The oddball effect: Perceived duration and predictive coding

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When a unique “oddball” stimulus is embedded in a train of repeated standard stimuli, its duration can seem relatively exaggerated (V. Pariyadath & D. Eagleman, 2007; P. U. Tse, J. Intriligator, J. Rivest, & P. Cavanagh, 2004). We explored the possibility of a link between this and signal intensity reductions at low levels of visual processing. In Experiment 1, we used Troxler fading as a metric of signal intensity—the apparent fading of a stimulus with prolonged viewing (I. P. V. Troxler, 1804). Fading was exaggerated by presenting oddball and standard stimuli to different eyes. However, there was no fading difference when standard stimuli were presented persistently or intermittently. These results contrast with oddball effects, which were insensitive to eye of origin, and which were contingent on intermittent standard stimuli. In Experiment 2, we show that oddball effects can be elicited with oddballs that are less intense versions of repetitive stimuli, and in Experiment 3, we show that oddball effects can scale with the discrepancy between repeated and oddball stimuli. These observations discredit any oddball effect explanation predicated on low-level neural response magnitudes to individual stimuli. Instead, our data support the view that oddball effects are driven by predictive coding (V. Pariyadath & D. Eagleman, 2007), reflecting the discrepancy between expected and actual inputs.

Keywords: temporal vision, attention, duration perception


Introduction

Illusory distortions of duration can occur when viewing repetitive image sequences. For instance, if the same stimulus is shown intermittently for fixed intervals, the initial presentation can seem to persist for longer than subsequent presentations (Rose & Summers, 1995). Similarly, if a single presentation of an oddball stimulus (a picture of a cow for instance) is presented within a train of repeated presentations of a standard stimulus (a picture of a building for instance), then the oddball can seem to persist for longer than the repeated presentations of the standard stimulus (Eagleman & Pariyadath, 2009; Pariyadath & Eagleman, 2007, 2008; Tse, Intriligator, Rivest, & Cavanagh, 2004; see online Supplementary Movie 1). We will refer to this as the oddball effect.

Stimulus repetition might encourage predictive coding (Pariyadath & Eagleman, 2007; Srinivasan, Laughlin, & Dubs, 1982). In effect, the prediction would be that a repetitive stimulus will repeat. One proposal is that prediction results in a more efficient neural code for repeated stimuli, thereby reducing metabolic costs (Grill-Spector, Henson, & Martin, 2006). If perceived duration were in some way related to the amount of energy expended in representing a stimulus, this would result in unique oddball stimuli having a longer perceived duration than repeated stimuli, which are encoded more efficiently (Eagleman & Pariyadath, 2009; Pariyadath & Eagleman, 2007). These proposals have been linked to reductions in neural responsiveness to repeated stimuli as measured via cortical brain imaging (Henson & Rugg, 2003; Rainer & Miller, 2000). However, neural adaptation is a general property of visual processing, so it is possible that adaptation-related reductions in responsiveness might be reflected at lower, sub-cortical, levels of visual processing and that these might contribute to oddball effects.

One way to track the responsiveness of neurons at low levels of visual processing is to examine the phenomenon of Troxler fading (Eagleman, Jacobson, & Sejnowski, 2004; Troxler, 1804). This refers to the gradual fading of visual input under persistent viewing. While the effects of Troxler fading are particularly apparent in the periphery of vision, where small involuntary eye movements are less effective in changing the receptive fields used to encode input (Martinez-Conde, Macknik, Troncoso, & Dyer, 2006), fading actually occurs right across the visual field, including foveal vision (Krauskopf, 1963; Simons et al.,
2006). The major determinant of fading would seem to be neural adaptation at low levels of visual processing (Clarke & Belcher, 1962; Gonzalez et al., 2007; Martinez-Conde, Macknik, & Hubel, 2002; Martinez-Conde et al., 2006), although fading can be modulated by higher level operations (De Weerd, Smith, & Greenberg, 2006; Lou, 1999; Mennemeier et al., 1994).

