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Sustained neural activity correlates with rapid perceptual learning of auditory patterns

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Abstract

Recurring structures forming regular patterns are common in sounds. Learning such patterns is thought to be crucial for accurate auditory perceptual organization (scene analysis) and efficient recognition and prediction of sounds. The current study investigated the behavioral and neural signatures of rapid perceptual learning of regular patterns in sounds. In six behavioral and EEG experiments with over 120 human participants from both sexes, we show that individuals are faster to detect regular patterns, are more sensitive to pattern deviations, and are more accurate at judging the temporal order of pattern onset relative to a visual stimulus when patterns are repeated compared to novel. Sustained neural activity indexed perceptual learning in two ways. First, sustained activity increased earlier for repeated compared to novel regular patterns when participants attended to sounds, but not when they ignored them; this earlier response increase mirrored the rapid perceptual learning we observed behaviorally. Second, the magnitude of sustained activity was reduced for repeated compared to novel patterns, independent of whether participants attended to or ignored sounds. The reduction in the magnitude of sustained activity appeared only for later stimulus presentations, suggesting it is not directly related to perceptual learning, but to processes enabled by learning. Our study thus reveals neural markers of perceptual learning of auditory patterns, and of processes that may be related to reduced novelty or better prediction of learned auditory patterns.

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Significance statement

Perceptual learning of regular patterns in sounds may optimize perception, but not much is known about the underlying neural processes. We observed several behavioral indices of perceptual learning, including faster pattern detection and increased sensitivity to pattern deviations for repeated compared to novel patterns. Sustained neural activity – indexing pattern processing – increased earlier for repeated than novel patterns, mirroring perceptual learning observed behaviorally. The magnitude of sustained activity was reduced for repeated relative to novel patterns. This reduction appeared only for later stimulus presentations, suggesting it is not directly related to perceptual learning. Our study thus neurally characterizes the perceptual learning of auditory patterns and of subsequent processes that may index reduced novelty or increased prediction of learned auditory patterns.

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Introduction

Natural sounds such as speech and music are rich in structured amplitude and frequency motifs that recur over time – here referred to as regular patterns (Rosen, 1992; Topbas et al., 2012; Broze and Huron, 2013). Sensitivity to regular patterns is thought to optimize auditory perception (Smith and Lewicki, 2006; Kluender et al., 2013) by enabling, for example, segregation of sound streams (Snyder and Alain, 2007; Bendixen, 2014), detection of acoustic changes (Schröger, 2005; Winkler et al., 2009; Herrmann et al., 2020), and recognition and prediction of sounds (Jones and Boltz, 1989; Henry and Herrmann, 2014; Nobre and van Ede, 2018). Learning of regular patterns may also benefit perception, for example, by increasing detection sensitivity and reducing detection time of recognizable sounds (Agus et al., 2010; Bianco et al., 2020). The current study is concerned with the neural substrates of processes that are related to perceptual learning of regular auditory patterns.

Sustained neural activity is a key signature associated with the processing of regular patterns in sounds. Sustained activity increases shortly after the onset of a regular pattern and has been observed for a variety of patterns, including reoccurring sequences of tone pips (Barascud et al., 2016; Southwell et al., 2017; Herrmann and Johnsrude, 2018b; Southwell and Chait, 2018), coherent chord patterns (Teki et al., 2016), and periodic amplitude and frequency modulations (Gutschalk et al., 2002; Ross et al., 2002; Herrmann and Johnsrude, 2018b; Herrmann et al., 2019). The underlying neural generators involve auditory cortex (Pantev et al., 1994; Pantev et al., 1996; Gutschalk et al., 2002; Barascud et al., 2016), and possibly also parietal cortex, frontal cortex, and hippocampus (Tiitinen et al., 2012; Barascud et al., 2016; Teki et al., 2016). Whether and how sustained neural activity changes as a consequence of perceptual learning of regular patterns is unclear.

Perceptual learning of regular auditory patterns is typically rapid, at least in experimental contexts, indicated by faster response times and higher detection sensitivity for repeated than novel patterns after only a few pattern repetitions (Agus et al., 2010; Kang et al., 2017; Bianco et al., 2020). We would expect sustained neural activity to increase earlier when patterns are repeated compared to novel, if sustained activity reflects perceptual learning of regular patterns. In addition, memory for regular patterns can be long-lasting – for weeks in experimental contexts (Agus et al., 2010; Bianco et al., 2020) – and such memories may also affect the magnitude of pattern-related sustained activity. Here, we examine whether the onset time and magnitude of sustained neural activity to regular patterns in tone-pip sequences changes over multiple repetitions.

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Finally, perceptual learning of regular patterns may be implicit: learning may occur when patterns are task irrelevant (Bianco et al., 2020) or when individuals ignore sounds (Andrillon et al., 2017). Pattern-related increases in sustained neural activity have been observed when individuals ignore sounds containing patterns (Barascud et al., 2016; Herrmann and Johnsrude, 2018b; Southwell and Chait, 2018), but it is unclear whether changes in sustained activity over multiple repetitions of regular patterns depend on participants' attention.

In a series of six behavioral and EEG experiments, we investigate whether and how sustained activity is affected by the repetition of a regular pattern and whether a person's attentional state mediates the relationship between pattern repetition and sustained activity. Perceptual learning is probed by contrasting behavior and sustained neural activity between regular patterns that are repeated across trials and patterns that are novel on each trial. We expect that the repetition of regular patterns across trials (compared to novel patterns) provides perceptual benefits, for example, for the detection of patterns and in sensitivity to pattern deviations. Moreover, we expect sustained activity to increase earlier for repeated compared to novel patterns and that the magnitude of sustained activity differs between repeated and novel patterns. This study provides a detailed account of changes in sustained neural activity associated with perceptual learning of auditory patterns.

General Methods & Materials

Participants

Participants gave written informed consent prior to the experiment and received course credit, or were paid $5 CAD per half-hour for their participation. Participants reported normal hearing abilities. The study was conducted in accordance with the Declaration of Helsinki, the Canadian Tri-Council Policy Statement on Ethical Conduct for Research Involving Humans (TCPS2-2014), and was approved by the local Nonmedical Research Ethics Board of the University of Western Ontario (protocol ID: 106570).

Stimulation apparatus

Behavioral and EEG recordings were carried out in a sound-attenuating booth. Sounds were presented via Sennheiser (HD 25-SP II) headphones and a Steinberg UR22 (Experiment I) or an RME Fireface 400 (Experiments II-VI) external sound card. Stimulation was run using Psychtoolbox in MATLAB (MathWorks Inc.).

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Acoustic stimulation and procedure

At the beginning of an experimental session, a methods-of-limits procedure was used to estimate the participant's hearing threshold. Details of the procedure are described in detail in previous work (Herrmann and Johnsrude, 2018a). Acoustic stimuli were presented at 55 dB above the individual's hearing threshold, that is, at 55 dB sensation level.

Experimental stimuli were 4.8-s long tone sequences that each consisted of 120 tones arranged in twelve sets of ten tones (see also Barascud et al., 2016; Herrmann and Johnsrude, 2018b; Southwell and Chait, 2018). Each set had a duration of 0.4 s (0.04 s individual tone duration; 0.007 s rise time; 0.007 s fall time), with no gap between tones or sets. The frequency of each tone was one of 200 values ranging from 700 to 2500 Hz (logarithmically spaced).

Acoustic stimuli were presented in 'Novel' and 'Repeat' conditions that occurred with equal probability (50%). For each stimulus, 10 new frequency values were randomly selected for each of the first 4–8 sets (depending on the specific experiment; see below), and then 10 new random frequency values were selected and repeated for the remaining sets, thereby creating a regular pattern (the serial order of tone frequencies was identical in these repeating sets; Figure 1A). Hence, each stimulus of the Novel and Repeat conditions started as a sequence of tones with random frequencies, and transitioned part-way through to a regular pattern of tone frequencies. Critically, in the 'Novel' condition, a new set of 10 random frequency values that created the regular pattern section of the stimulus was selected for each trial. In the 'Repeat' condition, the same set of 10 random frequency values that created the regular pattern section of the stimulus was utilized for each trial. Hence, all sounds of the Novel and Repeat conditions contained a regular pattern, but the pattern was different for each trial (Novel) or repeated across trials (Repeat).

