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Frequency-Based Neural Discrimination in Fast Periodic Visual Stimulation

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Abstract

Humans capitalize on statistical cues to discriminate fundamental units of information within complex streams of sensory input. We sought neural evidence for this phenomenon by combining fast periodic visual stimulation (FPVS) and EEG recordings. Skilled readers were exposed to sequences of linguistic items with decreasing familiarity, presented at a fast rate and periodically interleaved with oddballs. Crucially, each sequence comprised stimuli of the same category, and the only distinction between base and oddball items was the frequency of occurrence of individual tokens within a stream. Frequency-domain analyses revealed robust neural responses at the oddball presentation rate in all conditions, reflecting the discrimination between two locally-emerged groups of items purely informed by token frequency. Results provide evidence for a fundamental frequency-tuned mechanism that operates under high temporal constraints and could underpin category bootstrapping. Concurrently, they showcase the potential of FPVS for providing a direct neural measure of implicit statistical learning.

Keywords: Fast periodic visual stimulation, statistical learning, implicit learning, category bootstrapping, frequency effect

1. Introduction

The human brain can learn implicitly and effortlessly from the statistical properties of an input stream. Known as implicit statistical learning, this remarkable, domain-general ability helps us make sense of the highly complex and ever-flowing sensory environment to which we are exposed, by enabling us to discover fundamental units of information (for recent reviews, see Armstrong et al., 2017; Aslin, 2017; Christiansen, 2019; Frost et al., 2019; Newport, 2016). Arguably, the most familiar experimental demonstrations of such a phenomenon come from language research, attesting our ability to detect conditional relations between elements in the input. For example, guided only by differences in the transitional probabilities (TPs) between syllables, we can extract out of a continuous stream of sounds multi-syllabic units that correspond to words, and differentiate them from nonwords (Saffran et al., 1996; for analogous findings in the visual modality with shapes, see Kirkham, Slemmer, & Johnson, 2002; Siegelman & Frost, 2015; Turk-Browne, Jungé, & Scholl, 2005).

In addition to these, however, there are a host of statistical relations that can influence learning (Thiessen et al., 2013). By relying on the frequency distributions of phonemes in the input, for example, we are able to discover categorical prototypes (and boundaries), and distinguish between different phonemic categories (Maye et al., 2002; for analogous findings in the visual modality with low-level stimuli, see Rosenthal et al., 2001). In the current study, we examine whether distributional information can elicit implicit statistical learning in the context of an increasingly popular methodology that combines electrophysiological recording with Fast Periodic Visual Stimulation (FPVS).

Capitalizing on the principle of neural entrainment (for a review, see Norcia et al., 2015), the FPVS approach uses frequency tagging to effectively capture visual discrimination processes at the level of the brain (for a review see, Rossion, 2014). In particular, this involves presenting sequences of base stimuli (i.e., a set of visual items) at a fast periodic frequency rate F interleaved with oddball stimuli (i.e., a set of items that differ from base stimuli on a dimension of interest), inserted at fixed

intervals (every n item) and thus appearing at a slower periodic rate (F/n). A few minutes of stimulation are sufficient to evoke robust neural responses (i.e., steady state visual evoked potentials, SSVEP; Regan 1966) that are clearly and objectively identifiable at the predefined base and oddball stimulation frequencies and their harmonics. Critically, the presence of a neural response at the oddball frequency reflects the brain's ability to discriminate between oddballs and base stimuli and is selective to the dimension that differentiates them. Finally, this neural discrimination response is obtained implicitly in the absence of task-induced measures, and it is thus devoid of potential contamination from other cognitive and decisional processes.

This highly sensitive and behavior-free approach has become particularly popular for probing category-selective processing at the level of perception (see also Coll et al., 2019; Van der Donck et al., 2020; Stothart et al., 2017 for higher-level categorization in emotion and semantic processing) and has provided important insights into the neural representation of stimuli such as faces, objects, and words, in studies with healthy adults (Jacques et al., 2016; Liu-Shuang et al., 2014; Lochy et al., 2015; Retter & Rossion, 2016; Rossion et al., 2015; Stacchi et al., 2019) and children (Lochy et al., 2016), as well as clinical populations (Lochy et al., 2018; Liu-Shuang et al., 2016; Stothart & Smith, 2020).

Beyond pre-established categorical differences, however, an important and outstanding question is whether this approach can also capture the *emergence of a novel distinction*. The FPVS-oddball design provides a context that can easily foster implicit statistical learning. Extensively used to explore the neural mechanisms that underlie the detection of novelty in our perceptual environment (i.e., mismatch negativity; for reviews see, Kimura et al., 2011; Kremlacek et al., 2016; Näätänen et al., 2007; Stefanics et al., 2014), the oddball paradigm features oddballs as rare deviants in a stream of frequent, standard events. A typical 60-second FPVS sequence, for example, with a base presentation rate of 6 Hz and an oddball embedded periodically every 5th item (i.e., $6/5 = 1.2$ Hz), comprises a total of 360 stimuli, out of which 288 are base stimuli and only 72 appear as oddballs.

Differences in the frequency with which oddball and base stimuli occur in a given input stream are therefore inherent in the nature of the experimental paradigm. Importantly, this relative frequency-of-occurrence difference constitutes a source of distributional information on the basis of which oddballs (i.e., a group of infrequent stimuli) could be differentiated from base stimuli (i.e., a group of frequent stimuli), independently (or in the absence) of any pre-existing difference between them. But is the brain capable of such fast and implicit statistical learning simply based on the frequency-of-occurrence of perceptual events? And if so, is this frequency difference sufficient to elicit a neural discrimination response? To address these questions, we adopted a simple modification of the classic FPVS-oddball paradigm by exposing participants to *homogeneous* streams of stimuli, insofar all the items were drawn from the same category (e.g., word oddballs embedded in a sequence of words). Crucially, base and oddball types could be differentiated *only* by their respective frequency-of-occurrence within a presentation stream: oddball tokens appeared four times less often than base tokens (see Figure 1). Item assignment to oddball and base stimuli was performed randomly across participants who were engaged in an orthogonal task. Under these conditions and in the absence of other pre-existing or systematic distinctions between base and oddball stimuli, neural entrainment at the oddball stimulation frequency would index a selective discrimination response between two newly emerged groups of stimuli, generated purely on the basis of the statistical structure of the input stream.