In the following sequence of experiments, we investigate the possibility that the oddball effect is shaped by reductions in neural responsiveness due to adaptation at early stages of visual processing. We find no evidence for such a relationship.

**Experiment 1a: Eye or origin, flicker, and Troxler fading**

In Experiment 1a, we use an indirect measure of Troxler fading (Troxler, 1804) as a metric of adaptation at low levels of visual processing. As such processing is monocular, the effects of Troxler fading should be most apparent when a faded target is contrasted with retinally co-localized comparators that are shown to the opposite, as opposed to the same, eye.

In addition to looking at eye of origin effects, we will also look at the impact of presenting standard stimuli either persistently, or as a train of discrete intermittent events. Low-level neural adaptation should occur in both cases. Determining the extent to which this is true for the last of an intermittent train of standard stimuli may provide a useful basis for predicting oddball effects in subsequent experiments.

**Methods**

There were thirteen participants, one author and twelve volunteers who were naive as to the purpose of the experiment. All had normal or corrected-to-normal visual acuity. Stimuli were generated using a ViSaGe stimulus generator (Cambridge Research Systems) and presented on a gamma corrected 19" Sony Trinitron Multiscan G420 monitor (resolution 1280 × 1024, refresh rate 120 Hz).

Participants were seated in a darkened room and viewed stimuli from a distance of ~50 cm through an individually adjusted stereoscope. Participants’ heads were restrained by a chin rest. Participants were asked to fixate binocular red (CIE x = 0.62, y = 0.35, Y = 17) crosshairs, subtending 0.43 dva, throughout a run of trials.

Stimuli consisted of white (CIE x = 0.28, y = 0.29, Y = 98) monocular bars, subtending 2.3 degrees of visual angle (dva) in height and 0.7 dva in width. These were presented inside binocular red circles (see Figure 1). The background of the display was gray (CIE x = 0.28, y = 0.29, Y = 30).

Standard stimuli were either presented persistently for 7 s (Static presentations, see Figures 1a and 1b), or intermittently for 500 ms at a time, separated by blank inter-stimulus intervals (ISIs) of 200 ms (Flicker presentations, see Figures 1c and 1d). Flicker presentations consisted of a train of 10 standard stimuli. The orientation of Standard stimuli (vertical or horizontal) was determined at random on a trial-by-trial basis. The eye to which Standard stimuli were presented alternated, also on a trial-by-trial basis.

Standard stimulus presentations were followed by a 200-ms blank ISI, and then by a 500-ms presentation of a Comparison stimulus. The orientation of the Comparison was either the same as the preceding Standard stimulus (Baseline condition) or orthogonal to it (Oddball conditions). Comparison stimuli were also either presented to the same eye (Baseline and Same Eye conditions) or to the other eye (Diff Eye conditions) relative to the Standard stimulus.

Comparison stimuli were surrounded by a white square frame (subtending 3.1 dva, frame width 0.43 dva). During a run of trials, the luminance of the frame was manipulated.

![Figure 1](jov.arvojournals.org)
(between 53, 71, 93, 102, 111, and 120 cd/m²) according to the method of constant stimuli. A run of trials consisted of 300 individual trials, 60 for each of the 5 experimental conditions (Baseline, Same Eye Static, Same Eye Flicker, Diff Eye Static, and Diff Eye Flicker). Each participant completed two runs of trials.

On each trial, participants judged if the surrounding frame or Comparison stimulus was brighter. Responses provided distributions of apparent Comparison stimulus brightness as a function of frame brightness. We fitted logistic functions to these distributions and took 50% points as estimates of the subjective brightness of Comparison stimuli in each experimental condition. As we expected greatest fading in the Baseline condition, wherein the Comparison stimulus was the same orientation and was presented to the same eye as the Standard stimulus, we expressed brightness estimates for the other four oddball conditions relative to Baseline estimates. Proportions greater than 1 show less evidence of fading than Baseline. Our baseline measures are a fairly typical measure of Troxler fading, whereas other conditions can be taken as measures of the degree to which Troxler fading is disrupted by the relevant manipulations.