Participants listened to stimuli in four (Experiment I) or six blocks (Experiments II-V), and participants could take a break between blocks. The set of 10 random frequency values used to create a 'Repeat' pattern was changed for each block (but was constant within a block). The frequency values used were randomly chosen for each participant.

EEG recordings & analysis

Scalp EEG was recorded from 16 electrodes (Ag/Ag–Cl-electrodes; 10-20 placement) and additionally from the left and right mastoids using a BioSemi EEG system (Amsterdam, The Netherlands). Data were recorded at a sampling rate of 1024 Hz. The online low-pass filter was set at 208 Hz. Electrodes were

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referenced online to a monopolar reference feedback loop connecting a driven passive sensor and a common-mode-sense (CMS) active sensor, both located posteriorly on the scalp.

MATLAB software (v7.14; MathWorks, Inc.) was used for offline data analysis. Data were filtered with an elliptic filter to suppress line noise at 60 Hz. Data were re-referenced by averaging the two mastoid channels and subtracting the average separately from each of the 16 channels. Data were low-pass filtered at 22 Hz (211 points, Kaiser window) and high-pass filtered at 0.7 Hz (2449 points). Data were divided into epochs ranging from -1 to 5.8 s, time locked to sound onset. Independent components analysis (runica method, Makeig et al., 1996; logistic infomax algorithm, Bell and Sejnowski, 1995; Fieldtrip implementation Oostenveld et al., 2011) was used to identify activity related to blinks and horizontal eye movements. This analysis pipeline was used only for the identification of artifact components.

For the main data analysis, raw data were filtered with the elliptic filter for line noise suppression and with a 7-Hz low-pass filter (501 points, Hann window), re-referenced to the averaged mastoids, before dividing data into epochs ranging from -1 to 5.8 s. High-pass filtering was omitted and data low-pass filtered at 7 Hz, because sustained activity is a low-frequency response (Barascud et al., 2016; Herrmann and Johnsrude, 2018b; Southwell and Chait, 2018). Blink and eye-movement components from the independent components analysis identified using the high-pass filtered data were excluded. Epochs that exceeded a signal change of more than 200 µV for any electrode were excluded from analyses.

In order to analyze differences in sustained activity between the Novel and Repeat conditions following the transition from the random section to the regular section of the stimulus, we extracted data epochs ranging from -0.5 to 2 s time-locked to the transition onset within the sound. Single-trial time courses were averaged separately for Novel and for Repeat trials. Mean time courses were baseline-corrected by subtracting the mean signal in the -0.5 to 0 s time window from the signal at each time point of the epoch (separately for each channel). Data were averaged across a fronto-central electrode cluster (F4, Fz, F3, C4, Cz, C3) that is sensitive to regularity-related sustained activity (Herrmann and Johnsrude, 2018b).

Data analysis focused on two time windows. An early time window, ranging from 0.3 to 0.8 s post-transition onset, was used to determine whether regularity-related sustained activity is exhibited earlier for the Repeat than for the Novel condition. This time window was chosen because it takes about 1.5 sets (0.6 s) to elicit regularity-related sustained activity after transitioning from a random to a regular

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tone sequence (Barascud et al., 2016). Neural-response amplitudes within the 0.3–0.8-s time window were averaged. Latency analysis was not possible, because of the slow and sustained nature of response, but any difference in response latency between two time courses will be reflected in amplitude changes for a fixed analysis time window. The second time window, ranging from 1 to 2 s post-transition onset, was used to determine whether the magnitude of regularity-related sustained activity differs between the Repeat and the Novel conditions. Neural-response amplitudes within the 1–2-s time window were averaged. Neural activity between these two time windows, ranging from 0.8–1 s, was not analyzed because latency and magnitude effects in this time window may overlap and cancel each other out.

Experimental design and statistical analysis

A paired samples t-test was used to compare amplitudes between the Novel and the Repeat conditions, separately for the 0.3-0.8 s and the 1-2 s time windows. Repeated-measures ANOVAs were used to investigate effects of conditions across experiments (see below). Effect sizes are provided as partial η^2 for ANOVAs and as r_e ($r_{equivalent}$) for t-tests (Rosenthal and Rubin, 2003). r_e is equivalent to the square root of partial η^2 for ANOVAs. This study was not pre-registered. Data in BIDS format (Pernet et al., 2019) are available at https://osf.io/9fmz5/.

Experiment I: Faster detection for repeated than novel regular patterns

Experiment I aimed to replicate previous behavioral work that demonstrates improved detection of a repeated compared to a novel regular pattern (Agus et al., 2010; Bianco et al., 2020) so that we can be sufficiently confident about the sensitivity of our experimental paradigm for characterization of behavioral benefits and neural signatures of perceptual learning.

Methods and materials

Participants

Nineteen participants took part in Experiment I (median age: 20 years; range: 19–22 years; 6 female). Data from one additional participant were excluded because no response was made in more than 25% of trials.

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Stimuli and procedure

Participants listened to the 4.8-s sounds in four blocks. Each block comprised 80 trials, 40 Novel (different regular pattern on each trial) and 40 Repeated (same regular pattern on each trial). Sounds transitioned from the random section to the regular pattern at one of five times (counterbalanced across conditions): 1.6, 2, 2.4, 2.8, or 3.2 s, thus introducing a regular pattern at set 5, 6, 7, 8, or 9, respectively. Trials within each block were randomized such that a maximum of three trials from one condition could occur in a row. Participants were instructed to respond as quickly as possible via key press when they detected the regular pattern. Only responses made within 2 s after pattern onset were considered. Response times were estimated relative to the onset of the first tone of the regular pattern (i.e., 1.6, 2, 2.4, 2.8, or 3.2 s). The interval between two successive sounds was 2 s.

To measure simple change-detection response time, participants heard twenty 4.8-s sounds, in which constituent tones were fixed at one of two frequencies in a single control block. The tones of the first 5, 6, 8, or 9 sets were fixed at 1323 Hz; tones in the remaining sets were all fixed at 1600 Hz. Participants indicated via button press, as quickly as possible, when the switch from one fixed frequency to another happened. Response times were averaged across control trials to estimate the response time to a non-demanding stimulus change, so as to estimate the time it takes for a change to reach awareness and to be translated into motor output (Barascud et al., 2016).

The mean response time from the control block was subtracted from the response time of each trial in the Novel and Repeat conditions in order to normalize response times for the time of awareness and motor processes. For each condition, response times were averaged across the four stimulation blocks, separately for each of the 40 trials per condition presented within a block. This led to two 40-trial response time courses as a function of stimulus presentation. Response times were smoothed using a 7-point rectangular window. A paired t-test was used to compare response times between the Novel and the Repeat conditions at each of the 40 trial positions. False discovery rate was used to account for multiple comparisons (Benjamini and Hochberg, 1995; Genovese et al., 2002).

Considering that a maximum of three trials of the same condition could occur in a row, we also investigated whether any response-time benefit for repeated over novel regular patterns may be driven by trials that are preceded by the same condition or whether the response-time benefit is also presented for trials preceded by a different condition. Response times were analyzed using a repeated measures ANOVA with factors Condition (Novel, Repeat) and Previous Condition (Same, Different).

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Results

Response times associated with the stimulus presentation order are depicted in Figure 1B. At the very beginning of a stimulation block, response times did not differ between Novel and Repeat trials, but by the time they had heard 4-5 repetitions of a unique regular pattern, participants responded significantly faster compared to novel regular patterns (Figure 1B).

The repeated-measures ANOVA revealed faster response times for repeated compared to novel patterns (effect of Condition: $F_{1,18} = 162.958$, $p < 1^{e-8}$, $\eta^2_p = 0.902$) and faster response times when the previous trial was the same compared to the different condition (effect of Previous Condition: $F_{1,18} = 12.581$, $p = 0.002$, $\eta^2_p = 0.411$), but no interaction ($F_{1,18} = 0.655$, $p = 0.429$, $\eta^2_p = 0.035$; Figure 1C). The data suggest that the response-time benefit for repeated regular patterns is not due entirely to the same condition on a previous trial, but that individuals detect the onset of repeated patterns faster even when novel patterns are presented in-between.