In order to determine whether or not the emergence of such differential signal stems from a primary learning mechanism that applies to any perceptual event, participants were exposed to four types of linguistic stimuli: (1) familiar words; (2) pronounceable letter strings that are not attested as words in the lexicon (Pseudowords); (3) unpronounceable consonant strings (Nonwords), and (4) strings of letter-like, non-alphabetic characters (Pseudofonts; see Figure 1 for examples). We hypothesized that if sensitivity to local token frequency in the context of FPVS-oddball designs is

influenced by stimulus familiarity, then discrimination responses would be modulated as stimuli become increasingly similar to well-established neural representations (i.e., more word-like).

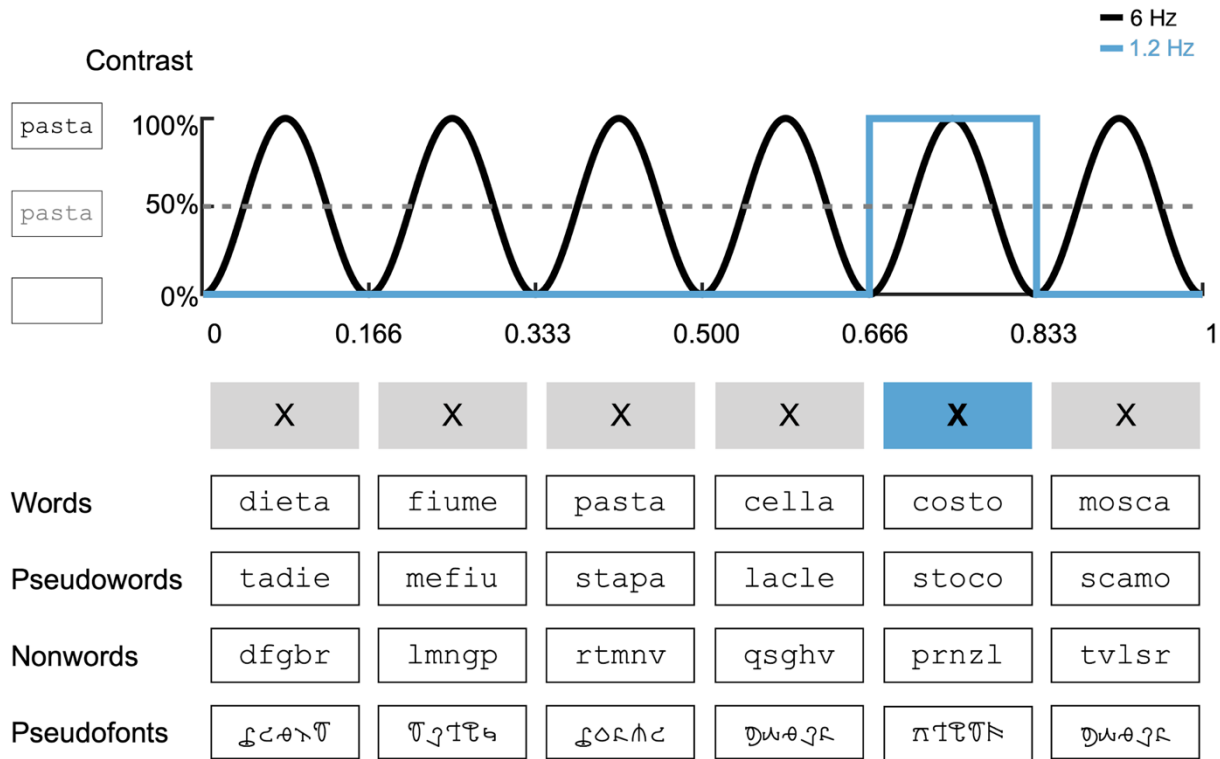


Figure 1. Experimental paradigm. In each sequence, stimuli were presented by sinusoidal contrast modulation at 6 Hz during 60 s. Each stimulus reached full contrast 83 ms after its onset and faded out completely after 166 ms (the duration of one cycle). Oddball stimuli appeared every fifth item at a frequency rate of 1.2 Hz (6/5 Hz). Differently from the classical FPVS-oddball design in which oddballs are embedded in a sequence of base stimuli that belong to a different category, in the present study oddballs and base stimuli were randomly drawn from the same category (X embedded in X; oddball is highlighted for illustration) and differed only in terms of their token frequency. A stimulation sequence comprised 360 stimuli with each base token repeated 36 times and each oddball token 9 times. Presentation order was pseudo-randomized to avoid immediate repetition. Examples are given for the four different conditions used in the experiment.

2. Materials and Methods

2.1 Participants

Thirty paid volunteers (7 males; age: $M = 24.8$, $SD = 4.02$) took part in the experiment after giving written informed consent. All participants were right-handed and native speakers of Italian, reporting having normal or corrected-to-normal vision and no history of linguistic or neurological impairment. Participants remained unaware of the goals of the experiment until the end of the session. The present study was approved by the SISSA Ethics Committee.

2.2 Stimuli

Experimental stimuli comprised four categories: Words, Pseudowords, Nonwords, and Pseudofonts. Each category consisted of 16 items, all five-elements long. Words (e.g., *pasta*) were selected to be frequent singular nouns (\log_{10} frequency: $M = 3.29$, $SD = 0.12$), made up of frequently occurring letter combinations (mean \log_{10} bigram frequency: $M = 6.08$, $SD = 0.47$). Pseudowords (e.g., *stapa*) were constructed by rearranging the letters of the word stimuli to form novel pronounceable letter strings, also with frequent letter combinations (mean \log_{10} bigram frequency: $M = 6.31$, $SD = 0.59$). Nonwords (e.g., *qnlvd*) were constructed by sampling random consonants without replacement, resulting in unpronounceable letter strings with rare or non-existent letter combinations (mean \log_{10} bigram frequency: $M = 4.07$; $SD = 1.63$). Finally, pseudofont strings (e.g., *vaifm*), were constructed by combining characters from the BACS-2 serif artificial script (Vidal et al., 2017), which were designed to closely match the visual characteristics of Latin characters (i.e., number of strokes, junctions, terminations, and serifs).