Results and discussion

Proportional brightness estimates, averaged across participants, are shown in Figure 2. These data show that apparent oddball brightness was affected by eye of origin, such that oddballs seemed dimmer when presented to the same eye as the Standard stimulus ($F_{1,11} = 10.93, p = 0.007$). These effects contrast with stimulus presentation style (Static or Flicker), which had no impact on apparent oddball brightness ($F_{1,11} = 0.10, p = 0.76$).

If we assume a link between the oddball effect and low-level adaptation, and we take the results of Experiment 1a as a metric of the latter, we can make oddball predictions for similar experimental conditions. Our paradigm will involve sequential presentations of Standard and oddball stimuli, either following a persistent Standard stimulus presentation and a small number of intermittent Standard stimulus presentations or following a longer train of intermittent Standard stimulus presentations. We would expect equivalent oddball effects across these styles of stimulus presentation, as both persistent and intermittent presentations resulted in equivalent magnitudes of fading in Experiment 1a. However, we would expect greater oddball effects when oddballs and Standard stimuli are presented to different eyes, as these conditions resulted in less fading relative to same eye presentations.

Experiment 1b: Eye of origin and the oddball effect

Details for Experiment 1b were as for Experiment 1a, with the following exceptions.

Standard and oddball stimuli had the same luminance (98 cd/m²). Flicker presentations (see Figure 3a) consisted of 16 sequential presentations, separated by 200-ms ISIs. During these trials, Standard stimuli were presented for 500 ms and oddball stimuli were presented on either the 12th, 13th, or 14th presentation, determined at random on a trial-by-trial basis.

Static presentations (see Figure 3b) consisted of an initial long Standard stimulus presentation (6.1 s) followed by a 200-ms ISI and then 7 shorter intermittent stimulus presentations. These consisted of 6 Standard stimulus presentations (500 ms) and an oddball stimulus, presented on either the 5th, 6th, or 7th presentation, all separated by 200-ms ISIs.

During a run of trials, the duration of oddball presentations was manipulated (250, 400, 450, 500, 550,
700, or 1000 ms) according to the method of constant stimuli. A run of trials consisted of 224 individual trials, 56 for each of the 4 experimental conditions (Same Eye Static, Same Eye Flicker, Diff Eye Static, and Diff Eye Flicker). Each participant completed two runs of trials.

On each trial, participants judged if the oddball presentation had been longer or shorter than the immediately preceding Standard stimulus (500 ms). Participant responses provided distributions of apparent oddball duration. We fitted Weibull functions to these distributions and took 50% points as estimates of subjective oddball, relative to Standard stimulus, duration in each experimental condition. We quantified oddball effects as the difference between these estimates and the veridical interval (500 ms).

**Results and discussion**

In Figure 4, we have shown oddball effects for each experimental condition. These data show that the style of stimulus presentation was critical for the oddball effect ($F_{1,12} = 18.52, p = 0.001$), with robust oddball effects in Flicker presentations ($M = 57 \pm 9$ ms) and no evidence of an effect in Static presentations ($M = 4 \pm 14$ ms). These effects contrast with the inefficacy of eye of origin ($F_{1,12} = 0.95, p = 0.35$).

The results of Experiments 1a and 1b are marked by a double dissociation. Eye of origin has a robust impact on Troxler fading (Troxler, 1804) but does not shape the oddball effect. In contrast, presentation style (involving either an initial protracted presentation or a train of intermittent presentations) is critical for the oddball but has no impact on Troxler fading. This double dissociation suggests that the two phenomena are driven by independent processes. If we take Troxler fading as a metric of low-level visual adaptation (Clarke & Belcher, 1962; Martinez-Conde et al., 2002, 2006), consistent with the efficacy of eye of origin in our data, then this suggests that the oddball effect is not strongly influenced by low-level visual adaptation.

