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Research report

Predicting the unknown: Novelty processing depends on expectations

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ABSTRACT

Fulfilled predictions lead to neural suppression akin to repetition suppression, but it is currently unclear if such effects generalize to broader stimulus categories in the absence of exact expectations. In particular, does expecting novelty alter the way novel stimuli are processed? In the present study, the effects of expectations on novelty processing were investigated using event-related potentials, while controlling for the effect of repetition. Sequences of five stimuli were presented in a continuous way, such that the last stimulus of a 5-stimulus sequence was followed by the first stimulus of a new 5-stimulus sequence without interruption. The 5-stimulus sequence was predictable: the first three stimuli were preceded by a cue indicating that the next stimulus was likely to be a standard stimulus, and the last two by a cue indicating that the next stimulus was likely to be novel. On some trials a cue typically predicting a standard was in fact followed by an unexpected novel stimulus. This design allowed to investigate the independent effects of (violated) expectations and repetition on novelty processing. The initial detection of expected novels was enhanced compared to unexpected novels, as indexed by a larger anterior N2. In contrast, the orienting response, as reflected by a novelty P3, was reduced for expected compared to unexpected novels. Although the novel stimuli were never repeated themselves, they could be presented after one another in the sequence. Such a category repetition affected the processing of novelty, as evidenced by an enhanced anterior N2, and a reduced novelty P3 for novels preceded by other novels. Taken together, the current study shows that novelty processing is influenced by expectations.

1. Introduction

Generally, the visual world is highly structured, such that observers can form reliable expectations regarding upcoming stimulation. For example, a red traffic light can be expected to turn green at some point. Such expectations alter neural processing of information: Typically, stimuli expected by observers generate less neural activity than stimuli that are surprising (Summerfield and de Lange, 2014; Summerfield et al., 2008). It remains unclear, however, if the effects of expectations are generalizable to broader stimulus categories, when no specific sensory template can be activated by expectations.

A category of stimuli for which observers by definition cannot form specific expectations is novel stimuli. Truly novel stimuli, stimuli that have never been seen, are unknown and can therefore not be predicted. Nonetheless, forming expectations about novel stimuli may be important because new stimuli can be an unknown threat or source of reward, and therefore rapidly detecting and responding to novelty is essential for survival (Panksepp, 1998). Indeed, novel stimuli are typically prioritized over familiar stimuli by attracting attention (Escera et al., 1998; Escera et al., 2001; Friedman et al., 2001; Ranganath and Rainer, 2003; Yago et al., 2003), and generate differential neural activity very early during processing (Xiang and Brown, 1998). Orienting towards novel stimuli has been believed to be an involuntary process (San Miguel et al., 2008).

Predictions and expectations can also bias processing of subsequent stimuli, by activating sensory templates (Carlsson et al., 2000; Kok et al., 2017). This raises the possibility that enhanced responses to novel stimuli may in fact be due to their *unpredictability* (as they do not match with any active template) rather than their novelty per se. In fact, several studies have suggested that the event-related potentials (ERPs) traditionally believed to reflect novelty processing actually reflect a violation of expectations rather than the mere detection of novelty (Cycowicz and Friedman, 2007; Escera et al., 2001; Schomaker and Meeter, 2015; Schomaker et al., 2014).

The brain's response to novelty has been investigated since the seventies of the previous century using the ERP technique. This technique allows for the discrimination of different aspects of the orienting response towards novelty with a high temporal

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resolution. ERP studies of novelty typically use the three-stimulus novelty oddball paradigm (Courchesne et al., 1975; the current study's task differs in various ways from the novelty oddball task, as will be discussed below). In this paradigm, participants have the task to respond to an infrequent target stimulus, which in the visual version of the task typically is a simple geometric figure, such as a triangle. Targets are embedded in a random sequence of frequent standard stimuli (typically also geometric figures), and infrequent task-irrelevant novel stimuli. In the visual version of the task, novel stimuli typically consist of bizarre drawings or figures that the participants could not possibly have seen before. These novel stimuli evoke at least two novelty-associated ERP components, a frontally peaking negative-going component around 250–350 ms, referred to as the anterior N2 or N2b (Folstein and Van Petten, 2008), and a later positive-going frontrocentral component around 300–550 ms, referred to as the novelty P3 (Friedman et al., 2001). The anterior N2 has been interpreted to reflect the automatic detection of novelty (Chong et al., 2008; Escera et al., 2001; Schomaker et al., 2014; Tarbi et al., 2011) or the strong neural responses generated by novel stimuli (Schomaker and Meeter, 2014; Schomaker et al., 2014), while the novelty P3 has been suggested to reflect the involuntary orientation towards and the conscious evaluation of novel events (Courchesne et al., 1975; Escera et al., 2000; Escera et al., 1998; Friedman et al., 2001). In terms of timing and topography, the novelty P3 is very similar to the P3a component which is elicited by deviant task-irrelevant stimuli (Squires et al., 1975). In fact, several studies have found that the two components cannot be distinguished (Combs and Polich, 2006; Goldstein et al., 2002; Simons et al.,2001), though see Barry et al. (2016). The novelty P3 has been traditionally associated with processing of stimulus novelty (Courchesne et al., 1975), but more recent studies have suggested it can is also be affected by top-down attentional factors (Chong et al., 2008), working memory load (Schomaker and Meeter, 2014; Tarbi et al., 2011; Lv et al., 2010), and stimulus complexity (Barkaszi et al., 2013).