2.3 Experimental Paradigm and Procedure

A schematic illustration of the experimental paradigm is shown in Figure 1. Stimuli were presented in sequences of 360 stimuli, 72 of which were oddballs and 288 base stimuli. Base and oddball stimuli in a given sequence belonged to the same category (e.g., word oddballs embedded in a stream of word base stimuli) and differed only in terms of how often their respective tokens ($N = 8$) appeared in the stream, with oddball tokens presented four times less frequently (i.e., 9 repetitions of each oddball token) than base tokens (i.e., 36 repetitions of each base token). The selection of base and oddball tokens involved randomly drawing two sets of 8 unique items from each stimulus category. In order to account for any systematic differences between oddball and base tokens, this procedure was performed separately for each individual participant. Once drawn, the selection of oddball and base tokens was held constant across all experimental trials for the same participant.

An experimental trial comprised a stimulation sequence, presented for 60 seconds. In each trial, stimuli were presented by sinusoidal contrast modulation at a frequency of 6 Hz, with each stimulation cycle (i.e., from a 94% light grey background to full contrast and back) reaching full contrast after 83 ms and lasting a total of 166.66 ms. An oddball stimulus was embedded every five base stimuli (i.e., oddball frequency of 1.2 Hz, thus every 833 ms). The presentation order of the stimuli was pseudo-randomized so as to eliminate consecutive item repetitions: base repetitions were separated by a minimum of 4 base stimuli, whereas oddball repetitions were separated by at least 2 oddball presentations (i.e., minimum distance 14 items). There were 5 experimental trials per condition such that the total stimulation time was 20 minutes: 60 s (trial duration) X 4 conditions (Words, Pseudowords, Nonwords, Pseudofonts) X 5 trials. Experimental trials were presented in random order

and were separated by a 30-second break. Each break ended with a 15-second countdown that indicated the beginning of the next trial.

Participants were run individually in a sound-attenuated and dimly illuminated room, seated at approximately 80 cm from a 27" BenQ XL2720Z monitor. Screen resolution was 1920 X 1080 pixels and refresh rate was set at 60 Hz. Stimulus display was administered by PsychToolbox-3 (Brainard, 1997, <http://psychtoolbox.org/>) on MATLAB R2015b (The MathWorks) in a Windows environment. All stimuli were presented at the center of the screen. All alphabetic stimuli (i.e., Words, Pseudowords and Nonwords) were presented in lowercase characters, using the fixed-width Courier New font, whereas Pseudofonts were presented in BACS-2 serif font. Both fonts were emboldened by 70% from their original character weight to improve visibility. Each stimulus subtended horizontal and vertical visual angles of 2.87 and 0.72 degrees, respectively.

Participants were instructed to fixate a small cross (12 pixels) presented continuously at the center of the screen, and to press a button as soon as they detected a change in its color (from blue to red and vice versa), which occurred randomly 6 times within each trial, independently of the oddball-base manipulation. The sole purpose of the color-change detection task was to ensure that the participant maintained a constant level of attention throughout the stimulation. Overall, participants' performance in the color-change detection task was highly accurate (accuracy: $M = 97.2\%$, $SD = 8$; reaction times: $M = 448$ ms, $SD = 73$) and comparable across the different experimental conditions (Words = 98.2%, $SD = 5$, reaction time: $M = 447$ ms, $SD = 73$; Pseudowords = 95.5%, $SD = 11$, reaction time: $M = 446$ ms, $SD = 71$; Nonwords = 98.3%, $SD = 6$, reaction time: $M = 447$ ms, $SD = 67$; Pseudofonts = 96.8%, $SD = 9$, reaction time: $M = 453$ ms, $SD = 80$).

2.4 EEG Acquisition and Preprocessing

Electroencephalographic (EEG) activity was acquired at a sampling rate of 256 Hz using an Active Two Biosemi system (Biosemi, Amsterdam, Netherlands) with 128 active electrodes mounted on an elastic cap and positioned according to the radial-ABC system locations. Two additional electrodes served as reference (Common Mode Sense active electrode, CMS) and ground (Driven Right Leg passive electrode, DRL). The magnitude of the offset of all electrodes, referenced to the common mode sense, was held below 20 mV.

EEG data preprocessing was performed in MATLAB (MathWorks, Inc) using a combination of custom script and the EEGLAB toolbox (Delorme & Makeig, 2004). Data from each subject were band-pass filtered (0.1–100 Hz), and artifact-ridden channels were removed by visual inspection of their time series and spectra. Eye blink, muscular and electrode-pop artifacts were removed using Independent Component Analysis. After cleaning, removed channels were replaced by using spherical interpolation, and data were segmented into 60-second epochs and re-referenced to the average of all electrodes. This procedure resulted in one dataset (5 trials of 60 seconds) per participant per condition. Data from one participant were excluded from the analyses due to excessive movement artifacts in the electrophysiological data.

2.5 Frequency Domain Analysis

Experimental trials were first averaged in the time domain, separately for each condition and each individual participant. This procedure served to reduce EEG activity that was not phase-locked to the stimulation. Data were then submitted to a Fast Fourier Transform and normalized amplitude spectra were extracted for each channel (absolute value of the FFT, divided by the number of data points). Given that the length of the epochs was 60 seconds, the frequency resolution was very high ($1/60 = 0.0167$ Hz). To account for noise variations across the frequency spectrum, a local baseline-

correction was applied, which involved subtracting from each frequency bin the mean of the surrounding 20 bins (10 from each side, excluding immediately adjacent bins and bins with minimum and maximum values; as in e.g., Dzhelyova & Rossion, 2014). Base and oddball responses were defined as the sum of the baseline-corrected amplitudes at the base (6 Hz) and oddball (1.2 Hz) stimulation frequencies and their corresponding first three harmonics (base: 12, 18, 24 Hz; oddball: 2.4, 3.6, 4.8 Hz).

