Event probabilities have a different impact on early and late electroencephalographic measures regarded as metrics of prediction

Blake W. Saurels
School of Psychology, The University of Queensland, Australia

Alan Johnston
School of Psychology, The University of Nottingham, United Kingdom

Kielan Yarrow
Department of Psychology, City, University of London, United Kingdom

Derek H. Arnold
School of Psychology, The University of Queensland, Australia

The oddball protocol has been used to study the neural and perceptual consequences of implicit predictions in the human brain. The protocol involves presenting a sequence of identical repeated events, that are eventually broken by a novel 'oddball' presentation. Oddball presentations have been linked to increased neural responding, and to an exaggeration of perceived duration relative to repeated events. Since the number of repeated events in such protocols is circumscribed, as more repeats are encountered the conditional probability of a further repeat decreases, whereas the conditional probability of an oddball increases. These facts have not been appreciated in many analyses of oddballs; repeats and oddballs have rather been treated as binary event categories. Here, we show that the human brain is sensitive to conditional event probabilities in an active, visual oddball paradigm. P300 responses (a relatively late component of visually evoked potentials measured with electroencephalography) tended to be greater for less likely oddballs and repeats. By contrast, P1 responses (an earlier component) increased for repeats as a goal-relevant target presentation neared, but this effect occurred even when repeat probabilities were held constant, and oddball P1 responses were invariant. We also found that later, more likely oddballs seemed to last longer, and this effect was largely independent of the number of preceding repeats. These findings speak against a repetition suppression account of the temporal oddball effect. Overall, our data highlight an impact of event probability on later, rather than earlier, electroencephalographic measures previously related to predictive processes – and the importance of considering conditional probabilities in sequential presentation paradigms.

Corresponding Author: Blake W. Saurels (blakewsaurels@gmail.com)

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INTRODUCTION

The oddball paradigm is perhaps the most popular method used to study the neural correlates of implicit predictions in the human brain (e.g., Garrido et al., 2009; Nordt et al., 2016; Stefanics et al., 2015; Tang et al., 2023). The paradigm involves presenting a sequence of identical repeated events (‘repeats’) that are broken by a novel ‘oddball’. When used in conjunction with electroencephalography (EEG), there are characteristic differences between patterns of electrical potentials evoked by oddballs and repeats that can be elicited by either visual (Polich, 2007) or auditory (Näätänen et al., 2007) stimulation.

One characteristic difference is that the brain seems to be less responsive to repeated sensory inputs (Desimone, 1996; Wiggs & Martin, 1998) – a phenomenon termed repetition suppression. This has also been observed using fMRI and single cell recordings (Buckner et al., 1998; Grill-Spector et al., 1999), and it can be detected using a sequence of just 2 identical presentations (Summerfield et al., 2011). EEG results relating to repetition suppression point to a reduction of occipital potentials as early as ~100 ms post visual stimulation (Tang et al, 2018). This is consistent with a reduced P1, the first positive potential evoked by visual stimulation, which is typically recorded by occipital sensors.

Repetition suppression has also been observed in relation to later potentials recorded by parietal sensors (~300ms post visual stimulation; Summerfield et al., 2011). The reduction of these potentials can be greater when the repeated events are more probable (Summerfield et al, 2008; Summerfield et al., 2011). This suggests that top-down expectations might play a role in this suppression, rather than the effect being a simple consequence of neural fatigue. This possibility is in line with contemporary theories, which posit that the human brain is disproportionately responsive to unexpected events, as these necessitate an updating of an internal model of the world (Bubic et al., 2010; Downing, 2007; Friston, 2005; Rao & Ballard, 1999; Yon, et al., 2023).

In relation to the modulation of later potentials, it is important to distinguish between active and passive oddball paradigms (Stefanics et al., 2015). In passive oddball paradigms, presentations are not attended (Garrido et al., 2009; Näätänen et al, 2001). In auditory tasks of this kind, oddballs elicit a mismatch negativity (MMN) – a decrease in evoked potentials recorded by central-frontal sensors from ~150-250 ms post auditory stimulation relative to repeats (Näätänen et al., 2007). In visual tasks, this potential is referred to as the visual MMN (vMMN), which is more variable, both in terms of its topography and timing (Astikainen et al., 2008; Male et al., 2020). There is even some evidence that a vMMN might not exist when eye movements and attention are adequately controlled (Male et al., 2020). The goal of passive oddball paradigms is to examine how the brain responds to unexpected events, while controlling for differences in endogenous attention. When observed, MMN is often taken as positive evidence for prediction-centred models of brain function, under the assumption that further repeats have come to be implicitly predicted by the brain after a sequence of repeated events, whereas oddballs are unexpected (Friston, 2005; Friston & Stephan, 2007; Garrido et al., 2009; Winkler, 2007).

In active oddball paradigms, presentations are attended, with participants typically making a judgement about the oddballs (Ernst et al., 2017; Saurels et al., 2022). Oddballs in these tasks tend to evoke a greater P300 – an increase in evoked potentials recorded by central-parietal sensors (and in some cases from central-frontal sensors) between ~300-600 ms post sensory stimulation (Duncan et al., 2009). This potential is thought to be endogenously driven (Levi-Aharoni et al., 2020), and it has been associated with attentional processing of target stimuli (Polich, 2007). The P300 has also been associated with the efficiency of encoding and memory (Paller et al., 1987), and with non-probabilistic expectations (Valakos et al., 2020). There is also evidence that the P300 is attuned to the probability of events (Donchin, 1981; Mars et al., 2008). Squires et al. (1976), for instance, used an active auditory oddball task where they found that P300 magnitudes were greater when oddballs were less likely.