Another factor that was found to influence the magnitude of the novelty P3, is context-derived expectations (Cycowicz and Friedman, 2007; Schomaker et al., 2014). For example, Schomaker et al. (2014) found that the novelty P3 component was strongly reduced when novels were frequent rather than rare. Still, each individual novel stimulus was presented just once – rather it was the frequency of *novel stimuli as a category* that affected the size of the novelty P3 component. A similar effect was found when the standard stimuli in an novelty oddball paradigm were complex, though not very novel, dot clouds as opposed to simple geometric figures (Schomaker et al., 2014). Interestingly, the anterior N2 was unaffected by these experimental manipulations, suggesting it more closely reflects the novelty of the stimulus itself (called *stimulus novelty* in Schomaker and Meeter, 2015), and is less dependent on contextual factors. Schomaker et al. (2014) explained their findings by changes in participants' expectations about upcoming stimuli. In conditions in which complex stimuli were frequent, upcoming stimuli were also expected to be complex. If the novelty P3 is mostly a response of *surprise* by unexpectedly complex stimuli (as hypothesized by Schomaker et al., 2014), a complex novel stimulus would elicit less of a novelty P3 in contexts that led participants to expect complex novel stimuli. Others have suggested, however, that it is in fact the later P3b component that reflects predictive surprise, and the following positive slow wave prediction updating, while the P3a (or novelty P3) was suggested to reflect belief updating Kolossa et al. (2017). If this is the case, expectations would modulate the P3b and/or positive slow wave rather than the novelty P3.

However, expectations were not directly manipulated in this previous study, nor in any other study showing effects of expectations (Cycowicz and Friedman, 2007), making it difficult to rule out alternative explanations. In particular changing the frequency with which stimuli occur not only manipulates expectations, it also alters the likelihood of a repetition (e.g., if 70% of stimuli in an experiment are novels, a novel is much more likely to be preceded by a novel than when only 10% of stimuli are novels). It could thus be that repetition suppression, rather than expectation, is the factor that reduces the novelty P3.

Previous studies thus suggest that novelty processing consists of a part that is a response to stimulus novelty itself (indexed by the anterior N2), but also of a part that is sensitive to expectations, indexed by the novelty P3. However, expectations were never experimentally manipulated, and findings were potentially confounded by the likelihood of repetitions (Cycowicz and Friedman, 2007; Schomaker et al., 2014). In the current study, we aimed to investigate the effects of expecting something new on novelty processing, and to rule out possible effects of repetition. We directly manipulated participants' expectations and investigated the brain's response to novel stimuli under such different conditions using ERPs. We used a task inspired by the novelty oddball task, including frequent standards, less-frequent novels, and infrequent targets. In contrast with the traditional novelty oddball task, expectations were actively manipulated: Each stimulus was preceded by a cue that predicted that the next stimulus would either be a standard or a novel stimulus. Additionally, stimuli were presented in an almost predictable sequence. On a few trials, novel stimuli were unexpectedly presented when both the cue and the position in the sequence would lead the observer to expect a standard stimulus. We investigated whether such unexpected novels were processed differently from expected novel stimuli, and whether these effects superseded those of repetition (i.e., of two novels following one another).

2. Methods

2.1. Participants

24 participants volunteered to take part in the study, but three were excluded due to noisy EEG data and one due to technical problems (see EEG analyses for details). Data of the remaining 20 participants was included in the analyses (5 male; age 21–29, mean = 23.4, sd = 2.2; 16 right-handed). All of them had normal or corrected to normal vision. Participants either received course credit or 8 Euros per hour per compensation. The study was performed in accordance with the ethical standards of the 1964 Declaration of Helsinki and in accordance with the ethical committee of the faculty of Behavioural and Movement Sciences at the Vrije Universiteit Amsterdam, the Netherlands. Participants all signed informed consent before their participation.

2.2. Stimuli

Two types of cues were presented: a green and yellow fixation cross that predicted standard or novel stimuli respectively (which color predicted what stimulus category was counterbalanced across participants). In addition, a rare non-cued target was presented on 12.5% of the trials in order to make sure that participants would attend all presented stimuli. The target could occur at any position in the sequence with equal probability. Novel stimuli were randomly drawn from a large set of fractal images, that were generated using the open-source program ChaosPro 4.0 (http://chaospro.de). The novel fractals were colorful, complex images without any semantic meaning. Both the standard and target stimulus were simple geometric forms, and consisted of triangles pointing in opposite direction (either upwards or downwards).

The pointing directions of the standard and target were counterbalanced across participants. The stimuli were presented in the center of the screen; targets and standards at a viewing angle of about 0.9° and novels of about 31.3 × 23.8°.

2.3. Procedure & design

The experiment took place in a Faraday-shielded, sound-attenuated room with subdued lighting. The task was programmed using E-Prime 2.0 software (Psychology Software Tools Inc., Pittsburgh, PA, USA), and was presented on a 21 in. LCD monitor, at a viewing distance of about 80 cm, at a 120 Hz refresh rate.

Trials were organized in sequences of five, with standard and novel stimuli being presented at predictable positions within a sequence. The sequences of five stimuli were presented in a continuous way, such that the last stimulus of a 5-stimulus sequence was followed without interruption or pause by the first stimulus of a new 5-stimulus sequence. On the first three positions in a sequence, a 'standard' cue was presented (yellow or green fixation cross, counterbalanced across participants), followed with 75% likelihood by a standard stimulus, 12.5% by an unexpected novel stimulus, and 12.5% by a target stimulus. On the last two positions in a sequence, a 'novel' cue was presented that predicted a novel stimulus, followed with 87.5% likelihood by a novel and 12.5% likelihood a target stimulus. Although the 'novel'-cue predicted that most likely a novel stimulus would be presented, it did not predict which specific stimulus. In contrast, the 'standard'-cue predicted a specific stimulus, namely a triangle (either upwards/downwards pointing).