2.5.1 ROI Analysis

The EEG response at the base stimulation frequency was analyzed in an occipito-parietal area comprising twenty electrodes surrounding and including Oz (A23 in Biosemi's ABC labeling), the site typically showing maximal SSVEP responses (Norcia et al., 2015). The EEG response at the oddball stimulation frequency were examined in two predefined regions-of-interest (ROI). Following previous work that used the same type of visual stimuli (i.e., pseudofonts and letter strings, e.g., Lochy et al., 2015), the primary regions of interest for oddball responses comprised an area of five occipito-temporal sites including and around the electrode PO7 on the left, and PO8 on the right hemisphere (A10 and B7 respectively in Biosemi's ABC labeling).

Data analysis was conducted at two levels. First, in order to test the significance of the oddball response in each condition, the response of interest was averaged across the channels of each ROI for each participant, and then subjected to a one sample t-test. Second, differences between conditions were assessed through ANOVAs with Condition (Words, Pseudowords, Nonwords, Pseudofonts) as a within-groups factor. In the case of the response at the oddball frequency, the within-groups factor of Hemisphere (left, right) was also included. The absence of statistically significant effects was further corroborated via a JZS Bayes Factor (Rouder et al., 2009), which measures the relative evidence for the null vs. the alternative hypothesis, thus allowing to provide support for the null itself (Leppink et al., 2017). These analyses were performed using a Cauchy prior with the default scale value of $r = 0.5$. We

report the relative evidence in favor of the null (BF01), where a value of 1 implies equal relative evidence and values above 3 indicate evidence in favor of the null.

2.5.2 Cluster Permutation Test

To assess the presence of an effect in electrodes besides the ones included in the ROIs, the presence of an oddball response was additionally tested using a non-parametric clustering method (Bullmore et al., 1999) as implemented in the FieldTrip toolbox for EEG/MEG analyses (Oostenveld et al., 2011). This method provides an intuitive and straightforward solution to the multiple-comparisons problem. It relies on the fact that a true effect should not be isolated, but should instead spread over adjacent electrodes, and is implemented through the following steps: (i) a statistic of interest (a t-value and the corresponding p-value, in this case) is calculated for each channel; (ii) spatially neighboring channels that yield a significant result ($p < 0.05$) are grouped together into candidate clusters, and a cluster-level t-value is computed by summing their individual t-values; (iii) next, a random subset of channels have their values set to zero, and the procedure is repeated on this surrogate data. This is repeated a large number of times (5000, in this case) and each time the largest cluster-level t-value is retained, constructing in this way an empirical distribution of possible t-values under the null; (iv) finally, the p-values of the observed candidate clusters is calculated as the percentage of t-values from the null distribution that are more extreme than their cluster-level t-value (for more details, see Maris & Oostenveld, 2007).

2.5.2.1 Comparisons Across Conditions. In order to test for possible differences in the topographies of the effects across conditions, we first applied the cluster permutation method described above. Since no significant clusters emerged in any of the comparisons, we turned to the JZS Bayes Factor (using a default Cauchy prior with scale value of $r = 0.707$) to assess the evidence in favor of no difference between conditions. We calculated the Bayes Factor independently for each electrode and reported the number of electrodes showing evidence in favor of the null and in favor of the alternative

hypothesis. The analysis was performed using MATLAB functions retrieved from https://figshare.com/articles/dataset/Bayes_Factors_Matlab_functions/1357917.

3. Results

3.1 Base Stimulation Frequency

A response at the base stimulation frequency reflects the successful synchronization of the visual system to the periodic stimulation and serves to demonstrate a constant deployment of attentional resources. In all experimental conditions the base stimulation frequency (6 Hz) and its higher harmonics (12, 18 & 24 Hz) resulted in a clear response in the predefined region of interest around Oz (Words: $t(28) = 9.556$, $p < 0.001$, $g = 1.774$ [95% CI: 1.179 - 2.356]; Pseudowords: $t(28) = 9.707$, $p < 0.001$, $g = 1.802$ [95% CI: 1.202 - 2.390]; Nonwords: $t(28) = 13.173$, $p < 0.001$, $g = 2.446$ [95% CI: 1.706 - 3.174]; Pseudofonts: $t(28) = 14.522$, $p < 0.001$, $g = 2.696$ [95% CI: 2.696 - 3.482]). The scalp topography of the response was analogous to the one previously observed in studies that presented visual stimuli at the same or similar frequency rates (e.g., Liu-Shuang et al., 2014). A one-way ANOVA revealed an effect of Condition that was marginally significant ($F(2.12, 59.32) = 3.13$, $p = 0.048$, Greenhouse-Geisser corrected.) A subsequent JZS Bayes Factor analysis, however, revealed moderate evidence against the presence of this effect (BF01 = 6.289), and as such it was not submitted to further analyses.