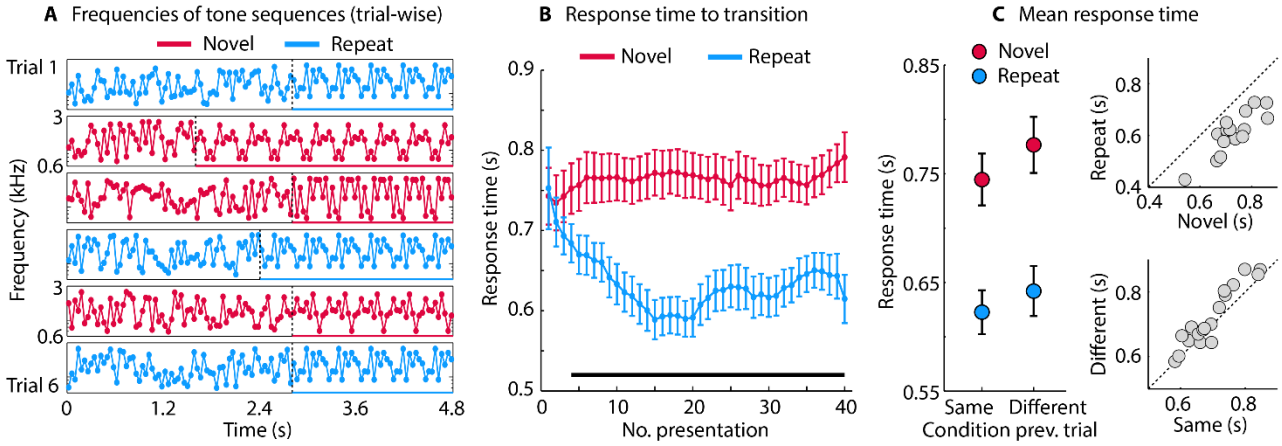

Figure 1: Stimuli and results of Experiment I. A: Tone frequencies for six sequential trials in a block of Experiment I. The black dotted vertical line indicates the onset of a regular pattern and the duration of the regular pattern is indicated by the colored solid line underneath each trial. In the Novel condition, a different regular pattern was presented on each trial. In the Repeat condition, the same regular pattern was present on each trial. The random section of the tone sequences was different from trial to trial for both conditions. **B:** Response times as a function of stimulus presentation (data are smoothed temporally with a 7-point rectangular window). The solid black line indicates a significant difference between novel and repeated regular patterns ($p \leq 0.05$; FDR corrected). **C:** Mean response time across all trials, separately for novel and repeated regular patterns and separately for trials preceded by a trial from the same or different condition.

The results of Experiment I are in line with previous work and show that individuals learn regular tone patterns over a few repetitions (Agus et al., 2010; Kang et al., 2017; Bianco et al., 2020), such that

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they are faster in detecting the pattern when they encounter it again (Bianco et al., 2020). Participants detected a repeated regular pattern about 0.12 s earlier than a novel regular pattern.

In the subsequent EEG experiments (II-V), we explore whether this perceptual benefit also manifests as earlier sustained activity and/or a change in magnitude of sustained activity in response to repeated compared to novel regular patterns.

Experiment II and III: Sustained activity during passive listening to novel and repeated patterns

Regularity-related sustained activity is typically investigated in passive-listening paradigms or under visual distraction (Barascud et al., 2016; Teki et al., 2016; Herrmann and Johnsrude, 2018b; Southwell and Chait, 2018). Experiment II and III of the current study thus investigate whether the repetition of a regular pattern alters sustained activity compared to a novel pattern under passive listening conditions. Novel and Repeat trials were randomly interspersed in Experiment II and blocked in Experiment III.

Methods and Materials

Participants

Eighteen individuals took part in Experiment II (median age: 21 years; range: 18–29 years; 13 female) and twenty different individuals participated in Experiment III (median age: 18 years; range: 18–23 years; 17 female). None of the participants who took part in Experiment II and III took part in Experiment I. Data from four additional participants were recorded for Experiment II, but due to technical problems no triggers were recorded, and the data could not be analyzed.

Stimuli and procedure

In Experiments II and III, EEG was recorded while participants listened passively to auditory stimuli and watched a muted, subtitled movie of their choice on a portable DVD player.

The stimulation procedure for Experiment II was identical to that in Experiment I, with a few exceptions. In each of six blocks, participants listened to 102 trials, 51 in each of the Novel and Repeat conditions. Sounds transitioned from the random section to the regular pattern at set 6, 7, or 8 (with equal probability). Participants thus listened to a total of 153 trials per condition. The inter-stimulus interval was 2 s.

Acoustic stimulation in Experiment III involved the blocked presentation of the Novel and Repeat conditions. We clustered all trials of each condition in order to investigate whether this would increase

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the effects of pattern repetition. In each of six blocks, participants listened to 72 trials, 36 trials in each of the Novel and Repeat conditions. In three blocks, Novel trials preceded Repeat trials, and this was reversed in the other three blocks. The ordering of the Novel and Repeat condition within the six blocks was counterbalanced across participants. Sounds from both conditions transitioned to a regular pattern at set 5, 6, or 7 (with equal probability). Half of the sounds also contained a pattern deviation in the 11th set that was generated by replacing the frequency of tones 105 to 108 with different randomly selected frequencies. The identical procedure was used in Experiment IV, where this pattern deviation served as a detection target.

Results

In Experiment II, neural responses did not differ between the Novel and the Repeat condition for the 0.3–0.8 s time window (t_{17} = 1.043, p = 0.312, r_e = 0.245) nor for the 1–2 s time window (t_{17} = 1.906, p = 0.074, r_e = 0.420; Figure 2A). The results were qualitatively similar for Experiment III, in which trials were blocked by condition: neural responses did not differ between the Novel and the Repeat conditions for the 0.3–0.8 s time window (t_{19} = 0.715, p = 0.483, r_e = 0.162) nor for the 1–2 s time window (t_{19} = 1.568, p = 0.133, r_e = 0.339; Figure 2B). The top part of Figure 2A and 2B shows, that in both experiments, sustained activity was less negative (i.e., reduced) in the Repeat compared to the Novel condition. One possibility for the absence of any effects in the 0.3–0.8 s and 1–2 s time windows may be a lack of statistical power in both experiments considered separately.

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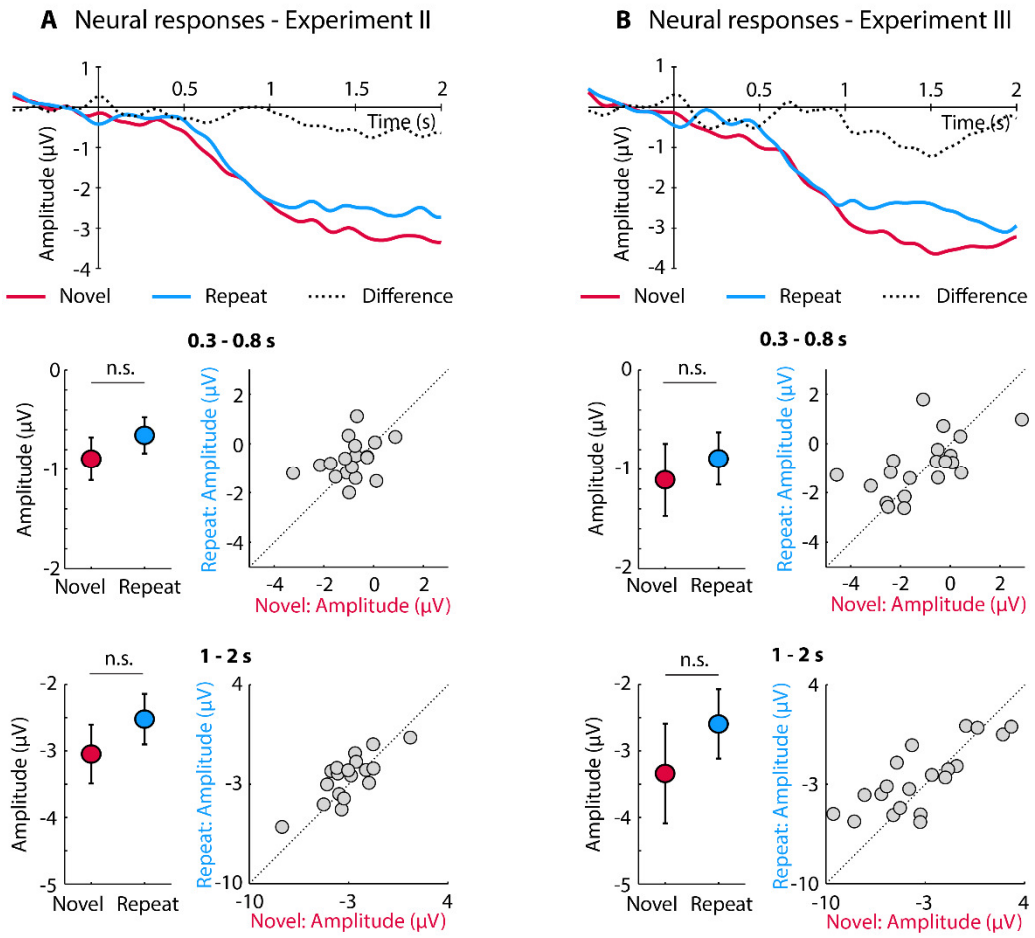

