularity x attention interaction did not reach significance ( $F(1,27) = 2.28, p = .14, \eta_p^2 = 0.08$ ).

### 3.2.3. Further analyses

The aforementioned findings based on PCA were confirmed in a traditional analysis on the peak amplitude of the N1/MMN and P2. Firstly, we identified three electrodes showing the most negative and positive responses on the grand averaged ERPs across all conditions independent of experimental manipulation over the time window of 70-130 ms for N1/MMN (i.e., C3, FC5, C5) and 160-240 ms for P2 (i.e., FCz, Cz, C2). Thereafter, we averaged the ERPs across these three electrodes for each participant/condition. Lastly, we identified the peak

amplitude within the time window of 70-130 ms for N1/MMN and 160-240 ms for P2 for each participant/condition, which was then submitted to a 2 (regular/irregular) x 2 (attended/unattended) x 2 (1st/2nd presentation) repeated-measures ANOVA (see Supplementary Material for statistical details).

To further examine whether the topographical distribution of the N1/MMN and P2 differed between conditions of interest, a 2 (regular/irregular) x 2 (attended/unattended) x 2 (1st/2nd presentation) x 3 (frontal/central/parietal) x 3 (left/midline/right) repeated-measures ANOVA was performed on the component scores at 9 representative sites (i.e., F3, Fz, F4, C3, Cz, C4, P3, Pz, P4).

On the N1/MMN, there was no three-way interaction between **regularity**, caudality, and laterality ( $F(3.06,82.47) = 1.83, p = .15, \eta_p^2 = 0.06$ ). Regularity interacted with caudality ( $F(1.21,32.78) = 33.07, p < .001, \eta_p^2 = 0.55$ ), but post hoc comparisons showed that the regularity effect was significant at all sites (frontal:  $t(27) = -8.07, p < .001$ ; central:  $t(27) = -6.17, p < .001$ ; parietal:  $t(27) = 2.88, p < .01$ ). Regularity interacted with laterality ( $F(1.60,43.13) = 5.01, p < .05, \eta_p^2 = 0.16$ ), but post hoc comparisons showed that the regularity effect was significant at all sites (left:  $t(27) = -5.40, p < .001$ ; midline:  $t(27) = -5.17, p < .001$ ; right:  $t(27) = -5.67, p < .001$ ). On the other hand, there was no three-way interaction between **attention**, caudality, and laterality ( $F(2.80,75.69) = 1.41, p = .25, \eta_p^2 = 0.05$ ). Moreover, attention did not interact with either caudality ( $F(1.18,31.84) = 0.95, p = .35, \eta_p^2 = 0.03$ ) or laterality ( $F(2,54) = 0.30, p = .75, \eta_p^2 = 0.01$ ). Therefore, there was little evidence that the aforementioned main effects of regularity and attention were influenced by the position of selected electrodes.

On the P2, the **regularity x repetition** effect did not interact with caudality ( $F(1,30,35.17) = 3.38, p = .06, \eta_p^2 = 0.11$ ) but it did interact with laterality ( $F(2,54) = 6.42, p < .01, \eta_p^2 = 0.19$ ). Tests of simple main effects showed that the regularity x repetition effect was non-significant at left sites but significant at midline and right sites (left:  $F(1,27) = 0.07, p = .79, \eta_p^2 < 0.01$ ; midline:  $F(1,27) = 11.52, p < .01, \eta_p^2 = 0.30$ ; right:  $F(1,27) = 11.24, p < .01, \eta_p^2 = 0.29$ ). Meanwhile, the **attention x repetition** effect did not interact with caudality ( $F(1.56,42.19) = 1.98, p = .16, \eta_p^2 = 0.07$ ) but it did interact with laterality ( $F(2,54) = 4.67, p < .05, \eta_p^2 = 0.15$ ). Tests of simple main effects showed that the attention x repetition effect was significant at all sites (left:  $F(1,27) = 4.57, p < .05, \eta_p^2 = 0.15$ ; midline:  $F(1,27) = 22.69, p < .001, \eta_p^2 = 0.46$ ; right:  $F(1,27) = 19.76, p < .001, \eta_p^2 = 0.42$ ).