On the 12.5% trials that a target stimulus was presented, a button press was required with either the left or right index finger (which finger was counterbalanced across participants). The target was only included to make sure that participants were paying attention to the stimuli. Both the novel and standard stimuli did not require a response. The cues were presented for a jittered interval of between 600 and 1200 ms. The following standard, novel or target stimulus was presented for 2000 ms, followed by another jittered intertrial interval of 600–1200 ms. If participants made an error, responding when there was no target or not responding to a target, a red cross was shown as feedback the first 200 ms of the intertrial interval.

Participants started with a practice block of 20 trials. Then, they saw a total of 360 standard, 340 novel, and 100 target stimuli. Of those 800 trials, a standard cue was presented on positions 1, 2 and 3 for a total of 480 times and a novel cue at positions 4 and 5 for 320 times. Participants could take a self-paced break between every 40 trials. Each block had a duration of about 2.4 min. The completion of the task took about 55 minutes.

2.4. EEG recordings

The EEG signal was recorded using a Biosemi system (Biosemi, Amsterdam, the Netherlands) with 64 electrodes with sintered Ag/AgCl tips, plugged into an Electrocap (Electro-Cap International Inc. Eaton, OH, USA). Electrode locations of the 64 channel Biosemi system correspond to the 10–20 system. Data were analyzed for the Fz, Cz, and Pz electrode.

The EEG signal was digitized with a sampling rate of 512 Hz with a gain setting of 1000, and later resampled to a rate of 500 Hz. During recording, electrode offset was kept below 20 μV (the Biosemi equivalent of impedance). The raw EEG data was digitally filtered using a 0.1 Hz basic finite impulse response 1000-point high-pass filter with a transition bandwidth of 0.01 Hz and a 24 dB roll-off per octave, and a 30 Hz low-pass filter with a transition bandwidth of 5 Hz and a 6 dB roll-off per octave. The data was offline re-referenced to the average of all 64 EEG electrodes. Horizontal and vertical eye movements were measured by bipolar electrodes placed at the outer corners of the eyes, and above and below the mid of the orbital sockets. These measurements were used to identify and remove blinks and eye movements.

2.5. EEG analysis

ERPs were computed from −200 ms pre-stimulus to 1000 ms post-stimulus, using the 200 ms before onset as a baseline. By visual inspection of the mean ERPs over all participants the time-window for the N2 component was defined from 270 to 310 ms post-stimulus, and for the novelty P3 a time-window of 380–440 ms was chosen. Mean amplitudes were calculated for these time-windows for novel and standard stimuli per participant. We also looked at the P3b component for targets, calculating a mean amplitude for a 420–470 ms time-window.

The data were cleaned and analyzed using EEGlab and ERPlab (Delorme ad Makeig, 2004; Lopez-Calderon and Luck, 2014). Artefacts were detected and rejected with a tool in ERPlab using a moving window of 200 ms and a window step of 100 ms, and an extreme value cut-off value of |125| μV. Artefacts were rejected on basis of the data of the Fz, Cz, and Pz electrodes in a −200 to 800 ms time-window. Eye movement measurements from the bipolar electrodes were used to check whether all blinks were removed by the moving window procedure, and else flagged for rejection. Using this procedure, an average of 6.86% (range = 2.1–23.0%; SD = 6.14%) of data was rejected per participant. Three participants were not included in any further analyses because the artefact detection criteria resulted in more than 25% data rejection (30.8–46.1%). ERPs were calculated for and analyses performed on the remaining data, using the ERP measurement tool in ERPlab (Lopez-Calderon and Luck, 2014).

In the current study we were interested in ERP components with similar topography, but opposite polarity. Specifically, any condition differences on the negative anterior N2 may affect the amplitudes of the later P3 components. To investigate this possible confound we performed a two-step temporospatial principal component analyses (PCA) using the ERP PCA Toolkit (EP Toolkit; Dien, 2010; Dien, 2012), in addition to the ERP analyses. This decomposition technique allows us to identify the different components that contribute to the ERP signal in time and topographic location for the novel stimuli, and to further identify differences in ERP components between novels, standards, and targets.

A priori knowledge regarding the peaking time, also based on the mean amplitude ERPs, and typical topography of the anterior N2, frontocentral novelty P3, and posterior P3b was used to identify the relevant PCA factors. Average condition data per subject for novels for −200 to 800 ms epochs including all EEG channels was entered in the PCA. Factors were only considered when they explained more than 0.1% of the data.

A temporospatial PCA was performed making use of the high temporal resolution of EEG for the first decomposition, and making use of spatial information in the second step (Dien, 1998, 2012). In the first step a temporal PCA was performed exploiting the high temporal resolution of EEG (Dien, 1998, 2012). A scree plot was used to display the variance explained by the factors using a parallel test for data reduction purposes (Cattell, 1966; Horn, 1965), and to determine how many factors to include in the temporal PCA. On basis of the scree test six factors, explaining 94.5% of the data, were included, and a Promax rotation with no Kaiser correction was used (Dien et al., 2003; Kayser and Tenke 2003). A rotation parameter (kappa) was set to three (Dien, 2010), to rotate the data to an oblique simple structure (Hendrickson and White, 1964). In a second step, a spatial PCA was performed on all six temporal factors using Infomax rotation (Dien et al., 2007). On basis of visual inspection of the scree plot six factors for each temporal factor

were retained in this step, accounting for 85.1% of the variance (note this is below 100% as not all factors were retained), and resulting in a total of 36 factors. Of these 36 factors, 27 explained more than 0.1% of the variance. Factors were then selected on basis of expected peaking time and peaking location for an anterior N2, novelty P3, and a target P3b (also see Schomaker and Meeter, 2014).