Figure 2: Results for neural responses in Experiment II (A) and III (B). The top row displays neural responses time locked to the onset of the regular pattern in sounds. Bottom parts show neural responses for Novel and Repeat conditions for the two time windows of interest: 0.3–0.8 s and 1–2 s. Sustained activity did not differ between conditions when data from each experiment were analyzed separately. Pooled data across experiments revealed a significant reduction in sustained activity for Repeat compared to Novel trials in the 1–2 s time window. n.s. – not significant

In order to increase statistical power, data from both experiments were submitted to an ANOVA with the within-subjects factor Condition (Novel, Repeat) and the between-subjects factor Experiment (Experiment II, III). For the 1–2s time window, this analysis revealed a significant reduction in sustained activity for the Repeat compared to the Novel condition ($F_{1,36} = 5.049$, $p = 0.031$, $\eta^2_p = 0.123$). The effect of Experiment ($F_{1,36} = 0.061$, $p = 0.806$, $\eta^2_p = 0.002$) and the Condition × Experiment interaction ($F_{1,36} = 0.151$, $p = 0.700$, $\eta^2_p = 0.004$) were not significant. No significant main effects or interaction were observed for the 0.3–0.8 s time window (all $F < 1.4$, $p > 0.2$, $\eta^2_p < 0.04$).

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In sum, the results of Experiment II and III show no signs of earlier sustained activity for the Repeat compared to the Novel condition (i.e., no effects for the 0.3–0.8 s time window, Figure 2A,B top). The analyses, however, revealed a small but significant reduction in sustained activity for repeated compared to novel regular patterns in the 1–2 s time window (data pooled across experiments). This reduction in the magnitude of sustained activity may not be directly related to perceptual learning (which was predicted to lead to earlier sustained activity), but to processes enabled by learning.

Previous work has demonstrated an increase in the magnitude of sustained activity for sounds with a regular pattern compared to sounds without under passive or distracted listening conditions (Barascud et al., 2016; Herrmann and Johnsrude, 2018b; Southwell and Chait, 2018), but this work did not investigate perceptual learning of regular patterns over multiple repetitions. Attention to the patterned sounds may be needed for individuals to learn patterns, such that the associated sustained activity occurs earlier compared to novel patterns. Accordingly, in Experiments IV and V, we required individuals to attend to the sounds.

In Experiment IV, participants had to detect a near-threshold deviation from a regular pattern. If learning a regular pattern strengthens its representation, deviation detection sensitivity should be higher for repeated than for novel patterns. In Experiment V, participants judged, for each sound, whether a visual disc, presented at one of several fixed times relative to pattern onset, precedes or follows the onset of the pattern. Experiment I (Figure 1) and previous work (Bianco et al., 2020) demonstrates that individuals detect a repeated pattern faster than a novel pattern. Hence, we expected that participants in Experiment V indicate an earlier disc time to correspond to the pattern onset for repeated than for novel patterns. In Experiment IV and V, if attention is effective at producing learning, we should see that sustained activity increases earlier for repeated compared to novel patterns. (The procedures of Experiment I could not be implemented for an active EEG task, because anticipation of a motor response increases sustained activity (Jahanshahi and Hallett, 2003; Lang, 2003) that may confound pattern-related sustained activity, and the motor response would occur at the time when pattern-related sustained activity emerges.)

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Experiment IV and V: Earlier sustained activity for repeated than novel patterns under attention

Methods and Materials

Participants

Thirty-two individuals took part in Experiment IV (median age: 18 years; range: 18–29 years; 16 female) and seventeen different individuals participated in Experiment V (median age: 18 years; range: 17–21 years; 13 female). None of the participants took part in any other experiment. Data from one additional participant for Experiment IV were recorded, but the corresponding log files for half of the experimental blocks were not stored due to technical problems. Data for this participant were thus not analyzed.

Stimuli and procedure

Acoustic stimulation in Experiment IV was identical to Experiment III: Novel and Repeated trials were blocked/clustered, with half of them including a deviation in the 11th set. In this experiment, participants were asked to indicate detection of the deviation with a keypress. Since preparation of a motor response could influence low-frequency sustained activity (Jahanshahi and Hallett, 2003; Lang, 2003), the behavioral response was delayed, and cued visually 0.01 s after sound offset. The visual cue consisted of a happy and a sad smiley-face icon presented side by side (Figure 3A). The happy smiley-face icon indicated the button for 'deviation present', whereas the sad smiley-face icon indicated the button for 'deviation absent'. The position of the happy and sad smiley-face icons (left vs. right) was random and participants did therefore not know which button to press prior to the visual response screen, and could thus not prepare any specific motor response (Herrmann et al., 2011a; Herrmann et al., 2011b). The next trial started 2.2 s after they had made a response. Participants performed 2-4 short training blocks to familiarize them with the task and to titrate the number of altered tones that made up the deviant so that participants would reach an ~80% detection rate (a median of 4 tones were used for the deviation).

The acoustic stimulation in Experiment V was similar to that in Experiment III and IV: Sounds had a duration of 4.8 s, each containing a regular pattern starting at set 6, 7, or 8 (with equal probability). Either a new pattern (Novel) or same pattern (Repeat) was presented on each trial, and trials for each condition (Novel, Repeat) were clustered within a stimulation block. On each trial, a disc (white on black background) was presented visually for 0.15 s at one of six times relative to the transition at which the sound changed to a regular pattern (-0.4, -0.14, 0.12, 0.38, 0.64, 0.9 s). Participants were asked to

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indicate whether the disc appeared after the onset of the regular pattern (Vroomen and Keetels, 2010; Patel and Chait, 2011). As in Experiment IV, the response was cued visually 0.01 s after sound offset, to avoid motor preparation. If the disk appeared after the sound transition, they pressed the button indicated by the happy smiley-face icon ("disc after transition"); otherwise they pressed the button indicated by the sad smiley-face icon (Figure 3A). The position of the two icons (left vs. right) was random. The next trial started 2.2 s after the participant had made a response. Participants performed 1-2 short training blocks to familiarize them with the task.

Behavioral data analysis

For Experiment IV, perceptual sensitivity (d') was calculated for Novel and Repeat conditions. A hit was defined as a correct 'deviation present' response. A false alarm was defined as an incorrect 'deviation present' response (i.e., when no deviation was present). A repeated-measures ANOVA with factors transition time (set 5, 6, or 7) and condition (Novel, Repeat) was calculated.

For Experiment V, the proportion of 'disc after transition' responses was calculated for each of the six disc times and two sound conditions (Novel, Repeat). For each participant, a logistic function was fit to the proportion data as a function of disc time relative to pattern onset, with intercept and slope as free parameters. Differences between Novel and Repeat conditions were tested separately for the intercept and slope using paired sample t-tests.