3.2 Oddball Stimulation Frequency

3.2.1 ROI Analysis

Results revealed a significant oddball response in both the predefined left and right occipitotemporal regions of interest (see Figure 2).¹ Tokens with a low frequency of occurrence successfully elicited an entrainment at the oddball stimulation frequency when the stream of stimulation consisted of Words embedded in Words (Left ROI: $t(28) = 4.16, p = 0.0003, g = 0.77$ [95% CI: 0.35 - 1.18]; Right ROI: $t(28) = 3.87, p = 0.0006, g = 0.72$ [95% CI: 0.30 - 1.12]), Pseudowords in Pseudowords (Left ROI: $t(28) = 3.46, p = 0.0017, g = 0.64$ [95% CI: 0.28 - 1.04]; Right ROI: $t(28) = 3.20, p = 0.0033, g = 0.59$ [95% CI: 0.19 - 0.99]), Nonwords in Nonwords (Left ROI: $t(28) = 2.55, p = 0.0164, g = 0.47$ [95% CI: 0.08 - 0.85]; Right ROI: $t(28) = 3.79, p = 0.0007, g = 0.70$ [95% CI: 0.29 - 1.10]), and Pseudofonts in Pseudofonts (Left ROI: $t(28) = 2.66, p = 0.0127, g = 0.49$ [95% CI: 0.10 - 0.88]; Right ROI: $t(28) = 2.79, p = 0.0093, g = 0.59$ [95% CI: 0.13 - 0.90]). A two-way ANOVA failed to indicate any significant effect of either Hemisphere ($F(1, 28) = 0.440, p = 0.5112, \eta^2 = 0.001$) or Condition ($F(1, 28) = 0.440, p = 0.2993, \eta^2 = 0.001$); additionally, the interaction between the two terms was not significant ($F(3, 84) = 2.343, p = 0.7885, \eta^2 = 0.015$). A JZS Bayes Factor analysis corroborated the absence of statistically significant effects for Hemisphere (BF01 = 6.134), Condition (BF01 = 5.617) and their interaction (BF01 = 250).

¹ As a sanity check, we examined whether, in addition to the oddball stimulation frequency at 1.2 Hz (every 5th item, 6/5 Hz), our data showed evidence for neural entrainment also at 1 Hz (every 6th item, 6/6 Hz), 1.5 Hz (every 4th item, 6/4 Hz), 2 Hz (every 3th item, 6/3 Hz), and 3Hz (every 2nd item, 6/2 Hz). Results showed only scattered evidence for entrainment at these frequencies. Of the 32 tests that we ran (4 frequencies x 2 ROI x 4 types of stimuli), only 7 were significant: at 1 Hz, Words, right ROI: $t(28) = 1.89, p = .035$; at 1.5 Hz, Pseudofonts, right ROI: $t(28) = 2.12, p = .021$; and at 3 Hz (Words, right ROI: $t(28) = 5.68, p < .001$, left ROI: $t(28) = 3.25, p = .001$; Pseudowords, right ROI: $t(28) = 1.83, p = .039$; Nonwords, right ROI: $t(28) = 2.33, p = .014$, left ROI: $t(28) = 1.70, p = .05$). This is in stark contrast with the very systematic emergence of a response at the frequency of oddball presentation.

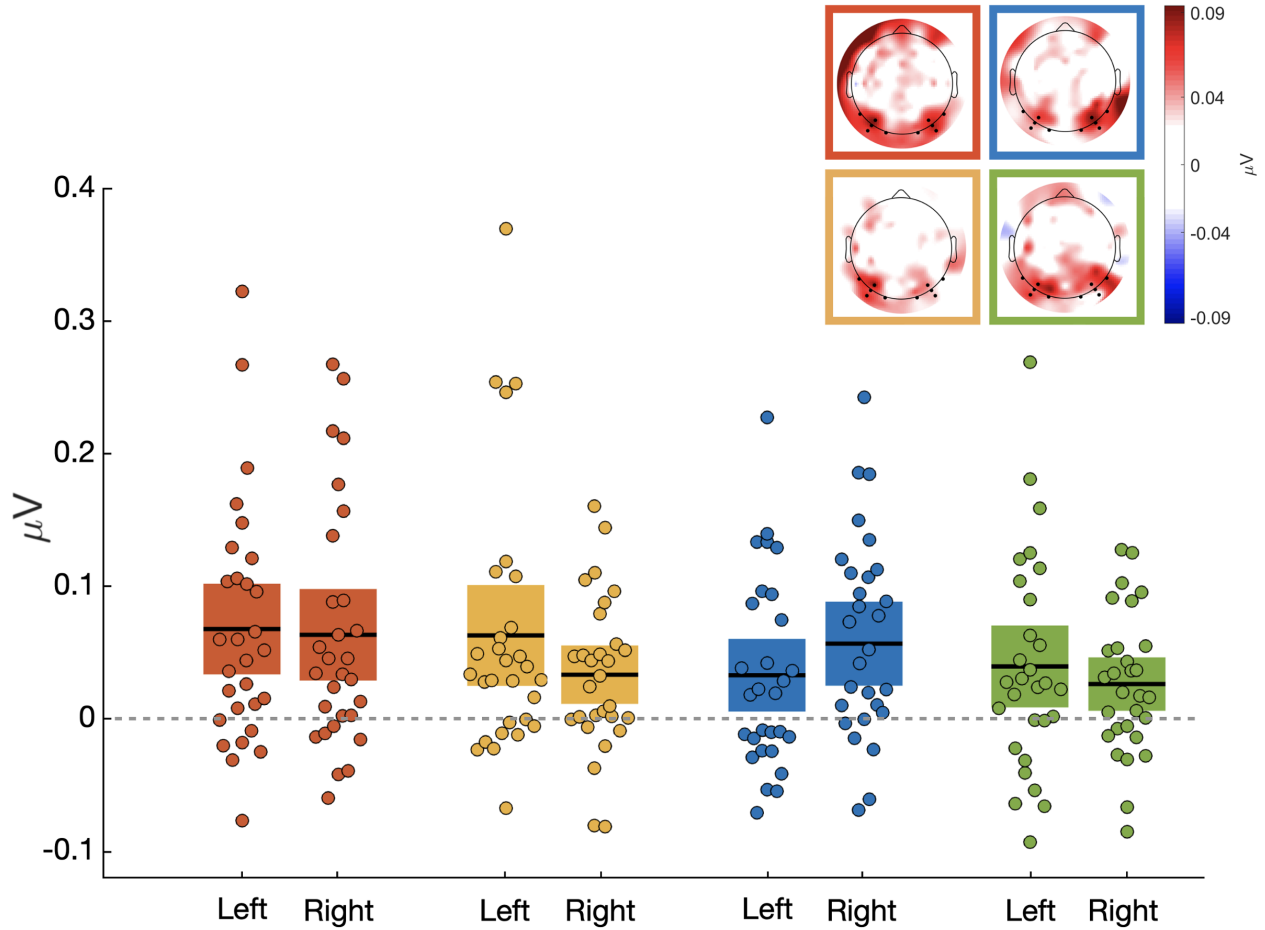


Figure 2. Grand-averaged token frequency response estimated as the summed baseline corrected amplitudes for the oddball frequency (1.2 Hz) and its harmonics (2.4, 3.6, 4.8 Hz) for the different conditions (Words in red, Pseudowords in yellow, Nonwords in blue, Pseudofonts in green) in the left and right occipito-temporal regions of interest, marked in the corresponding scalp topographies. Boxes depict the 95% t-interval around the mean and dots represent single participants. The dashed line illustrates the level of noise.