Active oddball paradigms allow researchers to test for differences between the perceptual experience of repeats and oddballs, which can be correlated with measures of neural activity. One example is that oddballs seem to have an exaggerated duration relative to repeats (the temporal oddball effect; Birngruber et al., 2018; Saurels et al., 2019; Saurels et al., 2022; Tse et al., 2004). It has been suggested that this effect is tied to repetition suppression (Pariyadath & Eagleman, 2007, 2012). Pariyadath and Eagleman (2012) examined this in a behavioural experiment, wherein oddballs were presented after a variable number of 'repeat' events (from 1 to 5). They found a positive linear relationship between the number of repeats preceding an oddball and the subjective dilation of oddball duration – the more repeats, the greater the relative exaggeration of oddball duration. This would seem to be consistent with mediation via repetition suppression, under the assumptions that perceived durations scale with the magnitude of neural responses, and that these are linearly reduced for increasing numbers of repetition (Pariyadath & Eagleman, 2007, 2012). So, oddball durations would not be exaggerated per se, rather the perceived duration of repeated events would be linearly reduced with increasing numbers of repetition. However, there is a viable alternative interpretation of these data – perhaps people learn that not all oddballs are equally improbable, and not all repeats are equally probable, and so they might have tried to anticipate oddballs.

In the behavioural task used by Pariyadath and Eagleman (2012), participants knew that oddballs were key to the task, as they had to judge the duration of these events. They might therefore have tried to anticipate these presentations. Given that an oddball would eventually be presented as participants saw more repeats, they might have appreciated that the probability of seeing an oddball eventually starts to increase. Formally, we can say that while the distribution of oddballs across sequence positions was uniform, the hazard function was not. Participants could therefore (consciously or unconsciously) have been increasingly anticipating the need to deploy attention, to accurately gauge the duration of an oddball, as more repeat events were encountered. Increased attention to later oddballs could explain the increase in their apparent duration relative to repeats (Tse et al., 2004). Under this explanation, the relationship between apparent oddball duration and repeat numbers should be moderated by the range of repeats used in trial sequences.

This illustrates the importance of considering the conditional probabilities of repeat and oddball events within sequential oddball paradigms. When repeat presentations are eventually interrupted by an oddball, people should eventually come to expect an oddball presentation. The point at which the probability of an oddball becomes greater than 0, and at which the probability of a repeat becomes less than 1, will depend on the minimum number of repeat events it is possible to see before an oddball. The way the probability of an oddball increases thereafter will depend on the maximum number of repeat events (and their distribution across positions).

Event likelihoods have been explicitly manipulated in paradigms that use sequential pairs of presentations (e.g., Saurels et al., 2022; Tang et al., 2018, also see Feuerriegel et al., 2021). However, the conditional probability of events is often overlooked in sequential oddball paradigms involving longer trains of events. In the passive oddball paradigms used to detect MMN, for example, oddball (‘deviant’) events are characterised as being inconsistent with predictions even when the conditional probability of an oddball, given the elapsed number of repeats, is greater than 50% (for MMN review, see Garrido et al., 2009). This treatment of data risks underestimating the true impact of the probability of encountering a given type of event (oddball or repeat).

There has been some work in the auditory domain that highlights these issues. Using a passive oddball task, Stadler et al. (2006) found that P300 activations were inversely related to event probability, such that repeated tones leading up to an inevitable oddball evoked increasingly large P300s. Schizophrenic patients, however, did not show this effect (Ford et al., 2010), in line with the theory that this population does not respond to event probabilities in the same way as neurotypical people (Jeon & Polich, 2003; Sterzer et al., 2018). In active oddball tasks, the influence of conditional (repeat and oddball) probabilities might be greater, as participants are tasked with actively monitoring inputs in these paradigms. This possibility has not been tested.

Research Questions and Task Overview

As far as we are aware, the conditional probability of encountering different event types (repeats and oddballs) has never been systematically investigated in an active visual oddball paradigm incorporating EEG. So, our primary aim was to determine if neural responses to repeats and oddballs would reflect the conditional probability of these events. By including a behavioural measure of time perception in our experiment, we are also able to assess the repetition suppression account of the temporal oddball effect, as this too is concerned with neural responses to events leading up to an oddball.

Participants completed 3 sessions of an active visual oddball task (see Figure 1). The number of repeats preceding oddballs varied across sessions – either 4-6 (*Session A* – colour coded as *magenta* throughout), 2-4 (*Session B – cyan*), or always 4 (*Session C – dark blue*). Participants were instructed to watch all events in each sequence and to report if the oddball, which varied in duration, seemed longer or shorter than preceding repeats. Oddballs were odd in that they were a different colour than preceding repeats. We recorded scalp electrical potentials with EEG.

Hypotheses

If the magnitude of visually evoked potentials in an active oddball task reflects the conditional probability of events, such that more probable events evoke smaller potentials, then we should be able to detect this by looking at responses to events at the tail end of sequences in Sessions A and B. Here, repeats become less likely, and so they should evoke progressively greater responses – whereas oddballs become more likely, and so they should evoke progressively smaller responses. In Session C however, participants know when the oddball will occur, so they can know with certainty when they will see a repeat or an oddball. However, recall that in our active task, participants must also consider the duration of repeats, and might focus on those repeats closest to the target where the fidelity of memory is best. The results of this session allow us to distinguish between the influences of conditional event probabilities and strategic changes leading up to a task-relevant event, which might reflect the engagement of top-down attentional processes (Baumgartner et al., 2018; Johnston & Venables, 1982; Luck et al., 1990). If anticipatory top-down attention is responsible for the changes in neural responding, in Session C there should be a tendency for greater evoked potentials to later repeats, as the task-relevant presentation nears, even though event probabilities are held constant.

A repetition suppression account of neural activity in active oddball paradigms, on the other hand, predicts a decrease in the magnitudes of visually evoked potentials with increasing repeat numbers. We should be able to detect this by looking at visual events at the tail ends of sequences, but also by comparing Session A, which has more repeats, to Sessions B and C.