Results

For Experiment IV, participants were more sensitive to deviations in the regular pattern when the transition to a regular pattern started earlier compared to later in the sound ($F_{2,62} = 5.525$, $p = 0.011$, $\eta^2_p = 0.151$, $\varepsilon = 0.793$), consistent with that the regular pattern being better represented when a higher number of regular sets occurred prior to the deviation. Critically, participants were more sensitive to deviations in the regular pattern for repeated compared to novel patterns ($F_{1,31} = 8.308$, $p = 0.007$, $\eta^2_p = 0.211$; Figure 3B; the interaction was not significant, $p > 0.4$). This suggests that the repetition of a regular pattern across trials also enhanced the representation of the regular pattern.

Analysis of neural responses revealed earlier sustained activity (measured as amplitude in the 0.3–0.8 s time window) for the Repeat compared to the Novel condition ($t_{31} = 2.458$, $p = 0.0198$, $r_e = 0.404$; Figure 3C). For the 1–2 s time window, regularity-related sustained activity was reduced (less negative) in the Repeat compared to the Novel condition; this difference trended towards significance ($t_{31} = 1.810$, $p = 0.080$, $r_e = 0.309$).

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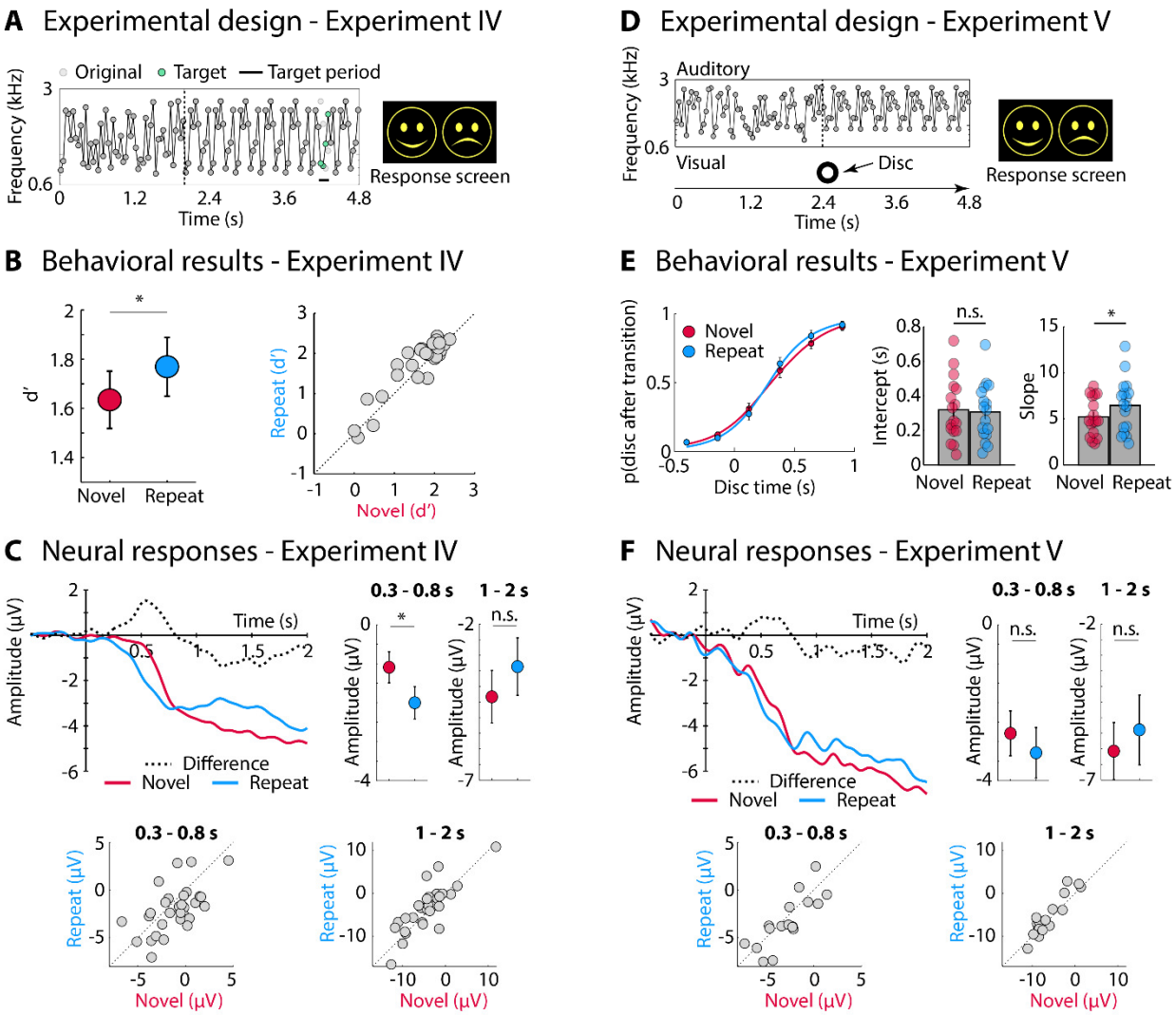

Figure 3: Experimental design and results for Experiment IV and V. A: Experimental design for Experiment IV. A deviation from the regular pattern was inserted into half of the trials by replacing several tone frequencies (median: 4 frequencies), in the 11th set of the sound. The example shows the frequencies for a sound that included a deviant; deviant is marked by the colored dots and the black horizontal line. After sound presentation, participants pressed the key for the happy smiley-face icon (deviation was present) or the key for the sad smiley-face icon (deviation was absent). **B:** Behavioral results indicated that sensitivity was higher for trials in the Repeat compared to Novel condition. **C:** Neural responses: time courses and mean activity. For the 0.3–0. 8 s time window, sustained activity increased earlier (i.e., measured as a more negative amplitude) in the Repeat than Novel condition. There was a trend towards reduced sustained activity for the Repeat compared to the Novel condition in the 1–2 s time window. **D:** Experimental design for Experiment IV. On each trial, a visual disc was presented at one of six times relative to the transition to a regular pattern within the sound. After sound presentation, participants pressed the key for the happy smiley-face icon (disc appeared after transition to regular pattern) or the key for the sad smiley-face icon (disc appear before transition to regular pattern). **E:** Behavioral results indicated a steeper slope for the Repeat compared to the Novel

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condition. **F:** Neural responses: time courses and mean activity for the two time windows of interest (0.3–0.8 s and 1–2 s; there was no significant difference). *$p \leq 0.05$, n.s. – not significant

In Experiment V, the estimated intercept of the logistic function between the Repeat and the Novel condition did not differ ($t_{16} = 0.496$, $p = 0.627$, $r_e = 0.123$). However, the slope of the logistic function fit was larger (i.e., steeper) for the Repeat compared to the Novel condition ($t_{16} = 2.464$, $p = 0.0255$, $r_e = 0.525$; Figure 3E), indicating that the timing of the visual disc relative to pattern onset could be estimated more accurately on Repeat trials. This may indicate a shorter audio-visual temporal integration window for the former relative to the latter (Vroomen and Keetels, 2010).

Sustained neural activity did not differ between Repeat and Novel conditions for the 0.3–0.8 s time window ($t_{16} = 1.286$, $p = 0.217$, $r_e = 0.306$) or for the 1–2 s time window ($t_{16} = 1.528$, $p = 0.146$, $r_e = 0.357$; Figure 3F).

As for the analysis of sustained activity for the passive-listening Experiments II and III, we pooled the data from Experiment IV and V to increase statistical power and calculated an ANOVA with the within-subjects factor Condition (Novel, Repeat) and the between-subjects factor Experiment (Experiment IV, V). For the 0.3–0.8 s time window, sustained activity was overall more negative in Experiment V than Experiment IV (effect of Experiment: $F_{1,47} = 5.209$, $p = 0.027$, $n^2_p = 0.100$). Critically, sustained activity was more negative – indicating shorter latency – in the Repeat compared to the Novel condition ($F_{1,47} = 5.855$, $p = 0.019$, $n^2_p = 0.111$), but there was no Condition × Experiment interaction ($F_{1,47} = 0.497$, $p = 0.484$, $n^2_p = 0.010$). These results suggest that an earlier increase in sustained activity for repeated compared to novel regular patterns requires a person to attend to the sounds, but that the specific attention task may matter less. The earlier increase in sustained activity due to pattern repetition is consistent with the faster detection of repeated compared to novel regular patterns in Experiment I that index perceptual learning (Figure 1).