3.2.2 Cluster Permutation Analysis

As illustrated in Figure 3, all four conditions revealed a strong and reliable response at the oddball stimulation frequency (1.2 Hz) and its higher harmonics (2.4, 3.6 & 4.8 Hz) reflecting sensitivity to the token frequency manipulation. In the Words condition, this emerged in four electrode

clusters located (i) in a posterior area that comprised occipito-temporo-parietal sites ($t(28) = 174.27$, $p = 0.0002$, $d = 0.58$, [95% CI: 0.18 - 0.97]); (ii) in central medial sites ($t(28) = 77.60$, $p = 0.007$, $d = 0.48$ [95% CI: 0.09 - 0.86]); (iii) over mid-frontal electrodes ($t(28) = 29.43$, $p = 0.408$, $d = 0.55$ [95% CI: 0.15 - 0.93]); and finally, (iv) in a small lateralized left-central region ($t(28) = 26.14$, $p = 0.0488$, $d = 0.49$ [95% CI: 0.10 - 0.87]). In the Pseudowords condition, the discrimination response emerged in one posterior cluster localized across occipito-temporo-parietal sites ($t(28) = 119.40$, $p = 0.0006$, $d = 0.50$ [95% CI: 0.11 - 0.89]). In the Nonwords condition, a significant response was elicited in two occipito-temporo-parietal clusters, one on the right ($t(28) = 58.42$, $p = 0.0128$, $d = 0.60$ [95% CI: 0.20 - 1.00]), and one on the left hemisphere ($t(28) = 37.95$, $p = 0.0314$, $d = 0.50$ [95% CI: 0.11 - 0.89]). Finally, Pseudofonts yielded a similar scalp topography as the Nonwords condition, again with one significant occipito-temporo-parietal cluster on the right ($t(28) = 87.30$, $p = 0.0008$, $d = 0.51$, [95% CI: 0.11 - 0.89]) and one on the left hemisphere ($t(28) = 26.07$, $p = 0.0434$, $d = 0.48$ [95% CI: 0.09 - 0.87]).

There were no candidate clusters to indicate significant differences in the distribution of the oddball response between conditions. This lack of statistical evidence was further corroborated by JZS Bayes Factor analyses, which provided evidence against cross-condition differences in the scalp topography of the oddball response (Electrodes showing evidence in favor of the null ($BF_{01} > 3$): Words vs. Pseudowords = 66, Words vs Nonwords = 73, Words vs Pseudofonts = 61; Pseudowords vs. Nonwords = 68, Pseudowords vs. Pseudofonts = 74; Nonwords vs. Pseudofonts = 84. Electrodes showing evidence in favor of the alternative ($BF_{10} > 3$): Words vs. Pseudowords = 0, Words vs Nonwords = 0, Words vs Pseudofonts = 0; Pseudowords vs. Nonwords = 1, Pseudowords vs. Pseudofonts = 1; Nonwords vs. Pseudofonts = 1).