As seen in **Figure 2**, the frontal channels show a frontocentral negativity following the P2 starting at around 300 ms which seems to be prominent for the regular, attended, and 1st presentation condition. For exploratory purpose, we performed a 2 (regular/irregular) x 2 (attended/unattended) x 2 (1st/2nd presentation) ANOVA on the N2 (i.e., PC2 accounting for 14.70% of the variance). There was no regularity x attention x repetition interaction ( $F(1,27) = 0.04, p = .84, \eta_p^2 < 0.01$ ). There was neither regularity x repetition interaction ( $F(1,27) = 0.45, p = .51, \eta_p^2 = 0.02$ ) nor attention x repetition interaction ( $F(1,27) = 1.47, p = .24, \eta_p^2 = 0.05$ ). However, there was a significant regularity x attention interaction ( $F(1,27) = 4.19, p \leq .05, \eta_p^2 = 0.13$ ). Posthoc comparisons showed that the N2 was larger (i.e., more negative) to regular than irregular stimuli in attended condition ( $t(27) = -3.68, p \leq .001$ ) but not unattended condition ( $t(27) = -0.92, p = .36$ ). The main effect of repetition did not reach significance ( $F(1,27) = 3.51, p = .07, \eta_p^2 = 0.12$ ).

#### 4. Discussion

Here we used EEG to examine the putative interaction of contextual regularity (as an external factor) and selective attention (as an internal factor) on the reduction of precision-weighted prediction errors upon stimulus repetition. Participants were presented with pairs of regular and irregular quartets in attended and unattended conditions. We found that contextual regularity and selective attention independently modulated the N1/MMN where repetition effect was absent. On the P2, the two factors respectively interacted with repetition effect without interacting with each other. The results suggested that these two factors separately affect the reduction of precision-weighted prediction errors.

#### **4.1. Both external and internal factors affected the precision-weighting mechanism**

The significant main effect of contextual regularity and selective attention on the N1/MMN suggested that the precision-weighting mechanism might be independently driven by external and internal factors. The topographical distributions of the N1/MMN further indicated that the two factors more likely affect the precision-weighting mechanism in different ways.

On the one hand, **contextual regularity** enhanced the N1/MMN independent of selective attention, suggesting that it increased the precision-weighting of prediction errors in an automatic fashion. The result is in line with previous reports that probe sounds triggered larger N1 when preceded by regular prime sounds than when preceded by random prime sounds (Hsu et al., 2015, 2018) and that deviant sounds triggered larger MMN when embedded in repetitive standard sequences than when embedded in equiprobable standard sequences (Jacobsen & Schröger, 2001; Quiroga-Martinez et al., 2019; see Näätänen et al., 2005 for reviews). Admittedly, the manipulation of contextual regularity in the current study (as well as previous research using the MMN paradigm) seemed to involve different amounts of local adaptation. Specifically, while regular context (cf. repetitive sequences preceding the MMN) consisted of

repetitive prime tones of fixed frequency, irregular context (cf. equiprobable sequences preceding the MMN) consisted of random-frequency prime tones. Thus, the observed increase in N1/MMN could, to an undetermined extent, result from the increase in repetition positivity to repetitive but not equiprobable standards (Baldeweg, 2007).

On the other hand, **selective attention** enhanced the N1/MMN independent of contextual regularity. This is in contrast with the idea that selective attention adjusts the precision-weighting of prediction errors synergistically with contextual regularity. For example, when participants performed a cover task of target detection based on the amplitude of continuous stimulus streams, selective attention was found to enhance the N1 to a larger extent for tones embedded in regular stimulus streams than tones embedded in random stimulus streams (Hsu et al., 2014b), speaking to the notion that selective attention amplified the gain of prediction errors to a larger extent in high regularity context than low regularity context. We speculate that whether selective attention could equally enhance prediction errors in low regularity context might be attributed to a number of procedural variations between studies. First, the cover task might be more taxing in the current study (i.e., detection of changes in frequency rather than amplitude). Second, it might be that the trials were of clearer structure in the current study (i.e., pairs of tone quartets rather than continuous stimulus streams). These factors could enlarge the amount of attentional enhancement in low regularity context which failed to reach significance in previous studies.