One temporospatial factor (TF1SF1) with strong frontal negativity peaking at 292 ms was identified as the anterior N2. The eigenvector of this factor explained 19.62% of the variance. In the P3 time-window, one temporospatial factor with a positive peak over central/parietal regions was identified, while no separate component peaking over frontal regions could be identified. The positive central/parietal component peaked at 382 ms (TF6SF2), and explained 0.22% of the data. As it was larger for novels than standards it was identified as the novelty P3 (also see Section 3). Another PCA positive component in the P3 time-window peaking over central/parietal electrodes at 472 ms was identified as a target P3b (TF3SF1; larger for targets than for standards or novels), explaining 6.63% of the data.

2.6. Statistical analyses

To confirm that novels elicited typical novelty responses we compared standard- and cued, uncued, repeated, and non-repeated novel-evoked ERPs with 2 * 3 repeated-measures ANOVAs with Stimulus (novel; standard) and Electrode (Fz; Cz; Pz) as factors.

We investigated the effects of expectations on processing of novel stimuli using a 2 * 3 repeated-measures ANOVA with Cue (novel; standard) and Electrode (Fz; Cz; Pz) as factors, for the mean N2 and P3 amplitudes separately. To test the null hypothesis, a statistical trend effect for the N2 was followed up by a Bayesian test using the statistical package JASP (Version 0.8.6; JASP Team, 2018). The Bayes factor for the null hypothesis (BF01) is reported.

To investigate the effects of repetition of the same category on novelty processing we performed a 2 * 3 ANOVA with Repetition (repeated; non-repeated) and Electrode (Fz; Cz; Pz) as factors, again for the N2 and P3 separately. Significant interactions were followed up by post-hoc *t*-tests per electrode site. The effects of cue type on average response times and hit rate were investigated using *t*-tests.

Finally, we checked whether the cues also affected the processing of the target stimulus as indexed by the P3b component. For this, we ran a 2 * 3 ANOVA with Cue (novel; standard) and Electrode (Fz; Cz; Pz) as factors, investigating the effects on the target P3b. We also ran post-hoc *t*-tests per electrode site. For all tests the Greenhouse-Geisser correction was applied when the sphericity assumption was violated. All main analyses were repeated for the PCA factor scores for the components identified as N2, P3, and P3b. Note that interaction effects cannot be investigated, since the spatial PCA results are represented by one virtual electrode covering the whole head.

3. Results

3.1. Behavioral data

Participants missed on average 5% of oddball stimuli. This was not different when a 'standard' or a 'novel' cue preceded the oddball, $t(23) = 0.18$, $p = .86$. They were equally fast in responding to the oddball after both cues, $t(23) = 0.64$, $p = .53$ (on average 570 ms after 'standard' cues and 569 ms after 'novel' cues).

3.2. ERPS

Fig. 1 shows the ERPs for novels preceded by a 'novel' and 'standard' cue, depicting the effects of expectations. Fig. 2 shows the ERPs for novels that were repeated or not, showing the effects of repetition. Fig. 3 shows the ERPs for targets preceded by a 'novel' and 'standard' cue, depicting the effects of expectations on target processing. All three figures show data at frontal, central and parietal midline electrodes.

Novel stimuli elicited a negative frontal and positive posterior peak in the N2 time-window, this component was absent for standard stimuli. In the P3 time-window both novels and standards elicited a positively going component, but the novels showed a larger peak-to-peak difference than the standards (this is sometimes referred to as the N2-P3 complex; see for example Azizian et al., 2006). First, analyses of the mean amplitudes of the N2 and P3 time-windows will be reported. Second, results of a PCA aimed to disentangle the overlap between the ERP components of interest are reported.

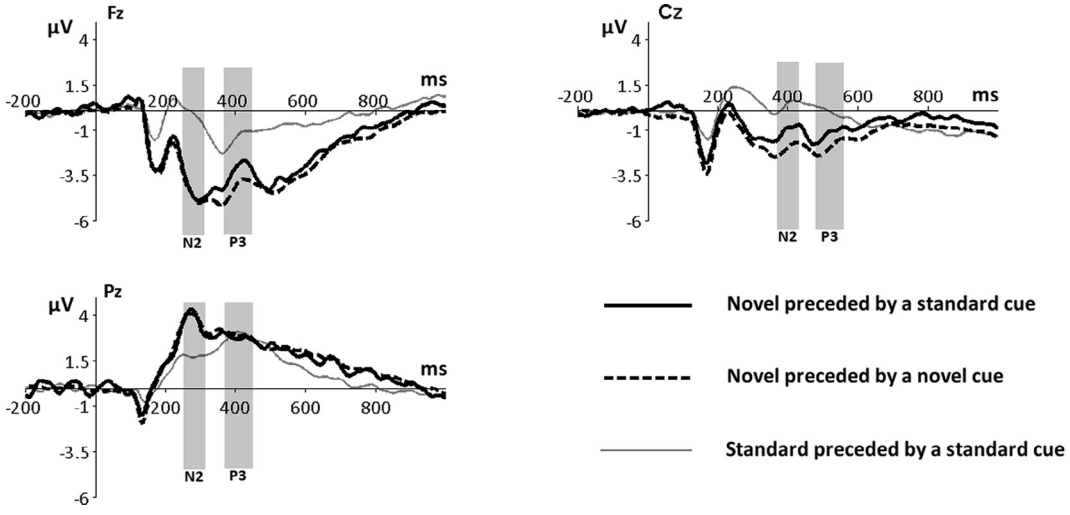

Fig. 1. Effects of expectations on novelty processing. ERPs for expected novel stimuli preceded by a 'novel' and unexpected novel stimuli preceded by a 'standard' cue at frontal (Fz), central (Cz), and posterior (Pz) electrode sites. The N2 and novelty P3 windows are highlighted.