For the 1–2 s time window, sustained activity was smaller (i.e., less negative) in the Repeat compared to the Novel condition ($F_{1,47} = 4.199$, $p = 0.046$, $n^2_p = 0.082$), but there was no effect of Experiment ($F_{1,47} = 1.906$, $p = 0.174$, $n^2_p = 0.039$) nor a Condition × Experiment interaction ($F_{1,47} = 0.128$, $p = 0.723$, $n^2_p = 0.003$). Reduced sustained activity for repeated compared to novel regular patterns in the 1–2 s time window resembles the reduction in sustained activity observed in Experiments II and III, when listeners ignored the sounds and focused on a visual movie. Reduced sustained activity due to the repetition of a regular patterns appears thus independent of a person's attentional state.

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Examining whether attention affects differences between Novel and Repeat conditions

The results from the previous sections demonstrate reduced regularity-related sustained activity for the Repeat compared to the Novel condition for the 1–2 s time window regardless of whether sounds are ignored (Experiments II and III) or attended (Experiments IV and V). An earlier increase in regularity-related sustained activity (measured as amplitude difference in the 0.3–0.8 s time window) for the Repeat compared to the Novel condition was observed only when participants attended to the sounds. In order to test directly whether the effect of condition (Novel vs. Repeat) on sustained activity differs between attention conditions, we calculated a repeated measures ANOVA with the within-subjects factor Condition (Novel vs. Repeat) and the between-subjects factor Attention (Ignore [Experiments II and III] vs. Attend [Experiments IV and V]).

Results

For the 0.3–0.8 s time window, the Condition × Attention interaction was significant ($F_{1,85} = 7.835$, $p = 0.006$, $\eta^2_p = 0.084$): the sustained activity increase for the Repeat compared to the Novel condition was present only when participants attended to the sounds (Figure 4). There was no main effect of Condition ($F_{1,84} = 0.001$, $p = 0.971$, $\eta^2_p < 0.001$). The same Condition × Attention interaction was observed when we limited our analysis to Experiment III (ignore) and Experiment IV (attend), in which sound stimulation was identical ($F_{1,50} = 4.571$, $p = 0.037$, $\eta^2_p = 0.084$).

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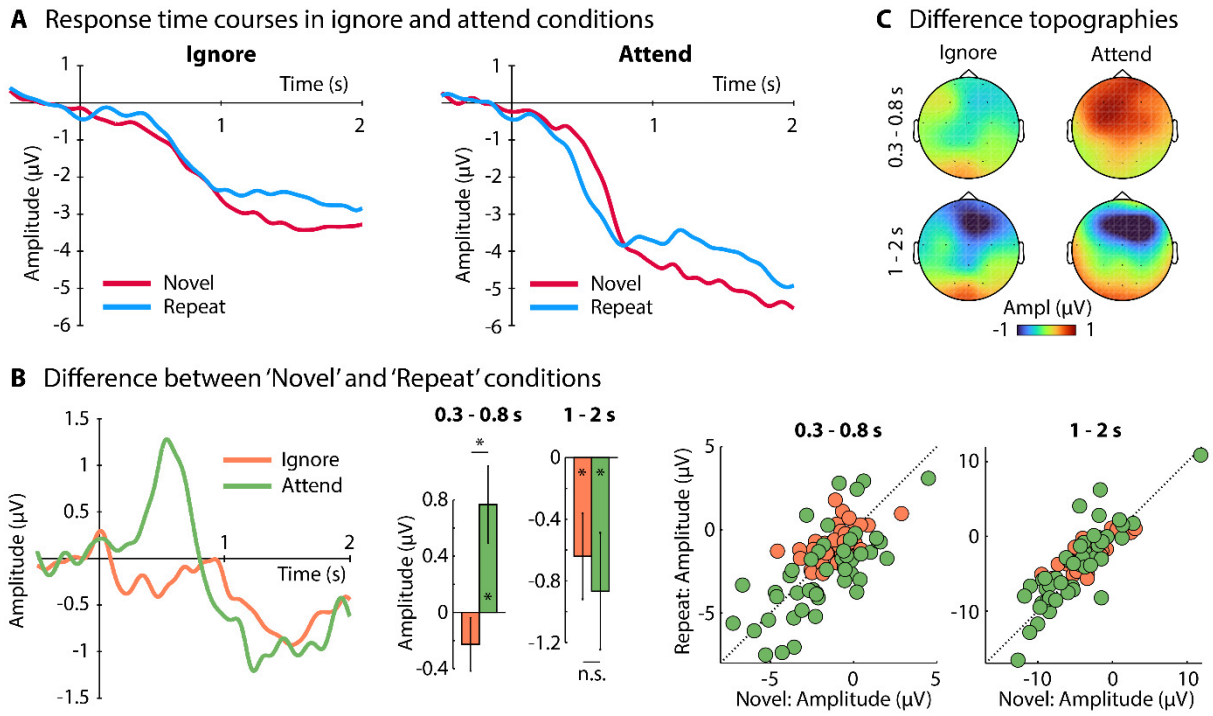

Figure 4: Effects of attention on regularity-related sustained activity in Novel and Repeat conditions. A: Time courses (collapsed across the two experiments in each case: Ignore: Experiments II and III; Attend: Experiments IV and V). **B:** Amplitude differences between Novel and Repeat condition: Time courses, bar graphs for time windows of interest (error bar reflects the standard error of the mean), and individual data points (each dot reflecting data from one participant). The asterisk within bars indicate a significant difference between Novel and Repeat conditions. For the 0.3–0.8 s time window, sustained activity was smaller (i.e., more positive) for the Novel than Repeat conditions when participants attended to sounds, but not when they ignored sounds (interaction $p \leq 0.05$). For the 1–2 s time window, sustained activity was reduced for the Repeat compared to the Novel condition, both when participants attended to, and ignored the sounds. **C:** Topographical distributions of the amplitude difference between Novel and Repeat conditions. *$p \leq 0.05$, n.s. – not significant

For the 1–2 s time window, the ANOVA revealed reduced sustained activity for the Repeat compared to Novel condition (main effect of Condition: $F_{1,85} = 9.247$, $p = 0.003$, $\eta^2_p = 0.098$), but attention did not appear to modulate the condition effect (Condition × Attention: $F_{1,85} = 0.210$, $p = 0.648$, $\eta^2_p = 0.002$; Figure 4).

In order to investigate the evolution of the difference between Repeat and Novel trials in sustained activity over the course of an experiment, trials of each condition (across experiments) were separated into two groups according to whether they occurred early (first half of the trials) or late (second half of trials) in a stimulation block. Trials within each group were averaged for each participant. A repeated-measures ANOVA was calculated using the within-subjects factors Condition (Novel vs.

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Repeat) and Time (Early, Late), and the between-subjects factor Attention (Attend, Ignore), separately for the two time windows of interest.

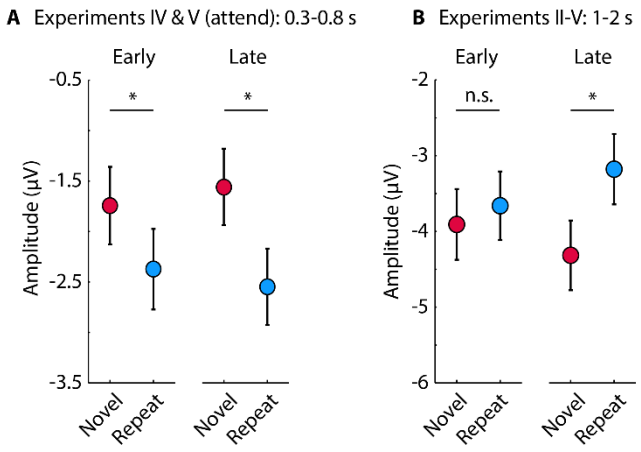

Figure 5: Comparison of sustained activity for Novel and Repeat conditions for early and late trials. A: Mean responses in the 0.3–0.8 s time window (Attend condition) were significantly increased (more negative) for the Repeat compared to the Novel condition for early as well as for later trials within a stimulation block. **B:** Mean responses in the 1–2 s time window (Attend and Ignore conditions) were significantly reduced (less negative) for the Repeat compared to the Novel condition for late, but not for early trials within a stimulation block. Error bars reflect the standard error of the mean. *p ≤ 0.05, n.s. – not significant

In the 0.3–0.8 s time window, the difference between the Novel and the Repeat conditions appears smaller for early compared to late trials, but it was significant for both early and late trials (early: $t_{48} = 2.056$, $p = 0.045$, $r_e = 0.285$; late: $t_{48} = 2.603$, $p = 0.012$, $r_e = 0.352$; Figure 5A), with no interaction ($p > 0.05$). The observation that sustained activity increased earlier for the Repeat compared to the Novel condition, and that this increase is apparent in the first half of the presented trials, is consistent with the behavioral results of Experiment I (Figure 1), indicating rapid perceptual learning.