Earlier reviews documented that multiple components might contribute to the scalp-recorded N1/MMN (Näätänen & Picton, 1987). The topographical distributions of the N1/MMN in the current study (**Figure 4A**) further indicated that certain subcomponents might be respectively more sensitive to the modulating effects of contextual regularity and selective attention.

Specifically, the main effect of contextual regularity seems to result from regular context eliciting vertex maxima but irregular context eliciting temporal maxima. Meanwhile, selective attention enhanced both vertex negativity in regular context and temporal negativity in irregular context. The pattern suggested that, although both contextual regularity (as an external factor) and selective attention (as an internal factor) can modulate the precision-weighting of prediction errors, the two factors function in different manners.

#### **4.2. Repetition effect (signalling the suppression of precision-weighted prediction errors) appeared on the P2**

To our surprise, repetition effect (signalling the reduction of precision-weighted prediction errors) was absent on the N1/MMN. The lack of repetition effect on the N1/MMN suggested that, in the current study, the brain can register the precision-weighted prediction errors (determined by contextual regularity and selective attention) disregarding the new/old status of the stimuli. Nevertheless, repetition effect soon appeared on the P2, where contextual regularity and selective attention respectively interacted with repetition effect without interacting with each other.

##### ***4.2.1. Contextual regularity controlled the presence/absence of repetition effect***

Repetition effect was significant in regular condition but not irregular condition. Moreover, it manifested as repetition enhancement rather than repetition suppression on the P2. At first glance, it seems contradictory to previous research reporting significant repetition suppression in high-precision context but not low-precision context on the N1m (Hsu et al., 2020) and N2m (Hsu et al., 2019). However, it is likely that the repetition enhancement of the P2 here and the repetition suppression of the N1m and N2m in previous studies can be attributed to a similar mechanism of repetition positivity (Costa-Faidella et al., 2011), where stimulus repetition

elicited more positive-going ERPs at 50-250 ms reflecting sensory memory trace formation in the auditory cortex (Haenschel et al., 2005; Baldeweg, 2006, 2007). Admittedly, it is unclear why the dissociation occurred at various latencies in the literature. It leaves an interesting question for future research to examine possible factors affecting the onset of such distinctive mechanism. Nevertheless, the more positive-going ERPs to stimulus repetition in regular condition but not irregular condition support the idea that the reduction of precision-weighted prediction errors via stimulus repetition depends on its initial precision status. Our brain seems more efficient at reducing precision-weighted prediction errors from a regular context than an irregular context. The current study further showed that such distinctive mechanism is independent of selective attention, so it might be automatic in nature.

#### ***4.2.2. Selective attention reversed the sign of repetition effect***

Repetition effect was significant in both attended and unattended condition, where there was a repetition enhancement in attended condition but a repetition suppression in unattended condition. This disagrees with previous research reporting that, when participants were presented with succession of repetitive tones (i.e., AADDBBXX), repetition suppression on the P2 was prominent only when there was a moderate level of attention (Hsu et al., 2014a). The discrepancy might result from the different time scales of stimulus repetition. In the current study, stimulus repetition was not presented in succession of repetitive tones but in pairs of tone quartets. Therefore, the repetition effect observed here might reflect less of spontaneous process but more of sensory memory trace formation regarding sound pattern. Meanwhile, previous functional magnetic resonance imaging (fMRI) studies in the visual domain similarly reported that selective attention reversed the prediction effect in early visual cortex, showing prediction enhancement when attended but prediction suppression when unattended (Kok et al., 2012). Altogether, the results suggested that selective attention modulates the gain of

prediction errors to repeated stimuli following the Matthew effect (i.e., the rich get richer and the poor get poorer). When attended, higher precision is assigned to the stimulus; stimulus repetition would further up-weight the already up-weighted prediction errors. When unattended, lower precision is assigned to the stimulus; stimulus repetition would further down-weight the already down-weighted prediction errors.

Interestingly, the reversed sign of repetition effect was also commonly shown in previous fMRI research manipulating stimulus quality. Specifically, the sign of repetition effect was reported to depend on stimulus visibility (Turk-Browne et al., 2007) and stimulus familiarity (Henson et al., 2000; Fiebach et al., 2005; Gagnepain et al., 2008; Soldan et al., 2008; Müller et al., 2013; Subramaniam et al., 2012). It was proposed that repeated stimuli without pre-existing representation (e.g., low visibility or unfamiliar stimuli) would elicit repetition enhancement indicating increased processing efforts, whereas repeated stimuli with pre-existing representation (e.g., high visibility or familiar stimuli) would elicit repetition suppression indicating that processing efforts are redirected to other novel information (Turk-Browne et al., 2008). The current study further demonstrated that selective attention is another factor that can reverse the sign of repetition effect.