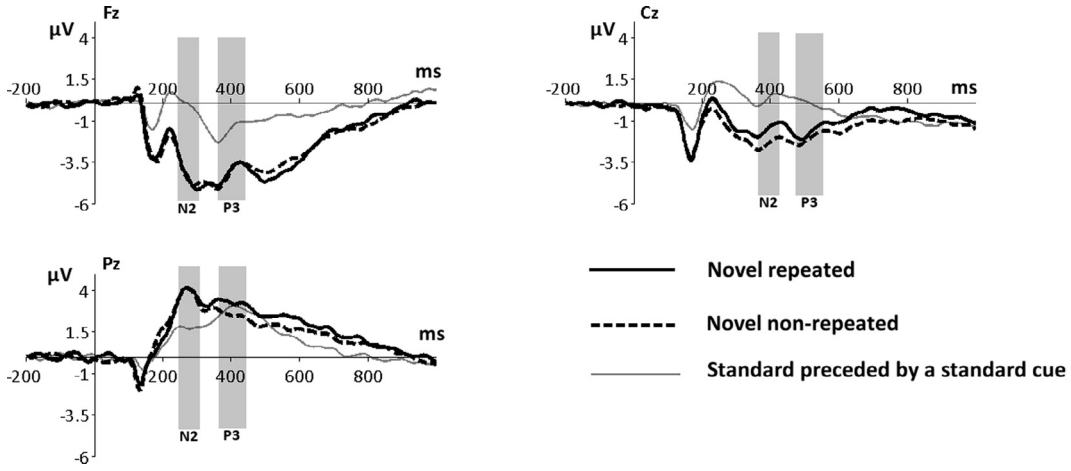

Fig. 2. Effects of repetition on novelty processing. ERPs for novel stimuli that were either repeated or not at Fz, Cz, and Pz electrode sites. The anterior N2 and novelty P3 time-windows are highlighted.

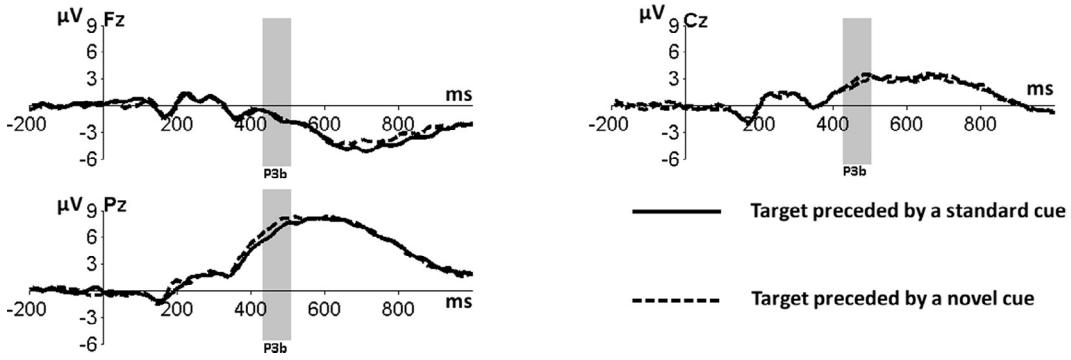

Fig. 3. Effects of expectations on target processing. Grand-average ERPs for target stimuli that were either preceded by a standard or novel cue at Fz, Cz, and Pz electrode sites. The target P3b time-windows are highlighted.

3.3. Mean amplitudes of peak time-windows

3.3.1. N2

Both uncued and cued novels elicited a larger anterior N2 than cued standards, $F(1,19) = 7.45$, $p = .013$, $\eta^2 = 0.28$, and $F(1,19) = 20.52$, $p < .001$, $\eta^2 = 0.52$ respectively. Similarly, repeated and non-repeated novels elicited a larger anterior N2 than standards, $F(1,19) = 27.70$, $p < .001$, $\eta^2 = 0.59$, and $F(1,19) = 15.33$, $p = .001$, $\eta^2 = 0.45$.

There was trend effect for a larger N2 amplitude for expected ('novel' cue; positions 4 and 5) versus unexpected ('standard' cue; positions 1–3) novels, $F(1,19) = 3.62$, $p = .072$, $\eta^2 = 0.16$. To further investigate this, we employed a Bayesian statistics approach. A repeated-measures ANOVA with Cue (novel; standard) and Electrode (Fz; Cz; Pz) as factors showed that there is substantial evidence for a null effect (BF01 = 5.676), suggesting that the effect of expectations on the N2 was not very strong. The N2 peaked anteriorly, as shown by a linear effect, $F(1,19) = 31.71$, $p < .001$, $\eta^2 = 0.63$. Electrode and cue did not interact ($p = .127$).

Although the same novel stimulus was never presented again, a novel could be presented after another novel stimulus, thus being repeated as a category of novels (this could happen at positions 5 and 1). Such a category repetition affected the anterior N2 amplitude, $F(1,19) = 9.96$, $p = .005$, $\eta^2 = 0.34$, with a larger N2 for non-repeated rather than repeated novels. Also in this analysis, the N2 was found to peak anteriorly as shown by a linear effect, $F(1,19) = 34.61$, $p < .001$, $\eta^2 = 0.65$. Repetition and electrode did not interact ($p = .177$).