The repetition suppression account of the temporal oddball effect also predicts a positive relationship between the number of repeats and the apparent duration of oddballs relative to repeats. Alternatively, this pattern might have emerged simply by conflating repetition number with oddball probability. If this is the case, we should observe the same pattern of oddball duration distortion for Sessions A and B, which have the same distribution of oddball probability at the ends of sequences, but different repeat numbers.

METHODS

Participants

Twenty volunteer participants (1 male; consistent with previous related investigations, such as Saurels et al., 2023; Stadler et al., 2006) were recruited for testing via a research participation scheme at the University of Queensland (in exchange for course credit or 40 AUD). All reported having normal or corrected-to-normal visual acuity (i.e., they were asked to wear their glasses or contact lenses if they would typically use these to read). Ages ranged from 18 to 27 (*M* ~ 20, *SD* ~ 2.3). Participants were informed that they could withdraw from the study at any time without penalty. The experiment was approved by the University of Queensland ethics committee, which adheres to the Australian Code for the Responsible Conduct of Research.

Stimuli and Apparatus

Stimuli were black (CIE: 0.272, 0.376, 5.016) or white (CIE: 0.285, 0.322, 138.05) circles presented against a grey background (CIE: 0.278, 0.333, 37.772). Circles had a diameter subtending ~15 degrees of visual angle (dva). Stimuli were presented on a calibrated 24” ASUS VG248QE 3D monitor, driven by a Psychtoolbox-3 (Kleiner et al., 2007) and custom Matlab R2015b software (The MathWorks, Natick, MA). The monitor had a resolution of 1920 x 1080 pixels and a refresh rate of 60Hz. Participants viewed stimuli from 57cm, from directly in front of the monitor with their chin placed on a chin rest. A Biosemi International ActiveTwo system was used to record EEG data (sampling rate: 1024 Hz), using a 10-20 distribution system for 64 electrodes.

Design and Procedure

The experiment was split into 3 sessions that differed in the number of repeats that could precede an oddball test presentation – either 4-6 (Session A), 2-4 (Session B), or always 4 repeats (Session C, see Figure 1). Participants were told about the possible number of repeats at the start of each session. The three types of session were completed in a counterbalanced order across participants.[1]

Oddballs were a different colour (black or white) relative to repeats, with the colours assigned to repeats and oddballs counterbalanced within each session. All repeat events persisted for 500ms. Oddball durations varied between 300 and 700ms, in 50ms intervals (9 possible test durations, equiprobable and presented in a random order, according to the method of constant stimuli). Presentations were separated by a 300ms inter-stimulus interval (ISI). Participants were encouraged to attend to all events, so that they could develop a good impression of the duration of repeats, which they had to compare to the perceived duration of the oddball presentation.

In each session participants saw each test duration 8 times for each number of repeats that were possible in the session. So, there were 216 trials (9 possible test durations x 8 presentations x 3 possible test positions) in Sessions A and B and 72 trials in Session C (9 possible test durations x 8 presentations) – for a total of 504 individual trials in the experiment.

At the end of each trial, participants were asked if they thought the oddball event had seemed to last longer (right click) or shorter (left click) than repeats. They were told that there would always be a difference in physical duration between the oddball test duration and repeats, but that on some trials it would be hard to detect. They were also told that there would not necessarily be an equal number of trials in which the oddball would be shorter or longer than standards.

Data Analysis

We calculated statistics using JASP (JASP Team, 2023).

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[1] Session orders A-B-C and B-A-C were completed once more than the other session orders.

Duration Judgement Function Fitting

For each test duration within each session, we calculated the proportion of trials on which each participant reported that the oddball had seemed to last longer than repeats. In Sessions A and B, this was done separately depending on the number of repeats preceding the oddball. We then fit cumulative Gaussian functions using psignifit (lambda & gamma free to vary between 0-0.5; Schütt et al., 2016) to individual datasets, and from these calculated the point of subjective equality (PSE) between repeat and oddball durations (i.e., the oddball duration at which participants were equally likely to report that oddballs had seemed longer or shorter than repeats – the 50% point of function fits). We then calculated a 'Duration Distortion Factor' (DDF) by taking the ratio of the physical repeat duration (500ms) relative to PSE estimates (as per Pariyadath & Eagleman, 2007 & 2012). For example, a PSE of 450ms would correspond to a DDF of 500:450 or of 1.11, indicating a duration distortion of ~11% for oddballs.

EEG Data Cleaning

EEG data were high (1 Hz) and low (40 Hz) pass filtered. Data were then subjected to an independent components analysis, implemented by the FieldTrip toolbox for Matlab (The Math Works and Inc., 2015; Oostenveld et al., 2011), to remove blink artefacts (positive patterns of activity at frontal electrodes). Electrode activity was then average referenced, to correct for baseline skin conductance levels. Data were then sorted into trials, and events within trials, via custom MATLAB code.

For ERP analyses, the response period for each event (700 ms) within each trial was baseline-corrected relative to the average of activity recorded by each sensor during a 100ms period prior to the onset of events. We excluded peaks that were ± 3 SDs from the mean for a given event number and session.

Cluster-based Permutation Analyses

As part of our analyses, we performed a cluster-based permutation analysis using the FieldTrip toolbox (Oostenveld et al., 2011) for MATLAB (settings: Monte Carlo method; test statistic set as the maximum of the cluster-level statistics; cluster alpha: .05; test alpha: .01; randomisations: 1000; minimum number of neighbourhood channels required sample inclusion in clustering algorithm: 3).

Transparency and Openness Statement

All data and code can be found at UQ eSpace.