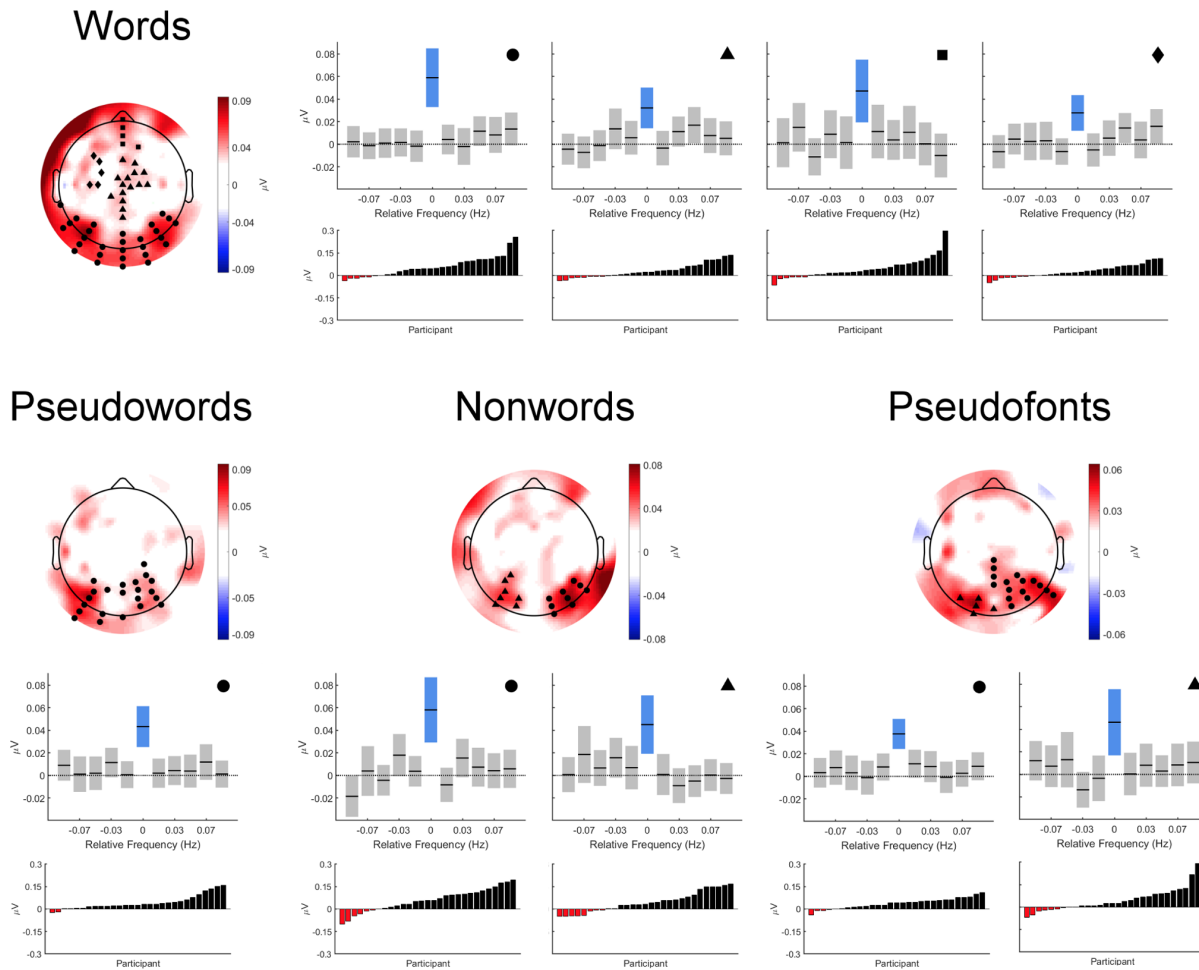


Figure 3. Grand-averaged token frequency response for the different conditions resulting from the cluster permutation test. In the scalp topographies different symbols depict the significant clusters. The plots represent the corresponding data with the oddball response centered at 0. Boxes depict the 95% t-interval around the mean and the dotted line illustrates the level of noise. For illustration purposes, the analogous response in the 10 neighboring frequency bins is displayed. The distribution of individual oddball responses for each participant in each cluster is also reported.

4. Discussion

The present study examined whether neural discrimination can be generated implicitly by the statistical structure of a rapidly changing visual stream. In an FPVS-oddball design, participants were exposed to rapid streams of visual stimuli (6Hz), embedded with oddballs that appeared periodically

every fifth item (1.2 Hz). Crucially, oddballs and base stimuli belonged to the same category and differed only in terms of the frequency with which their individual tokens occurred in the stream (i.e., oddball tokens appeared less often than base tokens). Results revealed a significant neural signal at the oddball stimulation rate and its harmonics, reflecting a selective response to oddballs relative to base stimuli. Such a response is of similar nature to the one observed in perceptual categorization studies, indexing the brain's ability to distinguish between two different categories of stimuli (e.g., words vs. nonwords, Lochy et al., 2015; faces vs. objects, Retter & Rossion, 2016). Importantly, however, in the absence of any pre-existing distinction, or other systematic differences (e.g., order of token presentation), between oddballs and base stimuli, the presence of an oddball response in the current study signifies the discrimination between two groups of items formed purely on the basis of their token frequency in the input stream: high versus low frequency tokens. Additionally, results showed that such a discrimination response was elicited across a wide span of stimuli, ranging from strings of unfamiliar, non-alphabetic characters to fully fledged, frequent words, indicating a frequency-based grouping that occurred independently of stimulus familiarity.

The observed frequency-of-occurrence effect emerged automatically, while participants engaged in an orthogonal task that did not require explicit processing of the experimental stimuli. Indeed, the ability of the human brain to implicitly learn from the statistical properties of an input stream is widely attested across a variety of research domains (e.g., Christiansen, 2019; Frost et al., 2019; see also Santolin & Saffran, 2018, for a review across species). Implicit statistical learning is attributed to a fundamental learning mechanism that enables us to discover patterns of regularity embedded in our sensory environment and appears to be involved in several key cognitive functions including category learning. A well-known illustration of this was provided by Maye et al. (2002), who showed that the frequency distribution of category exemplars to which infants are exposed influences the formation of phonemic category boundaries. Specifically, when infants were exposed to a bimodal

frequency distribution, whereby prototypical phonemes occurred frequently, and intermediate category phonemes (i.e., falling between phonemic categories) were infrequent, they were more likely to distinguish between prototypes of two phonemic categories. Conversely, when they were exposed to a unimodal frequency distribution, whereby intermediate category phonemes occurred most frequently, infants were less likely to make such distinction (see also, Maye et al., 2008; Rosenthal et al., 2001). Consistent with these findings, the present study provides evidence for participants' sensitivity to the distributional properties of the input. Remarkably, however, we show that even a simple frequency-of-occurrence difference appears to be sufficient to group separately stimuli that are otherwise indistinguishable. Furthermore, we demonstrate that this process operates dynamically on novel and familiar stimuli alike (i.e., overriding any previous representational knowledge). Direct support for this phenomenon is provided by a recent study conducted in the context of artificial grammar learning. In a series of experiments, Marino and colleagues (2020) showed that infants relied on the frequency which words occurred in the artificial grammar to implicitly categorize stimuli as functors and content words, as in real languages functor words appeared more frequently than content words. We suggest that these observations denote the deployment of a fundamental mechanism that is intimately tuned to frequency patterns and underpins abstract category bootstrapping. Using frequency as a potential cue to bootstrap categories can be easily conceptualized in the domain of language learning, whereby frequency-related effects are critical for the emergence of linguistic categories (for a theoretical discussion, see Ellis, 2002). Learning idioms, syntactic patterns, but also plausible word forms (i.e., comprising legal ortho-phonotactic patterns, prototypical bigrams or meaningful units) is an ability that hinges on how frequently a listener, or a reader, experiences instances of the existing categories in a linguistic system. Importantly, the discovery of such linguistic categories unfolds automatically and effortlessly, despite the lack of explicit instructions and of an overt intention to learn.