4. Novelty P3

Cued standards elicited a larger P3 than expected novels, $F(1,19) = 20.52$, $p < .001$, $\eta^2 = 0.52$, and unexpected novels, $F(1,19) = 7.45$, $p = .013$, $\eta^2 = 0.28$. Similarly, cued standards elicited a larger P3 than repeated and non-repeated novels, $F(1,19) = 27.07$, $p < 0.001$, $\eta^2 = 0.59$, and $F(1,19) = 11.35$, $p = .003$, $\eta^2 = 0.37$ respectively. Note that we observed robust differences on the N2 amplitude for novels and standards, therefore any differences on the P3 could be caused by the earlier differences in N2. This issue will be addressed with a PCA.

The cue was found to affect the processing of the novel stimuli, $F(1,19) = 8.26$, $p = .010$, $\eta^2 = 0.30$, with a larger novelty P3 for uncued than cued novel stimuli. The P3 was found to be larger posteriorly than frontally, as evidenced by a linear effect, $F(1,19) = 19.89$, $p < .001$, $\eta^2 = 0.51$, suggesting contributions of the P3b (PCAs were used to further address this possibility; also see Schomaker and Meeter, 2014; Schomaker et al., 2014). In addition, electrode site and the effects of cue type interacted, $F(1.32,25.04) = 4.02$, $p = .046$, $\eta^2 = 0.18$. This interaction was followed up by post-hoc comparisons for the different cue types per electrode site. Although the P3 peaked more posteriorly, the largest effects of cue type were found only for frontal (Fz) and central (Cz) regions, $t(19) = 2.63$, $p = .017$ and $t(19) = 3.24$, $p = .004$, respectively. No differences were observed at Pz ($p = .620$).

Category repetition also affected the P3 amplitude for novels, $F(1,19) = 11.99$, $p = .003$, $\eta^2 = 0.39$. Non-repeated novels elicited a larger P3 than repeated ones. Again the P3 was larger posteriorly

than anteriorly, as shown by a linear effect, $F(1,19) = 20.20$, $p < .001$, $\eta^2 = 0.52$. Repetition and electrode also interacted, $F(1.38,26.24) = 3.43$, $p = .043$, $\eta^2 = 0.14$. This was further investigated with post-hoc comparisons per electrode. In contrast to the frontocentral effects of expectations, the effects of repetition occurred more posteriorly at Pz, $t(19) = 2.71$, $p = .014$, and centrally at Cz, $t(19) = 3.62$, $p = .002$, but not anteriorly (Fz: $p = .829$).

5. Target P3b

No main effect of cue on the target P3b was observed ($p = .475$), suggesting that target processing was not affected by expectations regarding novelty. The target P3b peaked posteriorly, as shown by a linear effect, $F(1,19) = 29.00$, $p < .001$, $\eta^2 = 0.60$. Cue and electrode did not interact ($p = .571$).

5.1. PCA

To further investigate the relative contributions of the different novelty-related ERP components to the grand-average ERP signal, the analysis was repeated using the PCA factors identified as the N2, novelty P3, and target P3b. See methods for peak latency and location of the PCA factors. From now on the PCA factors will be referred to as the ERP components they are presumed to reflect. PCA waveforms and topographic plots for these three components are shown in Fig. 4.

5.2. N2

In line with the ERP mean amplitude analyses novels were found to elicit a larger N2 than standards in the PCA analyses. The N2 was larger for expected, $t(19) = 5.34$, $p < .001$, unexpected, $t(19) = 5.55$, $p < .001$, repeated, $t(19) = 6.15$, $p < .001$, and non-repeated novels, $t(19) = 4.74$, $p < .001$, compared to standards.

In line with the ERP mean-amplitude analyses, the novel-evoked N2 PCA component was larger for expected compared to unexpected novels, $F(1,19) = 13.74$, $p = .001$, $\eta^2 = 0.42$. The N2 peaked anteriorly, as shown by a linear effect, $F(1,19) = 33.10$, $p < .001$, $\eta^2 = 0.64$.