RESULTS

Neural Response to Improbable vs Probable Visual Events

While there are several typical neural markers seen in EEG recordings associated with errors of visual prediction (Garrido et al., 2009; Nordt et al., 2016; Polich, 2007), the spatial location on the scalp and timing of these markers can vary with the visual input used and the timing of presentations. So, in an effort start from an unbiased position, we first compared neural responses to improbable events (those that had a 50% or less chance of occurring) to neural responses to probable events (those that had a greater than 50% chance of occurring) using a cluster-based permutation analysis. Two positive spatiotemporal differences between neural responses to improbable relative to probable events were identified. The first was at ~73-133 ms post visual event onset at a cluster of occipital electrodes (see Figure 2A-B). This can be regarded as evidence for an occipital P1 difference (Di Russo et al., 2002) contingent on the probability of events. The second positive difference was at ~330-445 ms post visual event onset at a cluster of central-frontal electrodes (Figure 2C-D). This can be regarded as evidence for a central-frontal P300 difference (Duncan et al., 2009) contingent on the probability of events. This analysis also identified the dipole of the P1 difference: a negative central-frontal difference at the same time-point as the P1.

Neural Responses to Increasing Improbable Repeats

Using the information provided by the cluster test as to where and when neural markers associated with visual event probability could be found in our experiment, we were then able to narrow our scope of analysis to events at the end of oddball sequences – where repeat events become less likely and oddballs become more likely. To do this, we needed to quantify the P1 and P300 response for each visual event in oddball sequences. One common method is to average activity within a specific time window for relevant electrodes. However, a risk associated with this method is that individual differences can impact the timing and duration of ERP components, and data from sections of the ERP directly before or after the component of interest can add noise to the component estimate.

Instead, we took peak amplitudes as the metric for P1 and P300 strength. For each component, we averaged the activity across an equal number of electrodes (the 6 strongest contributors to each positive cluster; for occipital P1s: Oz, Iz O2, O1, PO8, & PO7; and for central-frontal P300s: FCz, FC1, FC2, C1, Cz, C2), and then across trials. We then found the peak amplitude for each event number, separately for repeats and oddballs, within the time-window for each component (to safely account for individual differences in latencies, we searched a time-window slightly wider than the range suggested by the cluster analysis: 50-200 ms for occipital P1s, and 300-500 ms for central-frontal P300s; visual inspection of the data suggested that we found the relevant component peak in all cases).

P1 Peaks for Repeats

Starting with repeats, Figure 3A depicts P1 peak amplitudes for the last 3 possible positions in a sequence where a repeat could have occurred (see table under the x-axis for actual sequences positions and event probabilities). Note that for Sessions A and B, the probability of seeing a repeat event decreased as participants saw more events, whereas it remained a certainty that they would see a repeat in Session C. We subjected these data to a 2-way within-subjects ANOVA, with repeat position from end of sequence (i.e., 3rd last, 2nd last, and last possible) and session type as IVs.

We found a main effect of position from end of sequence [$F_{(2,38)} = 28.85$, $p < .001$, $\eta^2_p = .603$], such that P1 strength progressively *increased* the later the repeat occurred [3rd last < 2nd last: $t = 4.48$, $p < .001$; 2nd last < last: $t = 3.08$, $p = .004$]. There was no main effect of session type

[$F_{(2,38)} = 1.12$, $p = .336$, $\eta^2_p = .056$], and there was no interaction [$F_{(4,76)} = 0.53$, $p = .716$, $\eta^2_p = .027$]. For good measure, we checked that there was a simple main effect of position from end of sequence for Session C, which there was [$F_{(2,38)} = 15.97$, $p < .001$]. As we see this progressive increase in P1 strength also occurred in Session C, even though the probability of a repeat remained a certainty in this session, this undermines the link between P1s and visual event probability.

P300 Peaks for Repeats

Figure 3B depicts P300 peak amplitudes for the last 3 possible positions in a sequence where a repeat could have occurred. We performed the same analysis for these P300 peaks, and again found a main effect of position from end of sequence [in the same direction as P1s; $F_{(2,38)} = 19.34$, $p < .001$, $\eta^2_p = .504$; 3rd last < 2nd last: $t = 2.33$, $p = .008$; 2nd last < last: $t = 3.83$, $p < .001$] and no main effect of session type [$F_{(2,38)} = 0.25$, $p = .781$, $\eta^2_p = .013$]. However, here we found an interaction [$F_{(4,76)} = 4.85$, $p = .002$, $\eta^2_p = .203$]. Follow-up analyses revealed a simple main effect of position from end of sequence for Session A [$F_{(2,38)} = 20$, $p < .001$] and Session B [$F_{(2,38)} = 12.66$, $p < .001$], but not for Session C [$F_{(2,38)} = 1.22$, $p = .308$]. The pattern of P300 peaks therefore aligns with a link to visual event probability.

Neural Responses to Increasing Probable Oddballs

P1 Peaks for Oddballs

We then examined neural responses to oddballs in the same way, the difference being that these became more probable as people saw more events. Starting with P1s (see Figure 3C), we subjected the data from Sessions A and B to an ANOVA with the same IVs as above and found no main effect of position from end of sequence [$F_{(2,38)} = 0.61$, $p = .55$, $\eta^2_p = .031$], no main effect of session type [$F_{(1,19)} = 0.08$, $p = .787$, $\eta^2_p = .004$] and no interaction [$F_{(2,38)} = 3.09$, $p = .057$, $\eta^2_p = .14$]. As there was only one possible oddball position in Session C, this was compared to the last possible oddball position in Sessions A and B via a separate one-way ANOVA. There was no effect of session type here either [$F_{(2,38)} = 0.69$, $p = .51$, $\eta^2_p = .035$]. These results align with the P1 results for repeats in Session C, in that they undermine a relationship between P1 strength and visual event probability.