The data also suggested that the detection of prediction errors in regular/irregular stimuli lead to differences in later emerging cognitive processes as reflected by the frontocentral negativity following the P2. This could be related to attention allocation, stimulus classification, and/or orienting processes.

### **4.3. Conclusion**

Overall, the current study demonstrated that contextual regularity (as an external factor) and selective attention (as an internal factor) more likely affect the reduction of precision-weighted prediction errors in distinct manners. While contextual regularity finetunes our efficiency at reducing precision-weighted prediction errors, selective attention seems to modulate the reduction process following the Matthew effect of accumulated advantage.

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## Tables

**Table 1.** Frequency of each tone.

	<b>C4</b>	<b>D4</b>	<b>E4</b>	<b>F4</b>	<b>G4</b>	<b>A4</b>	<b>B4</b>
<b>Frequency</b>	261.63	293.67	329.63	349.23	392.00	440.00	493.88
<b>(Hz)</b>							
	<b>C5</b>	<b>D5</b>	<b>E5</b>	<b>F5</b>	<b>G5</b>	<b>A5</b>	<b>B5</b>
<b>Frequency</b>	523.25	587.33	659.26	698.46	783.99	880.00	987.77
<b>(Hz)</b>							

**Table 2.** Range, mean, and *SD* of trial numbers after artefact rejection in each condition.

		<b>Attended</b>		<b>Unattended</b>	
		<b>1st</b>	<b>2nd</b>	<b>1st</b>	<b>2nd</b>
<b>Regular</b>	<b>Range</b>	60-90	57-90	57-90	61-90
	<b>Mean</b>	84.79	84.50	83.14	83.79
	<b><i>SD</i></b>	8.11	8.44	9.10	8.15
<b>Irregular</b>	<b>Range</b>	58-90	56-90	66-90	66-90
	<b>Mean</b>	84.82	85.43	85.21	85.14
	<b><i>SD</i></b>	9.11	8.84	6.49	7.11

**Table 3.** Mean (*SD*) of hit rate, false alarm rate, and *d'* in regular and irregular blocks when attended.

	<b>Regular</b>	<b>Irregular</b>
<b>Hit rate</b>	0.59 (0.21)	0.42 (0.16)
<b>False alarm rate</b>	0.03 (0.09)	0.03 (0.05)

<b><i>d'</i></b>	2.51 (0.90)	1.90 (0.57)
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**Table 4.** Mean (*SD*) of hit rate separately for prime1, prime2, prime3, and probe in regular and irregular blocks when attended.

	<b>Regular</b>				<b>Irregular</b>			
	<b>Prime 1</b>	<b>Prime 2</b>	<b>Prime 3</b>	<b>Probe</b>	<b>Prime 1</b>	<b>Prime 2</b>	<b>Prime 3</b>	<b>Probe</b>
<b>Hit</b>	0.56	0.65	0.76	0.40	0.23	0.73	0.48	0.26
<b>rate</b>	(0.36)	(0.33)	(0.24)	(0.33)	(0.22)	(0.32)	(0.25)	(0.26)

## Figure legends

**Figure 1.** (A) Schematic illustration of pairs of regular and irregular quartets. (B) On each trial, a pair of tone quartets (consisting of tones of 50-ms-duration) were presented with a 500 ms SOA. Each trial was followed by an ITI of 750 ms.

**Figure 2.** Grand average ERPs on three representative electrodes at midline (i.e., Fz, Cz, Pz) and M1. The N1/MMN and P2 are marked with arrows for ease of reference.

**Figure 3.** (A) Scree plot showing the eigenvalues of the 24 PCs in the temporal PCA. The 1st-4th PCs explain more than 5% of variance each and the 5th-13th PCs explain more than 1% of variance each. (B) Component loadings of the 24 PCs. The 1st-4th PCs are marked with red lines and the 5th-13th PCs are marked with blue lines. (C) Component score topographies, component loading latencies, and the proportion of variance explained in the first 13 PCs. PC4 and PC3 are respectively identified as components corresponding to the N1/MMN and the P2.