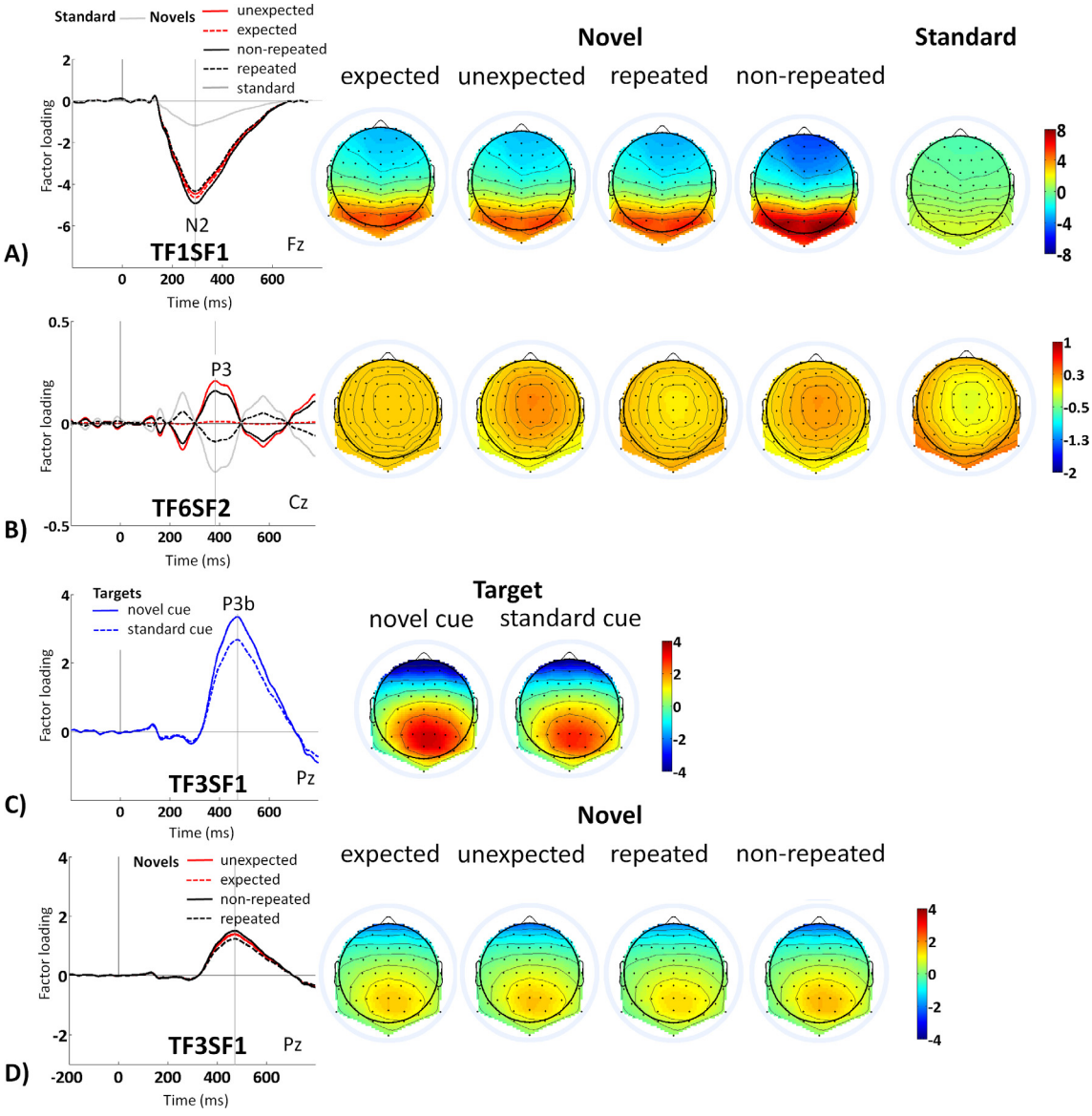

Fig. 4. PCA decomposition. Grand-average ERPs for novel stimuli that were expected, unexpected, repeated, and non-repeated, standard stimuli, and targets preceded either by a novel or standard cue. Next to the grand-average PCA waveforms topographic plots of the PCA factors are shown. A) The N2 PCA factor (TF1SF1) peaked at 292 ms. B) The P3 PCA factor (TF6SF3) peaked at 382 ms. C) The target P3b PCA factor (TF3SF1) with a peak at 472 ms. D) The P3b PCA factor for novels.

Also consistent with the ERP analyses, the N2 amplitude was larger for repeated compared to non-repeated novels, $F(1,19) = 13.89$, $p = .001$, $\eta^2 = 0.42$. The N2 peaked anteriorly as shown by a linear effect, $F(1,19) = 32.36$, $p < .001$, $\eta^2 = 0.63$.

6. Novelty P3

In contrast with the ERP mean amplitude analyses, the PCA results revealed that unexpected and non-repeated novels elicited a larger novelty P3 than standards, $t(19) = 4.11$, $p = .001$ and $t(19) = 2.92$, $p = .009$ respectively. No differences were observed for expected novels versus standards, $t(19) = 2.05$, $p = .055$, or repeated novels and standards ($p = .117$).

As for the mean-amplitude analyses, the novelty P3 was larger for novels that were not preceded by another novel (non-repeated) compared to novels that were (repeated), $F(1,19) = 9.51$, $p = .006$, $\eta^2 = 0.33$. Only a trend cueing effect was found for the novelty P3, with novels predicted by a standard cue (unexpected) eliciting a larger P3 than novels preceded by a novel cue (expected; $p = .090$).

7. Novel and target P3b

The P3b was larger for targets than novels, $t(19) = 2.23$, $p = .038$. Expectations nor repetitions did affect the P3b amplitude for novels ($p = .938$ and $p = .099$ respectively). No cueing effect was found for the novel-evoked P3b ($p = .938$). A trend effect of repetition was found, with non-repeated novels eliciting a larger P3b than repeated novels, $F(1,19) = 3.01$, $p = .099$, $\eta^2 = 0.14$. No main effect of cue on the target P3b was observed ($p = .119$). The target P3b peaked posteriorly, as shown by a linear effect, $F(1,19) = 23.88$, $p < .001$, $\eta^2 = 0.56$.

8. Discussion

Fulfilled predictions lead to neural repetition suppression and therefore may lead to response attenuation for expected stimuli (Summerfield et al., 2008). It is currently unclear, however, if the effects of expectations are generalizable to broader stimulus categories in the absence of exact expectations, as is the particular case for novel stimuli.

In the present study, we aimed to investigate the effects of expectations regarding a category of novel stimuli (always fractal images) on novelty processing using the ERP technique. Using a new task design we repeatedly presented series of five stimuli that were preceded by cues. The first three stimuli were preceded by a cue that indicated that a simple standard stimulus would most likely be presented next. The last two stimuli were preceded by a different cue, indicating that a novel stimulus would be likely to be presented next. Using this paradigm we could also investigate the effects of category repetition on novelty processing, as novel stimuli either followed one another, or followed a standard stimulus. Repetition and expectation were orthogonalized in this task, such that a novel stimulus could be expected or unexpected and repeated or not. This allowed us to investigate their relative contributions to the ERP components elicited by novel stimuli, including the anterior N2, P3, and P3b. Importantly, although we manipulated expectations regarding novelty, all novel stimuli were randomly drawn from the same stimulus category and were therefore physically comparable between conditions.