P300 Peaks for Oddballs

Lastly, we subjected the P300 data for oddballs (see Figure 3D) to the same analyses we did for P1s. A 2-way ANOVA that included data from Sessions A and B only revealed a main effect of position from end of sequence [$F_{(2,36)} = 6.77$, $p = .003$, $\eta^2_p = .273$], such that P300 strength *decreased* the later the oddball occurred. Follow-up tests revealed this difference was driven by a difference between oddballs that occurred in the earliest possible position (least likely) and both the 2nd last [3rd last < 2nd last: $t = 2.9$, $p = .006$] and last possible positions [3rd last < last: $t = 3.41$, $p = .002$]. There was no main effect of session type [$F_{(1,18)} = 0.08$, $p = .783$, $\eta^2_p = .004$], and there was no interaction [$F_{(2,36)} = 0.57$, $p = .573$, $\eta^2_p = .03$]. A separate one-way ANOVA revealed no difference between oddballs in Session C, to those in the last possible position in Sessions A and B [$F_{(2,36)} = 2.49$, $p = .097$, $\eta^2_p = .121$; this test violated the assumption of sphericity; following a Greenhouse-Geisser correction: $F_{(1.5,26.3)} = 2.49$, $p = .115$,

η^2_p = .121]. Consistent with the findings for repeats, the pattern of P300 peaks for oddballs aligns with a link to visual event probability.

Perceived Duration of Oddballs Relative to Repeats

We then wanted to see how our duration perception data accorded with the results of Pariyadath and Eagleman (2012). Figure 4 depicts duration judgement data as DDFs. These are ratios, so a DDF >1 indicates that oddballs seemed to last longer than preceding repeats (i.e., a DDF of 1.1 indicates that oddballs seemed 10% longer than repeats). We analysed these using the same structure of ANOVAs as above. A two-way ANOVA that included data from Sessions A and B revealed a main effect of position from end of sequence [$F_{(2,38)} = 68.27$, $p < .001$, $\eta^2_p = .782$], such that oddballs seemed longer relative to repeats when they occurred after more repeats [3rd last < 2nd last: $t = 8.37$, $p < .001$; 2nd last < last: $t = 2.88$, $p = .006$]. While there was no main effect of session [$F_{(1,19)} = 2.98$, $p = .1$, $\eta^2_p = .136$], there was an interaction [$F_{(2,38)} = 16.14$, $p < .001$, $\eta^2_p = .459$]. Follow-up analyses revealed a simple main effect of session was present for the earliest possible oddballs only [$F_{(2,38)} = 19.66$, $p < .001$], such that oddballs in the earliest possible position in Session A seemed longer than those in Session B. A separate one-way ANOVA revealed no difference between oddballs in Session C to those in the last possible position in Sessions A and B [$F_{(2,36)} = 0.5$, $p = .614$, $\eta^2_p = .027$]. To illustrate the dissociation from absolute repeat number, when Session C oddballs (always in the 5th position) were compared to oddballs in the 5th position of Sessions A and B [one-way ANOVA; $F_{(2,36)} = 11.98$, $p < .001$, $\eta^2_p = .4$], there was only a difference between Sessions C vs A [which had different event likelihoods; $t = 3.84$, $p < .001$], not for Sessions C vs B [which had the same event likelihood; $t = 0.7$, $p = .162$]. So, the results align with the previous finding that seeing more repeats within an oddball sequence with a circumscribed number of possible repeats makes the temporal oddball effect stronger. However, the lack of difference between sessions with more or less numbers of repeated events suggests that this is not a result of the number of repeats per se.

DISCUSSION

Initially, we found that the strength of occipital P1s (the first positive scalp potential measured for visual inputs), and central-frontal P300s (a later, positive scalp potential that has been associated with cognitive operations and event probability, see Polich, 2007) were both enhanced for improbable events, relative to probable ones, in this active oddball paradigm.

We then focussed on the tail ends of oddball sequences, where repeats became less likely and oddballs more likely. We found that P300 amplitudes tracked event probabilities here – they were greater for later repeats and earlier oddballs in Sessions A and B. There was also no difference in P300 strength between these two sessions, despite them having different numbers of repeats. In Session C, where people could know with certainty what they were about to see, P300s were unchanged across different stimulus positions for repeats, and unchanged compared to similarly certain presentations in other sessions for oddballs. In sum, P300s varied with conditional probability, but not with other factors when conditional probability was controlled.

By contrast, P1s did not track event probabilities – there was no difference in P1 strength for oddballs with different probabilities, and although P1s did increase as repeat probabilities decreased in Sessions A and B, there was an equivalent increase in P1 strength in Session C when event probabilities were held constant. This is suggestive of an influence of goal-directed / top-down attention (Baumgartner et al., 2018; Johnston & Venables, 1982; Luck et al., 1990), with P1 magnitudes increasing as participants increasingly attended to inputs as task-relevant presentations neared.

We found that oddballs that occurred later in sequences seemed longer. This might seem to be consistent with the repetition suppression account of the temporal oddball effect (i.e., later oddballs would seem relatively longer, as more repetitions have preceded them, resulting in more repetition suppression). However, neither P1 or P300 strengths decreased as people saw more repeats, and if these are regarded as a metric of neural response magnitudes, then our data are inconsistent with the predictions of the repetition suppression account of the temporal oddball effect.

Implications and Future Directions

P300s track visual event likelihood in active oddball sequences.

The P300 is known to be exaggerated for oddballs and for target events in active oddball paradigms, and it has been linked to attentive and to memory processes (Paller et al., 1987; Polich, 2007). The P300 is also greater for less frequent auditory oddballs (Squires et al., 1976). Here, we have shown that people are generally attuned to the conditional probability of visual events in an active, sequential oddball paradigm – resulting in exaggerated P300s for improbable oddballs, but also for improbable repeats.

P1 magnitudes might reflect the level of endogenous attention.