Rather than low-level adaptation, the main cause of the oddball effect might be predictive coding (Srinivasen et al., 1982). In effect, the prediction would be that a repetitive stimulus will repeat. If perceived duration were shaped by predictive coding (Eagleman & Pariyadath, 2009; Pariyadath & Eagleman, 2007), it should scale with the discrepancy between predicted and actual inputs. Accordingly, an oddball should seem to persist for longer than matched presentations of a repetitive standard stimulus even when the oddball is a less intense version of the standard. Note that if perceived durations were simply determined by the magnitudes of neural response to individual stimuli, one might predict that perceived duration should scale with stimulus intensity (Xuan, Zhang, ...
He, & Chen, 2007), as more intense inputs tend to excite greater responses across visual brain regions (Albrecht & Hamilton, 1982; Goodyear & Menon, 1998).

**Experiment 2: Bright and dim oddballs**

**Methods**

Details for Experiment 2 were as for Experiment 1, with the following exceptions.

There were twelve participants, two authors and ten volunteers who were naive as to the purpose of the experiment. Stimuli consisted of disks subtending 3.6 degrees of visual angle (dva) centered on a black display. The standard stimulus had a luminance of 60 cd/m². Oddball disk presentations had luminance intensities of 120 cd/m² (Bright oddballs) or 30 cd/m² (Dim oddballs).

Each trial consisted of 11 sequential disk presentations (see Figure 5). The standard disk was presented in all but one of the 11 repetitions, while an oddball stimulus was presented on the other occasion (either the 7th, 8th, 9th, or 10th presentation, determined at random on a trial-by-trial basis). Each presentation was separated by a blank 300-ms ISI. Standard stimuli were presented for 500 ms whereas oddballs were presented for 250, 380, 500, 750, or 1000 ms. At the conclusion of the trial, participants were asked to indicate whether the oddball presentation had been shorter or longer than the immediately preceding and subsequent standard disk presentations.

Each of the sampled oddball durations was presented 4 times, for each oddball condition, in a random order for each run of trials. Participants completed 3 runs of trials, providing 120 responses. Estimates of the oddball duration that was perceptually matched to that of the Standards were taken as the 50% points of Cumulative Gaussian functions fitted to individual data. Estimates of the oddball effect were then determined by subtracting individual PSE estimates from the standard duration (500 ms).

**Results and discussion**

As depicted in Figure 6, the perceived durations of both Bright ($M = 31 \pm 15$ ms) and Dim ($M = 51 \pm 14$ ms) oddballs were exaggerated relative to repeated presentations of the standard stimulus. Interestingly, while this effect was highly significant for Dim oddballs (single sample $t_{11} = 2.04, p = 0.004$), it was only marginally significant for Bright oddballs (single sample $t_{11} = 3.57, p = 0.066$). There was, however, no significant difference between oddball effect magnitudes for bright and dim stimuli (paired samples $t_{11} = 0.90, p = 0.39$).

These data show that an oddball presentation can seem to persist for longer than do matched presentations of a more intense repetitive stimulus. This is inconsistent with the responsiveness of visual brain regions to individual inputs (Albrecht & Hamilton, 1982; Goodyear & Menon, 1998). These data are, however, consistent with a link between perceived duration and predictive coding. Accordingly, perceived duration should scale with the magnitude of discrepancy between predicted and actual inputs. We
assessed this premise by using oriented stimuli to see if the oddball effect would scale with the angular difference between repetitive standard and oddball stimuli.

**Experiment 3: Oddballs and angular changes**

**Methods**

Details for Experiment 3 were as for Experiment 2, with the following exceptions.

There were eight participants, two authors and six volunteers who were naive as to the purpose of the experiment. Participants were asked to fixate a red cross-hair subtending 0.5 dva, located in the center of the screen. Standard stimuli consisted of white (CIE $x = 0.28$, $y = 0.29$, $Y = 120$) bars subtending 4.3 dva in height and 0.7 dva in width. The orientation of the standard stimulus was determined at random on a trial-by-trial basis. Oddball stimuli were gray (CIE $x = 0.28$, $y = 0.29$, $Y = 30$) and were either the same orientation as the standard, rotated $\pm 15^\circ$ from Standard, or $\pm 45^\circ$ from the Standard.