In the 1–2 s time window, the Condition × Time interaction was significant: $F_{1,85} = 4.483$, $p = 0.037$, $\eta^2_p = 0.050$; Figure 5B), with only late trials exhibiting a difference in sustained activity between Repeat and Novel trials ($t_{86} = 3.158$, $p = 0.002$, $r_e = 0.322$). No difference was evident for early trials ($t_{86} = 0.822$, $p = 0.413$, $r_e = 0.088$; Figure 5B). None of the other effects or interactions were significant (all $p > 0.5$). That sustained activity is reduced for the Repeat compared to the Novel condition only for late trials appears to differ from the behavioral results of Experiment I where reaction time differences were apparent already after a few trials (Figure 1). This may suggest that the reduced magnitude of sustained activity due to pattern repetition may not be directly related to perceptual learning, but processes that are enabled by learning.

In sum, these data suggest a striking functional difference between the onset of sustained activity which is sensitive to rapid perceptual learning when a person attend to sounds, and its magnitude, which seems to reflect processes that result from learning independent of a person's attentional state.

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Experiment VI:

One explanation of the reduction in sustained activity for the Repeat compared to the Novel condition in the 1–2 s time window observed in Experiments II-IV may be that participants were less surprised by the occurrence of a learned, repeated pattern compared to novel patterns. Experiment VI was conducted to test whether an effect of novelty, similar to that seen in the Novel condition in Experiments II-IV, could be induced by presenting sounds with a regular pattern either in a context in which regular patterns occur in 100% of the sounds (as in Experiments II-IV) or in a context in which regular patterns are rare, occurring only in 38% of sounds. We hypothesized that sustained activity would be reduced in the context with frequent compared to rare regular patterns, even when all patterns are unique. This would indicate that the reduction in sustained neural activity (1–2 s time window) for repeated compared to novel patterns in Experiments II-IV may be due to reduced surprise or anticipation of repetition (regardless of the specific pattern).

Participants

Twenty individuals took part in Experiment VI (median age: 19 years; range: 17–31 years; 15 female). None of these participated in Experiments I-IV.

Stimuli and procedure

All sounds were 4.8 s in duration and generated as 120 tone pips (twelve sets of ten tones each), as in Experiments I-IV. Two types of sounds were presented in Experiment VI: experimental sounds and context sounds (Figure 6). Experimental sounds – that is, those for which we analyzed sustained activity – transitioned from random tone frequencies to a regular pattern starting at set 6, 7, or 8 (with equal probability), as in Experiment II. A new regular pattern was selected for each sound similar to the Novel condition in Experiments I-IV. In each of six blocks, 39 experimental sounds were presented. Each block also contained 63 context sounds. Experimental sounds thus made up 38.2% of sounds per block. In half of the blocks, context sounds did not contain a regular pattern (RanContext condition), but rather 10 new tone frequencies were selected for each of the 12 sets. In the other half of the blocks, each context sound contained a regular pattern, starting at set 6, 7, or 8 (RegContext condition). Hence, the probability of a sound comprising a regular pattern was 100% in RegContext blocks and 38.2% in RanContext blocks. All regular patterns generated for context and experimental sounds were drawn randomly and were thus unique. Context sounds and experimental sounds were presented randomly within a block, such that no more than four sounds of the same type (context versus experimental

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sounds) could occur in succession. Blocks with different types of context sounds alternated. Starting context was counterbalanced across participants. Each participant listened passively to a total of 117 experimental sounds per context condition while watching a muted, subtitled movie of their choice.

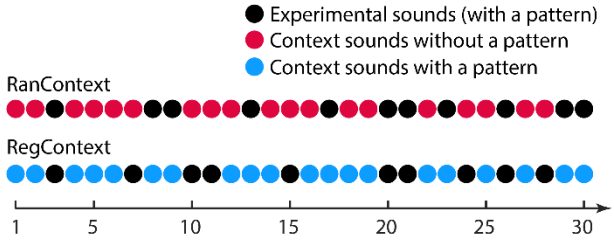

Figure 6: Experimental design of Experiment VI. The first 30 trials from one RanContext and one RegContext stimulation block from a sample participant. Each circle reflects one sound. Colored circles reflect context sounds that either comprised a regular pattern (RegContext) or not (RanContext). Black circles reflect experimental sounds of interest, which comprised a regular pattern. The probability of a sound comprising a regular pattern was 100% in RegContext blocks and 38.2% in RanContext blocks. Neural responses were analyzed only for experimental sounds (black circles).

Results

Neural-activity time courses in response to the onset of a regular pattern presented in RanContext and RegContext conditions are depicted in Figure 7A. Mean sustained activity in the 1–2-s time window was of lower magnitude in the RegContext compared to the RanContext, although this difference was not statistically significant ($t_{19} = 0.813$, $p = 0.426$, $r_e = 0.182$). In Experiments II-IV, the reduction in sustained activity for repeated compared to novel regular patterns has been a small (albeit consistent) effect. The test of the difference between RegContext and RanContext in Experiment VI was less powered, potentially explaining the absence of a statistical difference using a t-test. Nevertheless, the difference between RanContext and RegContext conditions (Experiment VI) and the difference between Novel and Repeat conditions (Experiments II-V) were very similar in the 1–2-s time window, reflected in the difference time course and the response mean, median, and range (Repetition effect: -0.768, -0.655, 15.241; Context effect: -0.720, -0.763, 15.836; Figure 7B). Moreover, the percentage of participants showing reduced sustained activity was comparable between experiment types (Experiments II-V vs. Experiment VI) and was reliably greater than 50% of the group size, which is what would be expected under the null hypothesis that reduced or increased sustained activity is equally likely: 56/87 (64.4%) participants demonstrate reduced sustained activity in the Repeat compared to the Novel condition in Experiments II-V (binomial test, $p = 0.0048$) and 14/20 (70%) of participants show reduced sustained activity in the RegContext compared to the RanContext in Experiment VI (binomial test, $p = 0.0578$). Finally, we compared the response differences between Experiments II-V and Experiment VI using a

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traditional (t_{105} = 0.073, p = 0.941) and a Bayesian independent samples t-test (BF_{10} = 0.254; JASP, 2020). The Bayesian t-test provides moderate evidence for the hypothesis that the reduction of sustained activity for repeated versus novel patterns (Experiments II-V) was of similar magnitude compared to the reduction of sustained activity for patterns occurring frequently (RegContext) versus less frequently (RanContext) in Experiment VI.

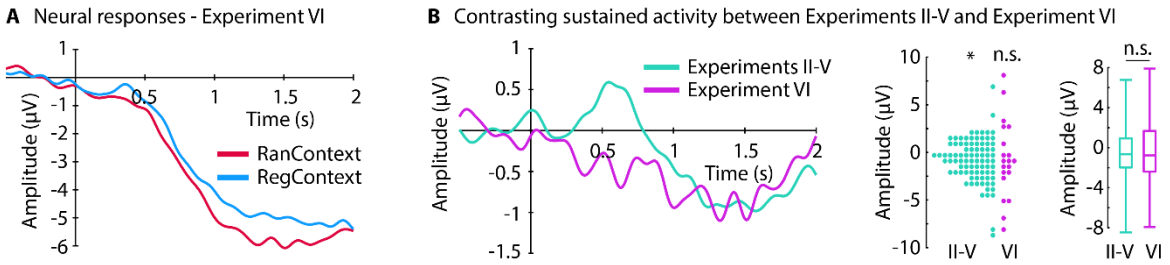

Figure 7: Neural responses in Experiment VI and comparison to responses in Experiment II-V. A: Neural activity time courses in response to a regular pattern, separately for sounds presented in the context of sounds without (RanContext) or with regular patterns (RegContext). RanContext and RegContext did not differ significantly. **B:** Difference time courses for Experiment II-V (Novel minus Repeat) and for Experiment VI (RanContext minus RegContext). Plots on the right show histograms (each dot reflects the data from one person) and box plots for the mean activity in the 1–2 s time window. Plots in panel B highlight the similarity in the magnitude of sustained activity for Experiment VI relative to Experiments II-V. *p ≤ 0.05, n.s. – not significant

General discussion

Here we investigated whether and how perceptual learning of regular patterns in sounds changes sustained neural activity, which is a well-established index of pattern processing (Gutschalk et al., 2002; Barascud et al., 2016; Southwell et al., 2017; Herrmann and Johnsrude, 2018b).