Evidence for implicit statistical learning in an FPVS-oddball paradigm constitutes a significant contribution to a field of research that, despite being in the limelight of cognitive science, has been confined to a small range of methodologies (for critical reviews, see Frost et al., 2019; Siegelman et al., 2018). In a typical SL experiment, learning is tested offline during a separate test-phase, which follows participants' passive exposure to an input stream. Furthermore, newly acquired knowledge is usually measured through participants' performance on a behavioral task that requires them to deliberate over learned material in order to make explicit decisions about stimuli that either follow or violate the regularities present in the input stream. However, these measures, in addition to learning, are likely to reflect cognitive operations that relate to participants' reflective and decision-making abilities (see, e.g., Christiansen, 2019). By contrast, with FVPS, learning can be derived directly from the exposure to the stream of information. Additionally, in the absence of a behavioral task that requires participants to engage the experimental stimuli, any neural signal that is elicited by the statistical structure of the input is not contaminated by other task-specific cognitive demands. Most notably, however, this new methodological approach opens up a new way to address questions that can lead to a further specification of the mechanisms that underpin statistical learning. In particular, the present findings provide novel evidence that statistical learning emerges under high temporal constraints and can thus operate on a timescale that has so far remained virtually unexplored: the presentation of a given stimulus lasted less than 166 ms and its processing was masked by both a preceding and a following stimulus. Can this type of learning unfold on an even faster timescale? Furthermore, the frequency difference that elicited neural grouping in the present study was 9 repetitions of each oddball token as opposed to 36 repetitions of each base token (i.e., 1/4 ratio). What might be the minimum relative difference required to give rise to the kind of discrimination response that was observed? Finally, beyond frequency of occurrence whether more elaborate statistics like the transitional probability of events can be learned implicitly under these stimulation conditions remains to be established.

In the same light, the present findings contribute to the statistical learning literature by stressing the importance of non-associative statistical cues —the distribution of token frequency, in this specific case— to implicit learning. Following on the path set by the earliest, seminal work in the field (e.g., Saffran et al., 1996; Reber, 1967), most statistical learning studies have focused their investigations on conditional statistics. Indeed, the substantial uniformity that characterizes this research field has been especially highlighted in a recent critical review by Frost et al., (2019), who discuss its impact on the scope of the empirical findings and ultimately, on advancing our understanding of the underlying statistical learning mechanisms. While the saliency of conditional statistics is indisputable (Avarguès-Weber et al., 2020), these are not the only type of statistics that learners attend (Thiessen et al., 2013). In this context, we consider the present set of data as a way to highlight the diversity of the probabilistic information that characterizes our perceptual world, and how powerful distributional cues —somewhat neglected in previous research on statistical learning— can be in driving our learning.

An additional aspect of our findings worth mentioning is the implications they carry for FVPS research. The susceptibility of the approach to the statistical structure of the stimulus sequence challenges previous evidence for category-selective neural discrimination to determine if, and to what extent, the evoked responses have been confounded by the relative token frequency of base and oddball stimuli or the presence of other embedded regularities. Concurrently, our findings call future FPVS work to account for implicit statistical learning phenomena in the design of the stimulation stream in order to avoid such contamination in the discrimination responses.

Finally, considering the potential neural mechanisms that underlie the emergence of the discrimination response in the present study, we suggest that this can be accounted for by a bottom-up process of context-dependent neural adaptation. The observed frequency-of-occurrence effect could index a difference in across-item repetition suppression (i.e., delayed repetition; Henson et al., 2004),

with the frequently repeated base tokens undergoing greater reduction in stimulus-evoked neuronal activity compared to oddball tokens, which were repeated less frequently (see also Radtke et al., 2020). Alternatively, the differential response to oddball stimuli could reflect an effect of expectation (or surprise), similar in kind to that observed in the MMN response (e.g., Kimura, et al., 2011; Stefanics et al., 2014) as interpreted within the framework of predictive coding models (e.g., Friston, 2005; Garrido et al., 2009). According to this, our brain generates expectations about incoming sensory events on the basis of our previous experiences. Encountering an unexpected, rare stimulus would thus result in a larger prediction error relative to a frequent and expected one. Within this framework, a frequency-based oddball response can be conceptualized as a difference in prediction error between stimuli with a high probability of occurrence (base tokens) versus stimuli with a low probability of occurrence (oddball tokens). Importantly, the generation of stimulus expectations in the current oddball design would arise from the distributional properties of the input via the integration of information across several stimuli (for further evidence of the effect of distributional statistics on MMN, see e.g., Koelsch et al., 2016).

Interestingly, using a more conventional oddball design Amado & Kovács (2016) demonstrated that the relative contribution of repetition suppression and expectation effects to the visual MMN is modulated by stimulus category. Specifically, they showed that in the case of faces and chairs, the visual MMN was largely due to repetition suppression, whereas in the case of single real and false (i.e., similar to our pseudofonts) letters, the vMMN was mainly explained by surprised-related differences. Separating the relative effects of these neural mechanisms on the FPVS-oddball response was beyond the scope of our study (but see, Feuerriegel et al., 2018). Nevertheless, we note that our results indicate that the observed frequency-based oddball response emerged equally for different stimulus categories, ranging from entirely novel (e.g., strings of pseudofonts) to very familiar (e.g., words) stimuli. This suggests that novel distributional information can be rapidly acquired in the context of an oddball

experiment, even if it departs from the distributions learned over a lifetime, attesting to the versatility of the brain when it comes to learning statistical information.

In conclusion, the present study capitalized on FPVS and EEG to provide evidence for neural discrimination based purely on the distribution of token frequency within a rapidly changing stream of visual stimuli. This discrimination response emerged implicitly and independently of stimulus familiarity, thus reflecting the operation of a fundamental mechanism that is prone to capture the statistical structure embedded in the environment. These findings showcase the potential of FVPS for providing a neural measure of implicit statistical learning and open up a new promising avenue for this line of research.

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6. Open Practices Statement

Data, materials and analysis scripts for the present study are available on the Open Science Framework at <https://osf.io/tcrq8/>. No part of the study procedures or analysis was pre-registered prior to the research being conducted.

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