**Figure 4.** (A) The N1/MMN and P2 component score topographies in each condition. Three electrodes showing the most negative and positive responses across all conditions independent of experimental manipulation are marked as white dots and black dots (**N1/MMN**: FC4, C3, FC3 with reversed polarity at M2, M1, O2; **P2**: FCz, Cz, FC2 with reversed polarity at F7, M1, T8). (B) The difference between the component maxima and its reversed polarity for the N1/MMN (left) and P2 (right). Error bars depict one standard deviation of the mean.

## Supplementary material

### ERP data

#### *N1/MMN peak amplitude*

There was no regularity x attention x repetition interaction ( $F(1,27) = 0.85, p = .36, \eta_p^2 = 0.03$ ) nor any two-way interaction (regularity x attention:  $F(1,27) = 0.62, p = .44, \eta_p^2 = 0.02$ ; regularity x repetition:  $F(1,27) = 0.48, p = .49, \eta_p^2 = 0.02$ ; attention x repetition:  $F(1,27) = 2.04, p = .16, \eta_p^2 = 0.07$ ). However, there was a significant main effect of **regularity** ( $F(1,27) = 10.78, p < .01, \eta_p^2 = 0.29$ ) where regularity enhanced the N1/MMN and a significant main effect of **attention** ( $F(1,27) = 4.83, p < .05, \eta_p^2 = 0.15$ ) where attention enhanced the N1/MMN. The main effect of repetition did not reach significance ( $F(1,27) = 0.77, p = .39, \eta_p^2 = 0.03$ ).

#### *P2 peak amplitude*

There was no regularity x attention x repetition interaction ( $F(1,27) = 1.08, p = .31, \eta_p^2 = 0.04$ ). However, there was a significant regularity x repetition interaction ( $F(1,27) = 4.97, p < .05, \eta_p^2 = 0.16$ ) and a significant attention x repetition interaction ( $F(1,27) = 13.63, p \leq .001, \eta_p^2 = 0.34$ ). For the **regularity x repetition** interaction, post hoc comparisons showed that repetition effect was significant in the regular condition ( $t(27) = -3.22, p < .01$ ) but not irregular condition ( $t(27) = -0.63, p = .53$ ). For the **attention x repetition** interaction, post hoc comparisons showed that repetition effect was significant in both attended condition ( $t(27) = -3.62, p \leq .001$ ) and unattended condition ( $t(27) = 2.19, p < .05$ ). Specifically, there was a repetition enhancement in attended condition but a repetition suppression in unattended condition. The regularity x attention interaction did not reach significance ( $F(1,27) = 0.11, p = .75, \eta_p^2 < 0.01$ ).

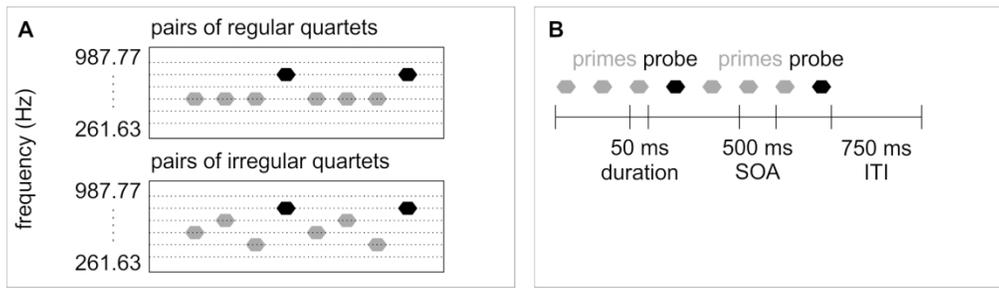


Figure 1. (A) Schematic illustration of pairs of regular and irregular quartets. (B) On each trial, a pair of tone quartets (consisting of tones of 50-ms-duration) were presented with a 500 ms SOA. Each trial was followed by an ITI of 750 ms.