9. Effects of expectations

In the current cueing paradigm participants could have ignored the cues as they were task-irrelevant (i.e. targets could be presented at any position in the sequence with equal probability); so were the novel stimuli. Nevertheless, we found effects of the cues on novelty processing in the ERP data, suggesting that participants actually formed expectations regarding the upcoming stimuli. Moreover, the cues did not affect target processing, while they did affect processing of novel stimuli, suggesting that the participants specifically formed expectations with regard to the occurrence of novel stimuli.

A statistical trend suggested that expectations enhanced the anterior N2 component, and this finding was corroborated by a Bayesian analysis and a PCA, suggesting that expectations enhanced the initial detection of novelty. This is in contrast with findings that the anterior N2 for novels is not affected by context manipulations that could affect expectations (Schomaker et al., 2014; Chong et al., 2008). Our current manipulation had a stronger effect on explicit expectations (i.e., a novel cue explicitly predicted the presentation of a novel stimulus and increased the odds of a novel 32-fold) than the earlier context manipulations had, which may explain the contrasting results.

In our previous work we already found that the P3 for novel stimuli was reduced when they could be expected because they were frequent (Schomaker et al., 2014). A problem with the interpretation of those results, however, was that expectations were not explicitly manipulated and novel stimuli were also more likely to follow one another in conditions when their frequency was higher. Another explanation could thus be that repetition rather than expectations reduced the novelty P3 in that study. In the current study, we explicitly manipulated expectations, and again found that expecting a novel stimulus reduces its processing as indexed by a smaller novelty P3. The current study's findings are thus consistent with previous suggestions that expectations can affect how novelty is processed (Cycowicz and Friedman, 2007; Schomaker et al., 2014). However, for the first time we could dissociate expectations and repetition in our design. We found that both reduced the novelty P3.

10. Effects of repetition

Repetition of novelty affected the anterior N2, as found by both the ERP and PCA analyses: A novel stimulus elicited a larger N2 when it was preceded by another novel, than after a standard stimulus. In contrast, the (novelty) P3 was larger for novels preceded by a standard stimulus than for novels preceded by a novel. Possibly, the effects of repetition may work through expectations, as the occurrence of a stimulus may affect expectations about which stimuli will be presented next (i.e. affect prediction updating). It is also possible that the effects of repetition of the P3 are due to habituation (Barry et al., 2016). Such low-level habituation effects, however, cannot entirely explain the effects of repetition, as the exact same novel stimulus was never presented again. Moreover, habituation would not explain the increase in N2 amplitude for a novel preceded by another novel.

11. Stimulus differences

Novel stimuli elicited a larger anterior N2 than standards. This is in line with the general interpretation that the anterior N2 signals stimulus novelty (Chong et al., 2008; Tarbi et al., 2011). Potentially, this difference could also be caused by stimulus size (Pfabigan et al., 2015), as novels were substantially larger than standards, and smaller stimuli typically elicit smaller ERP components (but note that novels were of similar size between expectation and repetition conditions). Regardless, the larger N2 for novels confounds the interpretation of the subsequent P3 component. Paradoxically, in the mean amplitude analyses we found that the

novel stimuli elicited a smaller P3 than standard stimuli. This may have been due to the larger N2 confounding interpretation of the subsequent P3. Indeed, using PCA we were able to identify a P3 component unconfounded by the earlier elicited N2 component, which resulted in a larger P3 for unexpected and non-repeated novels than for standards. In contrast, the PCA did not reveal differences between the P3 elicited by expected and repeated novels, relative to the P3 elicited by standard stimuli. These findings further suggest that both expectations and repetition negatively affect the size of the novelty P3.

12. Dissociating novelty ERP components

Both expectations and repetition had differential effects on the N2 and subsequent novelty P3. It is conceivable, however, that only one component was affected, and overlap between the two components resulted in a spurious effect seen in the other (e.g. the negative anterior N2 modulating the positive novelty P3 or vice versa). In addition, the P3 to novels peaked posteriorly, rather than anteriorly. A possible explanation for this is that the P3 to novels was confounded by contributions of other positive components (e.g. the P3b; also see Schomaker and Meeter, 2014; Schomaker et al., 2014). Alternatively, the effect may be caused by the P3 riding on the broad frontal-negative posterior-positive component that we interpreted as an N2. Our use of an average reference makes it additionally hard to interpret the topography of the results using ERP analyses.

However, our PCA further allowed us to disentangle the respective contributions of the anterior N2, and following positive components (e.g. P3, or P3b) to the ERP signal and to identify the effects of expectations and repetition on each. Factors reflecting an anterior N2, a central/parietal P3 component, and a posterior P3b were identified. The PCA for the anterior N2 was consistent with the ERP analyses of the N2. The N2 PCA factor also had a frontal-negative, and a posterior-positive part, suggesting that the posterior-positive part of the N2 may reflect its frontal-negative dipole. A novelty P3 PCA factor was identified that had a positive peak over central electrodes for unexpected and non-repeated novels, and a negative/neutral peak for expected and repeated novels, and standards. This provides further evidence that the positive-going peak seen in the ERP P3 time-window was caused by a 'positive' novelty P3 component. The novelty P3 factor was sensitive to repetition (reduced for novels preceded by other novels), and to expectations – although this only reached the level of a trend. As described above, an additional positive contribution, identified as the P3b, was found using PCA decomposition (targets > novels) which was not affected both by expectations or repetitions. These findings suggest that the novelty P3, but not the target P3b, is sensitive to effects of expectations and repetitions.

13. Conclusion

Taken together, the current findings suggest that novelty processing is not entirely automatic as it is affected by expectations and category repetition. Both expectation and repetition enhanced the initial processing of task-irrelevant novels (reflected in the N2), while reducing later processing that may reflect orienting towards novelty (reflected in the novelty P3).

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