Behavioral evidence of pattern learning

We observed several behavioral benefits associated with the repetition of a regular pattern that suggest perceptual learning. Detection of regular patterns was faster (Experiment I; Figure 1), sensitivity to pattern deviations higher (Experiment IV; Figure 3), and judgements about the temporal order of pattern onset relative to a visual stimulus more accurate (Experiment V; Figure 3) when participants listened to repeated compared to novel patterns. Perceptual benefits emerged rapidly after only a few repetitions of a regular pattern (Experiment I, Figure 1), which is consistent with previous work (Hawkey et al., 2004; Agus et al., 2010; Agus and Pressnitzer, 2013; Kang et al., 2017; Bianco et al., 2020). Moreover, faster

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response times for repeated than novel patterns in Experiment I were observed despite novel patterns being interspersed among repeated patterns, indicating some mechanism for the longer-term encoding of specific patterns, despite interference by other patterns with an identical temporal structure (cf. Agus et al., 2010; Viswanathan et al., 2016; Bianco et al., 2020).

Participants detected repeated regular patterns faster than novel patterns in Experiment I (Figure 1). We therefore expected when participants had to judge whether a visual disc, present at one of several fixed times relative to pattern onset, preceded or followed the onset of the pattern that they would indicate an earlier disc time to correspond to the pattern onset for repeated than for novel patterns. However, this was not observed. Earlier detection of a pattern onset was advantageous for performance in Experiment I, whereas Experiment V may not have provided such an obvious advantage because participants focused on audio-visual integration of the auditory pattern and the visual disc. Audio-visual integration may be a more complex process compared to auditory pattern detection alone, potentially decreasing sensitivity to changes in perceived timing. Interestingly, we observed that temporal order sensitivity (i.e., the slope of the psychometric function) – increased for repeated compared to novel patterns (Figure 3E), which may indicate a narrower audio-visual temporal integration window for the former relative to the latter (Vroomen and Keetels, 2010).

Early increase in sustained activity mirrors rapid perceptual learning

Sustained neural activity is larger when individuals listen to sounds containing a regular pattern compared to sounds without a regular pattern (Pantev et al., 1994; Pantev et al., 1996; Gutschalk et al., 2002; Ross et al., 2002; Barascud et al., 2016; Sohoglu and Chait, 2016; Teki et al., 2016; Southwell et al., 2017; Herrmann and Johnsrude, 2018b; Southwell and Chait, 2018; Herrmann et al., 2019). Here, we investigated whether sustained neural activity changes when listeners learn a repeated regular pattern.

We observed that sustained activity increased earlier for repeated compared to novel patterns when participants attended to but not when they ignored the sounds (Figure 4). The earlier increase in sustained activity for repeated compared to novel patterns was present for trials within the first half of a stimulation block (Figure 5) and thus mirrors the pattern of response times observed in Experiment I (Figure 1; cf. Agus et al., 2010; Bianco et al., 2020). The earlier increase in sustained activity may thus index processes related to rapid perceptual learning.

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Reduced sustained activity due to pattern repetition

We observed reduced sustained activity 1–2 s after pattern onset for repeated compared to novel patterns, both when participants actively or passively listened to sounds (Figure 4). The data are in line with work showing that perceptual learning in adulthood, including learning of auditory patterns similar to the ones used here, can occur in the absence of attention or when patterns are task irrelevant (Seitz and Dinse, 2007; Andrillon et al., 2017; Bianco et al., 2020). Because repeated patterns are more predictable than novel patterns, the reduction in sustained activity for repeated relative to novel patterns is consistent with a predictive coding account, in which responses to predictable events are reduced compared to responses to novel events (Friston, 2005; Baldeweg, 2006; Bubic et al., 2010; Arnal and Giraud, 2012; see also Heilbron and Chait, 2018). Behavioral benefits for repeated over novel patterns could reflect successful prediction.

The repetition-related reduction in sustained activity 1–2 s post pattern onset was limited to late sound trials only (Figure 5), contrary to repetition-related behavioral benefits that manifest after a few trials (Experiment I; Figure 1; cf. Agus et al., 2010; Bianco et al., 2020). These discrepant results suggest that reduced sustained activity for repeated compared to novel patterns may not be associated with the rapid perceptual learning observed behaviorally, but rather with a cognitive consequence of such learning, such as increased predictability or reduced novelty. In Experiment VI, we explored this possibility by measuring sustained activity for novel regular patterns occurring frequently (highly predictable) or infrequently (less predictable) within a presentation block. Indeed, we observed a reduction in sustained activity for the former compared to the latter (Figure 7). This reduction in sustained activity was small (and not statistically significant; potentially due to lower statistical power compared to the pooled Experiments II & III and IV & V). However, the effect in Experiment VI was comparable to the repetition-related reduction in sustained activity in Experiments II-V. Drawing firm conclusions about the functional meaning of reduced sustained activity is certainly not warranted at this point, but the results of Experiment VI may encourage exploration of the hypothesis that reduced sustained activity observed in Experiments II-V reflects reduced novelty or increased predictability following perceptual learning.

Speculations about underlying neural sources

The underlying sources of pattern-related sustained activity involves auditory cortices (Pantev et al., 1994; Pantev et al., 1996; Gutschalk et al., 2002; Barascud et al., 2016) and potentially higher-level brain regions including parietal cortex, frontal cortex, and hippocampus (Tiitinen et al., 2012; Barascud et al.,

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2016; Teki et al., 2016). Previous work suggests that there are two distinct regions, an anterior and a posterior one, in auditory cortex that generate sustained activity, but that only the anterior region is modulated by auditory patterns (Gutschalk et al., 2002). Our 16-channel EEG setup does not allow firm conclusions to be made about the underlying sources of the learning-related neural effects, but the frontal-central EEG distribution depicted in Figure 4C is consistent with a more anterior region of auditory cortex as well as with frontal cortex activity. From the topographical EEG distribution, however, it appears unlikely that parietal cortex is involved. Previous work suggests that perceptual learning recruits the hippocampus (Rose et al., 2011; Mundy et al., 2013; Larcombe et al., 2018), but whether or not the hippocampus contributes to long-term representations of auditory patterns and the sustained activity signatures thereof cannot be answered with our EEG setup. Other imaging modalities such as functional magnetic resonance imaging or lesion studies may be more suitable to assess the contribution of the hippocampus.

Conclusions

In a series of six behavioral and EEG experiments, we investigated the behavioral and neural signatures that index rapid perceptual learning of regular patterns in sounds. We show that participants detect regular patterns faster, are more sensitive to pattern deviations, and judge the temporal order of pattern onset and a visual stimulus more accurately for repeated compared to novel regular patterns. Sustained neural activity indexed perceptual learning in two ways. Sustained activity increased earlier for repeated compared to novel patterns when participants attended to sounds, but not when they ignored them. This effect mirrored the rapid perceptual learning we observed behaviorally. The magnitude of sustained activity was reduced for repeated compared to novel patterns both when participants attended to, and ignored, the sounds. This reduction of sustained activity appeared only in later phases of our experimental protocols, suggesting it is not directly related to rapid perceptual learning, but perhaps to cognitive processes enabled by learning. Our study thus reveals neural markers of perceptual learning of auditory patterns, and of processes that may be related to reduced novelty or better prediction of learned auditory patterns.

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Declaration of conflict of interest

None.

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