On each trial, there were 11 sequential stimulus presentations, with the oddball presented on the 7th, 8th, 9th, or 10th presentation (see Figure 7). Oddball stimuli were presented for 300, 400, 500, 750, or 900 ms, except for two participants who had difficulty with the task and were therefore presented with oddballs for 250, 380, 500, 750, or 1000 ms. Each run of trials consisted of 75 individual trials, with each oddball duration presented 5 times for each of the three oddball orientation conditions. Each participant completed 2 runs of trials.

Determination of oddball effect magnitudes was as described for Experiment 2.

**Results**

In this experiment, the luminance of oddballs was less intense than the repetitive standard stimuli. In addition, the orientation of the oddball was either the same as the Standard, rotated by $15^\circ$ from the Standard, or rotated by $45^\circ$ (see Figure 7). In each case, the perceived duration of the oddball was exaggerated relative to presentations of...
the more intense repetitive Standard (see Figure 8). More importantly, a repeated-measures ANOVA revealed a linear relationship between the magnitude of the oddball effect and the angular difference between oddball and standard stimuli ($F_{1,7} = 25.1, p = 0.002$).

### General discussion

Our data suggest that the oddball effect is not strongly influenced by low-level visual adaptation. For instance, we found no evidence that the magnitude of the oddball effect could be modulated via fading due to low-level visual adaptation (Experiment 1). Our data are also inconsistent with a simple link between neural response magnitudes, as predicted by responses to isolated inputs, and perceived duration. This is true because we were able to elicit an oddball effect using oddballs that were less intense versions of repetitive standard stimuli (Experiment 2). As these data are inconsistent with a strong link between the oddball and low-level visual adaptation, we suggest instead that the main cause of the oddball effect is predictive coding (Pariyadath & Eagleman, 2007). This is consistent with the linear relationship between perceived duration and the magnitude of angular difference between expected and actual inputs (Experiment 3).

#### Oddballs as a transient change in a persistent representation

Recently, it has been suggested that the oddball effect is linked to the relative magnitudes of neural response to different inputs (Eagleman, 2008; Eagleman & Pariyadath, 2009; Eagleman et al., 2005). According to this proposal, the oddball effect does not result from exaggerated oddball durations but from diminished standard stimulus durations. We believe our data pose an important caveat for this type of account. Specifically, we believe they caution against crouching any explanation of the oddball solely in terms of how the visual system responds to repeated standard, or indeed to oddball, stimuli. Instead, we believe our data implicate an operation that compares these inputs, so that an oddball can be judged as odd. Ultimately, we believe that Oddballs are treated by the visual system as a transient change in a persistent representation. We outline our reasoning below.

Our data suggest that the oddball effect cannot be explained by an account that considers repetitive standard stimulus and oddball presentations as separate and independent facts. If this were true, less intense oddballs should have a reduced apparent duration relative to more intense repetitive standard events, due to the tight relationship between the neural response magnitudes and luminance contrast for isolated inputs (Albrecht & Hamilton, 1982; Goodyear & Menon, 1998). Instead, we have found that less intense oddballs have an exaggerated perceived duration. We therefore suggest that the oddball is driven by a predictive analysis wherein repetitive standard and oddball stimuli are linked, not isolated, and in which perceived duration is related to the discrepancy between expected and actual inputs (Eagleman & Pariyadath, 2009; Pariyadath & Eagleman, 2007).

Our data, however, do not preclude the possibility of a relationship between neural response magnitudes and perceived duration (Eagleman, 2008). They simply suggest that such a relationship must not treat repetitive standard and oddball stimuli as independent facts. If, for instance, the luminance contrast of an input were predicted on the basis of previous inputs, any discrepancy between prediction and actual input might be treated as a change in a persistent representation. In that case, both increases and decreases in luminance contrast should result in exaggerated perceived durations, because both increases and decreases in the luminance contrast of a persistent representation result in increased brain activity (Haynes, Lotto, & Rees, 2004). Moreover, a transient decrement in the luminance contrast of a persistent stimulus results in a greater increase in brain activity than does a transient luminance contrast increment (Haynes et al., 2004). This precisely mirrors the trend in our data concerning the effects of luminance contrast on the oddball effect (see Figure 6).