It has been shown previously that P1 responses can be modulated by top-down attention (Baumgartner et al., 2018; Johnston & Venables, 1982; Luck et al., 1990). This aligns well with our finding that P1 responses increased as target oddballs approached – people likely preferentially attended oddballs and the directly preceding repeats, as these events were critical for the relative duration decision that was demanded of them on each trial. Changes in top-down attention could also explain why later, more certain oddballs seemed longer in our task, as these events were more likely to have been fully attended. This is in contrast to P300 responses, which were linked to conditional event probabilities.

Interplay between expectations and attention.

One of the challenges for researchers looking at how expectation might impact on neural, perceptual, and behavioural responding is how to manage attention (see Summerfield & Egner, 2009; Summerfield & Egner, 2016, for reviews). One approach has been to try to partition out the effects of attention, in order to look at the isolated impact of expectation. This has been attempted by directing attention away from the sensory inputs with varying probabilities that are targeted for analysis (e.g., Garrido et al., 2013; Richter & de Lange, 2019). These studies suggest that the human brain is in some ways more responsive to unlikely events (see Garrido et al., 2009; Friston, 2005). However, it is possible that people attend to these inputs to some unmeasured degree, creating ambiguity as to the cause of any modulation in responding. Moreover, while a focus on responses to unattended inputs does serve to increase our understanding of how distracted brains respond to task-irrelevant inputs, if we wish to additionally understand how predictive processes shape neural and behavioural responses in engaged people, we also need to consider how attention and expectations might interact.

Contemporary work that has actively manipulated attention has uncovered some surprising results in relation to predictive processes and event likelihoods. For instance, consider contemporary MMN research. Increases in the MMN to unattended, unexpected auditory inputs has previously been considered a ‘signature’ of prediction error within the predictive coding framework (Garrido et al., 2009). However, when visual inputs are used instead, the (v)MMN is *dependent* on attention (Male & O’Shea, 2023; Smout et al., 2019) – when attention is directed away from the unexpected visual input, the (v)MMN disappears. An analogous set of findings can be seen in fMRI research looking at increases in BOLD responses to unexpected inputs. This increase occurs when people can attend visual events (Richter et al., 2018; for a review see de Lange et al., 2018), or when their attention is not actively directed away from the visual input that is varying in likelihood (Kok et al., 2012). When attention is directed away though, the increased BOLD response to unexpected inputs disappears (Richter & de Lange, 2019). These results highlight that it would be unwise to generalise how the brain treats unexpected sensory information from results obtained in only attended or unattended contexts.

Our study used an active oddball task – so people had to pay attention to the visual events, but probably not equally. People knew, either approximately (Sessions A & B) or precisely (Session C) when a task-relevant oddball would occur, so they may have increasingly allocated top-down attention to events as an oddball presentation neared. What is interesting about our data is that the P1, an early ERP component, increased in the lead up to oddballs, but was not tied to event probabilities (as it still increased in Session C, when the probability of all events after the 1st was fully specified, and was not greater for more surprising oddballs). It has often been claimed, based on hierarchical predictive processing accounts of brain function (Rao & Ballard, 1999), that responding at early stages of sensory processing should be modulated by event probabilities (Alink, 2010; Clark, 2013). Instead, we found that the later P300 – which is often considered as a more ‘cognitive’ and endogenously driven evoked potential (Polich, 2007) – was linked to event probabilities. P300s were greatest for improbable oddballs that occurred earlier in sequences, rather than later, guaranteed ones that people would have been able to prepare to devote their full attention to.

This link, between a relatively late response and event probabilities, is consistent with other recent EEG findings. For instance, Alilović et al. (2019) found that event probabilities modulated EEG response measures ~240 ms post event onsets, whereas attention modulated responses from as early as ~130 ms post stimulus onset. Moreover, they did not detect any impact of event probabilities at the earliest stages of visual processing – indexed as the early phase of C1 (from 50-80 ms post event onset). Similar results exist for the auditory modality. Todorovic and de Lange (2012) found, using MEG, that event probabilities did not modulate responding until an intermediate stage of auditory processing. One contemporary theory that might account for these findings is the ‘opposing processes theory’ (Press et al., 2020). According to this account, the human brain balances a tendency to highlight what is informative (based on what it expects to encounter), with the need to veridically represent the external world, by weighting initial processing and perception toward probable inputs, but then biasing later processing toward improbable inputs.

It might be tempting to consider modulations of the later P300 component as an index of prediction error signals according to the predictive coding framework. We think this is tenuous for two reasons: 1) the relationship between P300 amplitudes and prediction outcomes is reversed when predictions are made explicitly (e.g., the person predicts they will see a white or black circle ahead of time), rather than being implicitly inferred from the statistics of the sensory environment – that is, P300s are greater for explicitly *expected,* rather than unexpected, visual events (Saurels et al., 2022). This was true even when the explicitly expected and unexpected events were equiprobable. And 2) looking at electrical potentials at the scalp or BOLD activity cannot tell us how ‘error’ units/neurons and ‘representation’ units/neurons are responding differently, and understanding how these dissociable units/neurons (if they exist) change their responding to different event probabilities is necessary for identifying a prediction error and prediction update sequence (see Walsh et al., 2020 for review). So, we cannot be sure if an enhanced P300 is necessarily indicative of a prediction error signal, or if it reflects some other composite of sensory and cognitive processes.

The repetition suppression account of the temporal oddball effect does not fit the neural or behavioural data.

Our findings undermine the repetition suppression account of the temporal oddball effect in two ways. First, we did not find a progressively reduced ERP component response to repeated inputs followed by an uptick for oddballs. Note that this does not speak against repetition suppression generally, simply that in this active, sequential oddball paradigm, which mirrors those used to make claims about repetition suppression driving the temporal oddball effect, we did not observe the pattern of neural activity predicted by this theory. Second, despite there being more repeats in Session A than Session B, we did not observe a general difference in temporal oddball effect strength between these sessions. This accords with the findings of Saurels et al. (2023), which show that seeing progressively more repeats before an oddball does not impact temporal oddball effect strength when controlling for anticipatory allocation of attention.