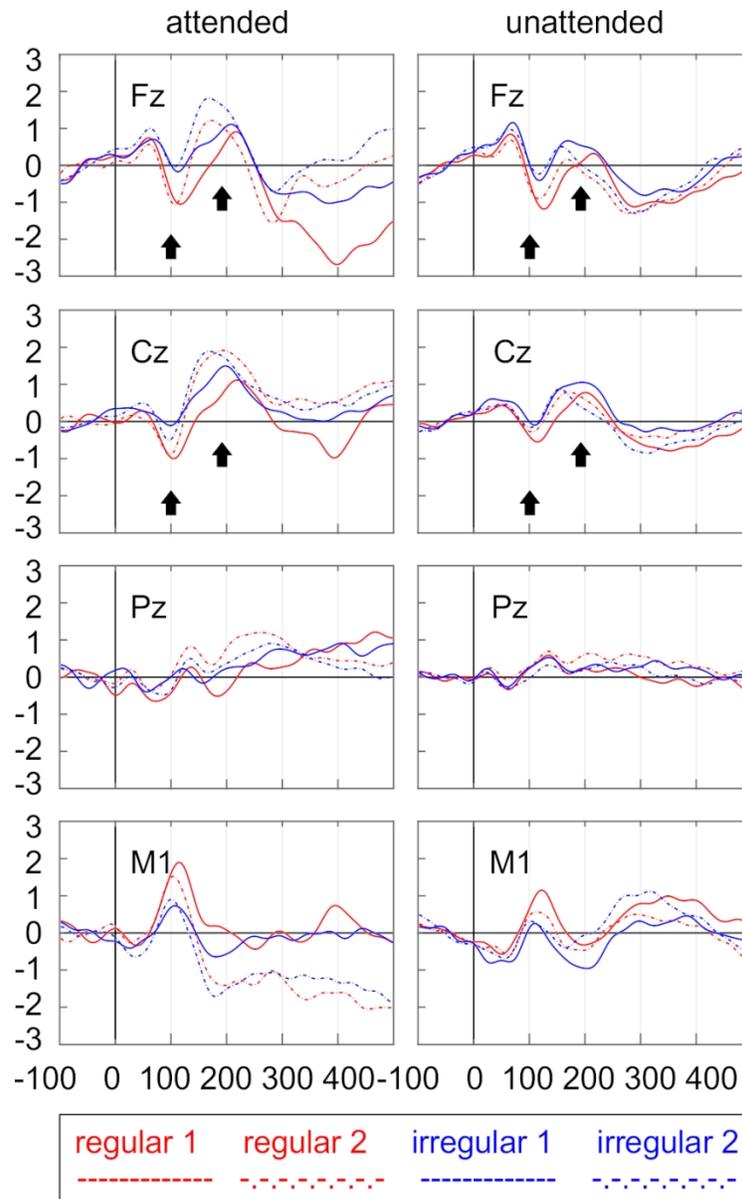


Figure 2. Grand average ERPs on three representative electrodes at midline (i.e., Fz, Cz, Pz) and M1. The N1/MMN and P2 are marked with arrows for ease of reference.