#### Orientation changes, the oddball, and low-level adaptation

Our data concerning Oddball effect variance with angular differences (between repetitive standards and oddballs) may seem to be consistent with low-level visual adaptation. Orientation-selective reductions in sensitivity have certainly been attributed to adaptation in primary visual cortex (Blakemore, Carpenter, & Georgeson, 1970; Coltheart, 1971; Fang, Murray, Kersten, & He, 2005). However, orientation adaptation is dramatically impacted by eye of origin, being substantially weakened when adaptor and
test are shown to different eyes (Bjorklund & Magnussen, 1981). In contrast, we have shown that the oddball effect is insensitive to eye of origin (see Figure 4). Note that this contrasts with apparent oddball intensity. Presumably because our oddball and standard stimuli in Experiment 1 were presented in the same retinal locations, oddball intensity was somewhat modulated by eye of origin (see Figure 3). Given this dissociation, between eye of origin sensitivity and insensitivity (for orientation adaptation and the oddball effect, respectively), we believe that the orientation tuning of the oddball effect (see Figure 8) reflects the discrepancy between predicted and unexpected inputs, rather than the influence of low-level visual adaptation.

Predicted input and attention

The oddball effect has previously been linked to enhanced attention (Tse et al., 2004; Ulrich, Nitschke, & Rammsayer, 2006). We believe our data are broadly consistent with such a relationship. One of the most important tasks performed by sensory processing is to serve as an alert when circumstances change. Both predictive coding and neural adaptation are implicated in this endeavor, as both are thought to result in more efficient neural representations (Desimone & Duncan, 1995; Grill-Spector et al., 2006; Srinivasan et al., 1982), which, in turn, should heighten sensitivity to change. Thus, if an input is rendered relatively unexpected due to predictive coding/neural adaptation, it might become more likely to attract exogenous attention.

While perhaps not explicitly stated, we believe that predictive coding is central to most attentional accounts of the oddball effect (Tse et al., 2004; Ulrich et al., 2006). These proposals suggest that attention is drawn toward oddball stimuli, which sets in train a process that exaggerates the oddball’s perceived duration. However, attention is only drawn toward the oddball because it is odd, in that it has a relatively low probability of being presented. We believe, therefore, that the initial process necessary for generating the oddball effect is not any attention-related processes that might be set in train by detecting an oddball but the predictive processes that make an oddball odd.

Of course this scheme would allow for a contribution of attention independent of predictability. For instance, if attention were drawn toward an input because of its ecological significance, that input might result in a greater neural response, and therefore in a relatively exaggerated perceived duration (see van Wassenhove, Buonomano, Shimojo, & Shams, 2008). In this instance, an exaggerated duration might ensue independent of predictibility. This does not, however, rule against predictability playing a causal role in situations wherein repetitive standard and oddball stimuli are equally matched in terms of ecological significance. Our demonstration that less intense oddballs can result in an enhanced perceived duration relative to more intense repetitive standard stimuli could be construed as an example of the opposite situation, of a less ecologically significant stimulus resulting in an enhanced duration, presumably because it is unexpected due to an anticipatory, predictive, code.

Conclusions

Our data are inconsistent with a strong causal link between the oddball effect and reductions in neural responsiveness at low levels of visual processing, as manipulations of eye of origin had no impact on oddball effect magnitude. Nor can the oddball effect be predicted on the basis of neural response magnitudes to individual inputs, as less intense oddballs have an exaggerated perceived duration relative to more intense repetitive standard stimuli. We do, however, find that the oddball effect scales with the angular difference between oddball and repetitive standard stimuli. Overall, we believe our data are consistent with perceived duration being shaped by a predictive code that treats an oddball stimulus as a transient change within a persistent representation.

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