We did find that improbable oddballs (those that appeared in the earliest position) in Session A (preceded by 4 repeats) seemed longer than equally improbable oddballs in Session B (preceded by only 2 repeats). One possibility is that repetition number might interact with visual event probability in this context, and that this might produce differences in neural and perceptual outcomes.

Statistical expectations in sequential oddball paradigms.

As illustrated in Figure 1, sequential oddball paradigms that have a prescribed range for the oddball presentation can encourage a statistically informed expectation. If people are attuned to event probabilities, they might begin to expect an oddball, and may not expect further repeats. To examine how the brain reacts to unexpected inputs, in MMN research for example, oddballs are typically considered as implicitly unexpected (Garrido et al., 2009; Stefanics et al., 2015), a dichotomous treatment of events which might underestimate the impact of conditional event probabilities. For instance, consider the interpretational differences if we had only examined a difference between repeats and oddballs, and ignored conditional probabilities and the possibility of task-relevant changes in attention.

Conclusions

From these findings we conclude that: 1) as not all oddballs are equally unexpected, and not all repeats are equally expected, we should be cautious about interpreting changes in brain activity from violations of repetition as an index of prediction error, and 2) the repetition suppression account of the temporal oddball effect does not match our behavioural or neural findings. The key takeaway is that while it may be an oversimplification to consider neural responses to *all* visual oddballs as indexing prediction error, our data shows that one previously examined neural response – the P300 – does index the *conditional probability* of visual events in these oddball tasks, in line with the general picture that the brain learns and modulates its responding to reflect the statistics of its environment.

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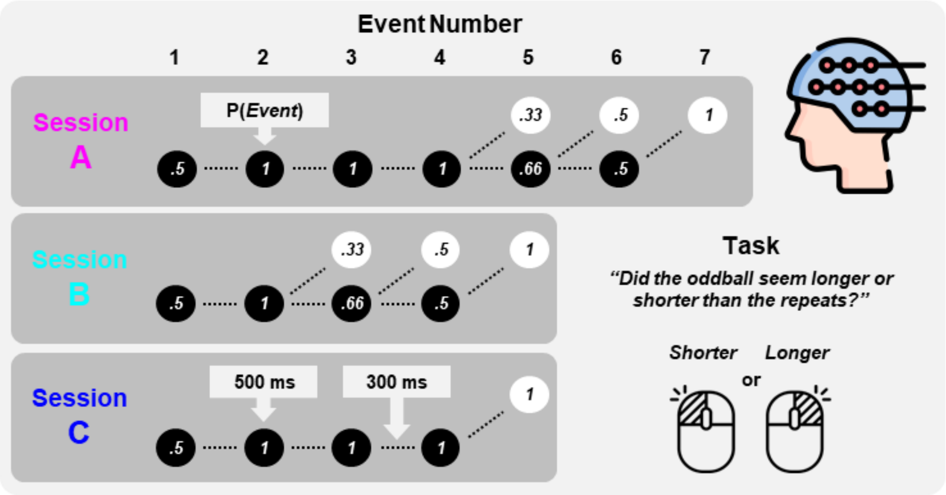

Figure 1. A depiction of the trial sequence options in each session. White circles represent oddballs, and black circles represent repeats. The numbers inside the circles denote the conditional probability of participants seeing a repeat or oddball at a given event number. Participants completed the duration judgement task at the end of each trial in all sessions.

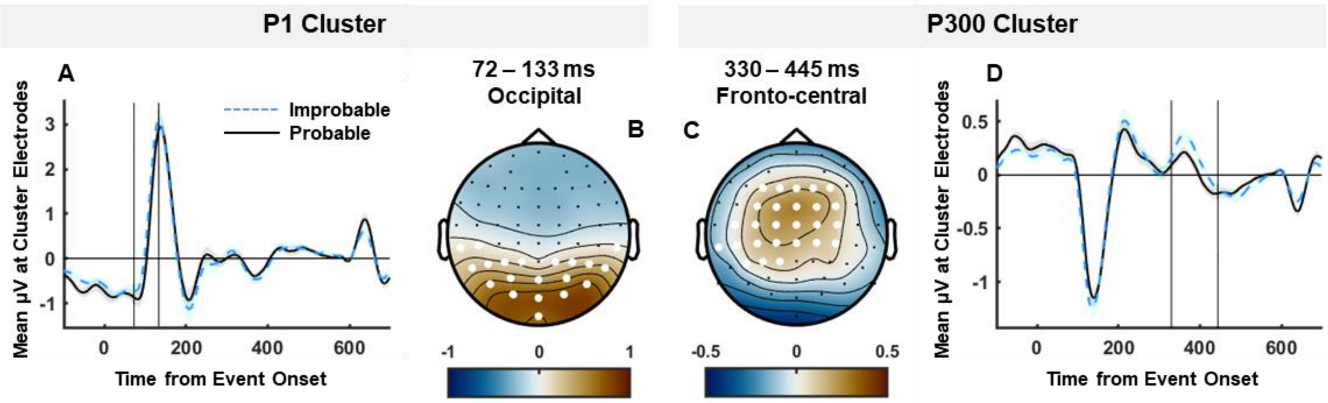

Figure 2. [A] Mean activity (µV) at P1 cluster electrodes for improbable and probable events as a function of time from event onset. Shaded areas depict SE. Vertical lines bound the cluster time-window. **[B]** Map of mean activity within the cluster time-window. White circles depict electrodes that contributed to the cluster. **[C D]** Same as A B, but for the P300 cluster.