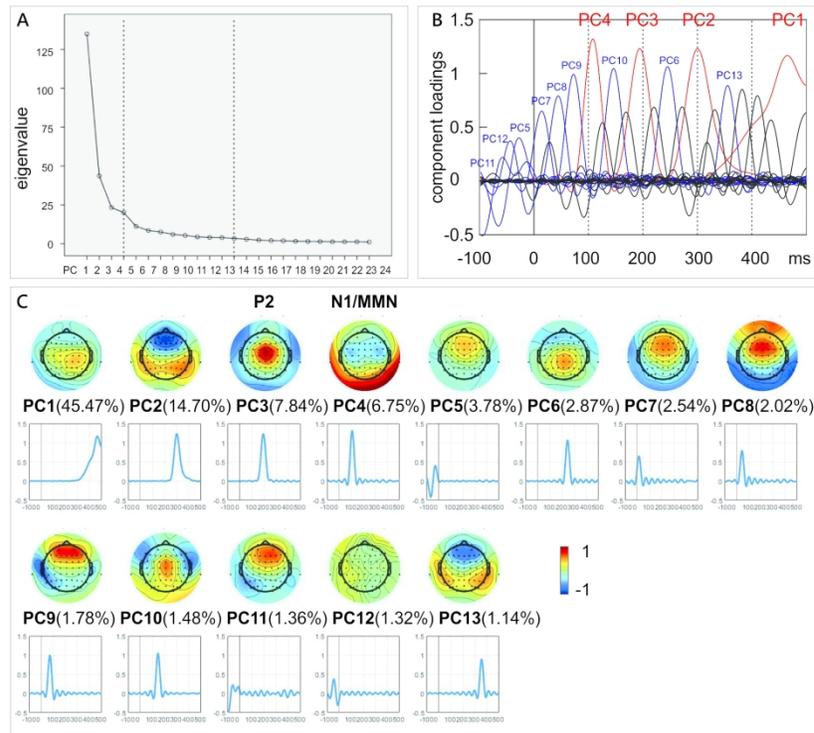


Figure 3. (A) Scree plot showing the eigenvalues of the 24 PCs in the temporal PCA. The 1st-4th PCs explains more than 5% of variance each and the 5th-13th PCs explains more than 1% of variance each. (B) Component loadings of the 24 PCs. The 1st-4th PCs are marked with red lines and the 5th-13th PCs are marked with blue lines. (C) Component score topographies, component loading latencies, and the proportion of variance explained in the first 13 PCs. PC4 and PC3 are respectively identified as components corresponding to the N1/MMN and the P2.

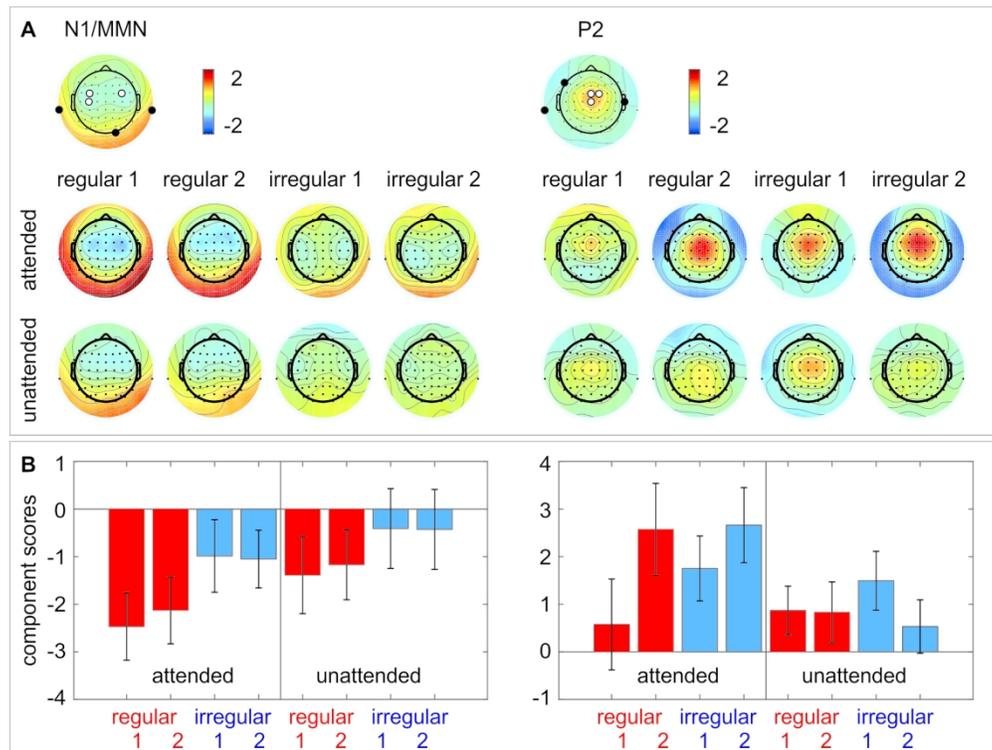


Figure 4. (A) The N1/MMN and P2 component score topographies in each condition. Three electrodes showing the most negative and positive responses across all conditions independent of experimental manipulation are marked as white dots and black dots (N1/MMN: FC4, C3, FC3 with reversed polarity at M2, M1, O2; P2: FCz, Cz, FC2 with reversed polarity at F7, M1, T8). (B) The difference between the component maxima and its reversed polarity for the N1/MMN (left) and P2 (right). Error bars depicts one standard deviation of the mean.