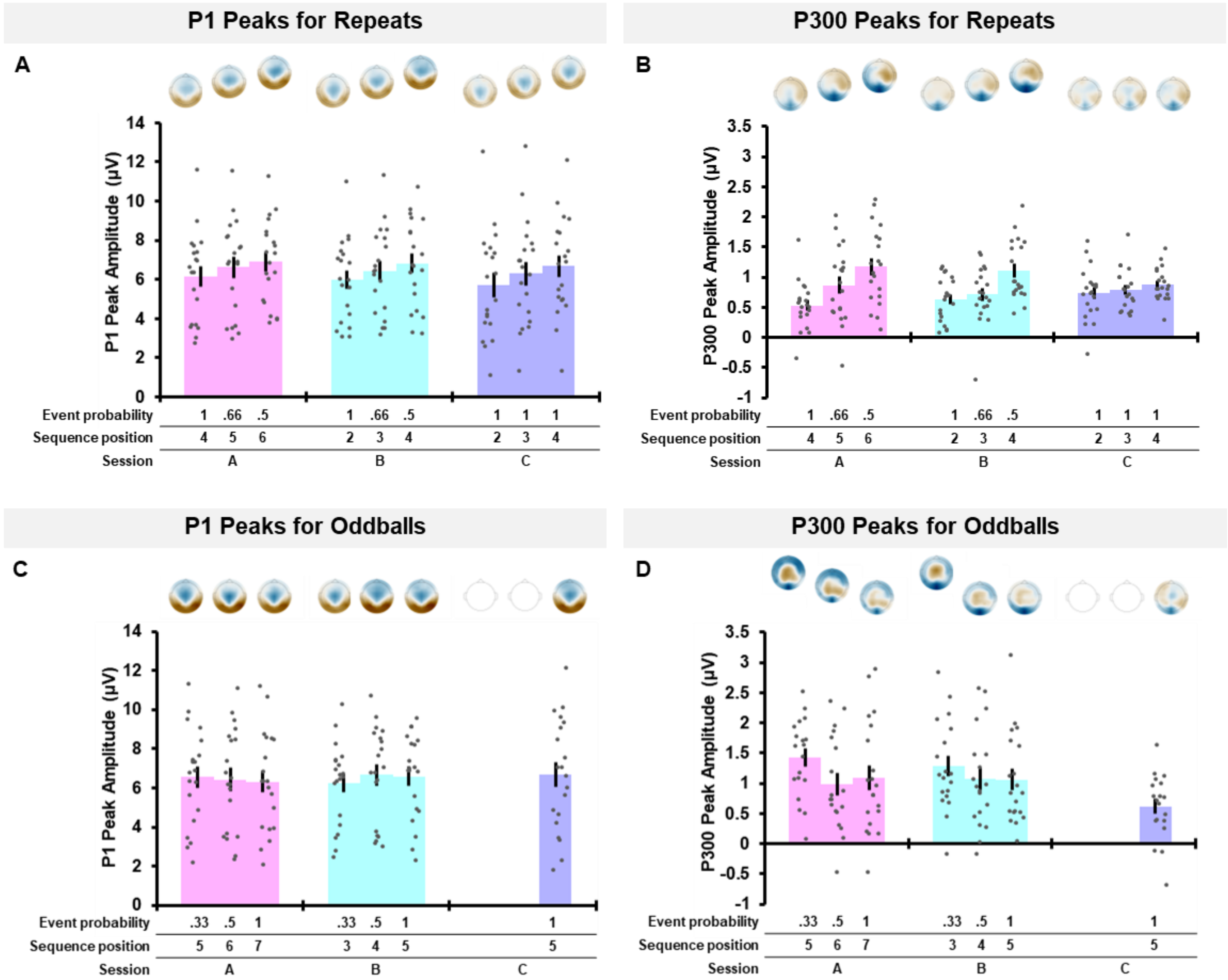

Figure 3. [A] P1 peak amplitudes (µV) for repeats at the tail ends of sequences (i.e., in the last 3 possible positions), grouped by session. Black error bars depict ±1 SE, and dots depict individual participants. Topographical maps above each bar depict the mean activity for the P1 cluster time-window, averaged across participants. The x-axis contains information about the event probability, sequence position, and session for each visual event. **[B]** P300 peaks for repeats. **[C]** P1 peaks for oddballs. **[D]** P300 peaks for oddballs. Note that oddballs can only occur at event number 5 in Session C.

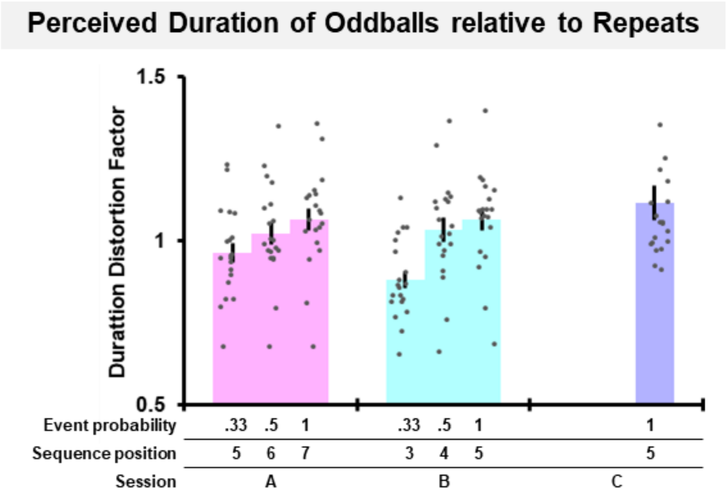

Figure 4. The duration distortion factor (a ratio of oddball perceived duration relative to repeats, where a value >1 indicates that oddballs seemed longer than the preceding repeats), for each oddball event, grouped by session. Black error bars depict ±1 SE, and dots depict individual participants. The x-axis contains information about the event probability, sequence position, and session for each visual event.