An Event-Related Potential Study of Onset Primacy in Visual Change Detection

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Abstract

Onset primacy is a behavioural phenomenon whereby humans identify the appearance of an object (onset) with greater efficiency than other kinds of visual change, such as the disappearance of an object (offset). The default mode hypothesis explains this phenomenon by postulating that the attentional system is optimised for onset detection in its initial state. The present study extended this hypothesis by combining a change detection task and measurement of the P300 event-related potential (ERP), which was thought to index the amount of processing resources available to detecting onsets and offsets. In an experiment, participants indicated the locations of onsets and offsets under the condition in which they occurred equally often in the same locations across trials. Although there was no reason to prioritise detecting one type of change over the other, onsets were detected more quickly and they evoked a larger P300 than offsets. These results suggest that processing resources are preferentially allocated to onset detection. This biased allocation may be a basis on which the attentional system defaults to the 'onset detection' mode. Possible contributions of other ERP components to onset primacy are also discussed in the article.

Keywords: attention, attentional capture, P3, P3b, P300

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The ability to direct attention within an environment provides an adaptive mechanism that is particularly useful for the detection of change. In the absence of effective visual change detection, it would be difficult to successfully navigate everyday life. Driving a car or crossing the road, for example, requires the ability to detect new obstacles as they appear in the visual field. Research involving visual search paradigms has indicated that humans are particularly adept at noticing new objects that abruptly enter their environment (Cole & Liversedge, 2006; Jonides & Yantis, 1988; Yantis & Jonides, 1984). Under certain conditions, however, even significant changes in visual scenes go unnoticed, through a phenomenon known as change blindness (Simons & Rensik, 2005). Behavioural studies have demonstrated that the sudden appearance of an object (object onset) is relatively robust to change blindness, while other types of change, such as the sudden disappearance of an object (object offset), are more likely to remain unnoticed (Cole & Kuhn, 2010; Cole & Liversedge, 2006). The comparative efficiency of onset over offset detection has been referred to in the literature as onset primacy (Cole, Kentridge, & Heywood, 2004; Donaldson & Yamamoto, 2012).

The persistence of onset primacy across experimental paradigms led Donaldson and Yamamoto (2016) to propose that onset detection is the default processing mode of the attentional system. To process other kinds of change, a shift is required from this default mode, resulting in a less efficient response. While the robust nature of onset primacy may be functionally adaptive, given that onset detection is advantageous in most situations, there are other situations in which offset detection may be more beneficial. For example, a lifeguard monitoring a crowded beach needs to notice the disappearing swimmer; a parent watching over a group of children in the playground needs to notice if one goes missing. As such, it is important to understand how and why onset primacy occurs by investigating the processes

that underlie onset and offset detection.

In pursuing this endeavour, the present study tested the validity of the default mode hypothesis (Donaldson & Yamamoto, 2016) by examining differences in neural activation with electroencephalography (EEG) while participants attempted to detect onsets and offsets. According to the default mode hypothesis, the system of neural processing should initially be optimised for detection of onsets, making relevant areas of the brain more responsive to onsets than offsets. This enhanced processing of onsets should be reflected in event-related potentials (ERPs) that are of theoretical relevance to visual change detection. Specifically, this study primarily focused on the P300 ERP as a neural marker of cognitive processes that underlie behavioural findings of onset primacy. Additionally, the P100 ERP was measured to examine whether early visual processes also contribute to onset primacy.

P300

The P300, which is also called the P3, is a positive deflection that typically occurs between 300–500 ms after the onset of sensory stimuli (Hopfinger & Mangun, 1998; Hopfinger & Maxwell, 2005; Koivisto & Revonsuo, 2003), though it could range more widely from 250 ms up to 900 ms (Polich, 2007). It is generally implicated in information processing that involves selective attention and may be evoked after exposure to auditory or visual stimuli. Given that the P300 varies in topographic distribution, it is often conceptualised as two separate subcomponents, the P3a, a frontal distribution associated with stimulus novelty, and the P3b, a temporal-parietal distribution associated with attention and memory processing (Polich, 2007). The latter component has also been observed over the occipital areas in studies of selective attention (Koivisto & Revonsuo, 2003). While the P3a novelty component may instinctively be of interest in a change detection paradigm, it is likely that novelty effects would quickly be habituated across the repetitive presentation of visual stimuli, making meaningful P3a components difficult to observe across averaged trials. The

P3b component, however, remains of particular interest. As such, consequent discussion of the P300 is largely focused on the P3b in this paper. For simplicity, the P3b component is referred to as P300 hereafter.

A key reason for focusing on the P300 is that its amplitude is a good index of the amount of processing resources available for performing a task. This is best demonstrated in dual-task studies in which participants are given two tasks to perform simultaneously (Isreal, Wickens, Chesney, & Donchin, 1980; Mangun & Hillyard, 1990; Sirevaag, Kramer, Coles, & Donchin, 1989; Wickens, Kramer, Vanasse, & Donchin, 1983). A typical finding from these studies is that the P300 evoked by a primary task decreased when a secondary task was made more difficult so that it demanded a greater degree of participants' attention (which, in turn, reduced their attention to the primary task). Notably, the P300 is modulated in the same way even when two tasks do not coincide strictly—there can be a delay of up to 1–1.5 s between them (Nash & Fernandez, 1996; Strayer & Kramer, 1990). Thus, these findings indicate that the P300 generally reflects the trade-off relationship between tasks when participants mentally prepare for performing both of the tasks, and its amplitude goes up and down as more and less resources are allocated to a task of interest. This idea is directly applicable to the current paradigm because there is similar reciprocity between onset and offset detection such that as observers improve their behavioural performance in detecting offsets through training, their efficiency in detecting onsets declines (Donaldson & Yamamoto, 2016). Taken together, it was postulated that P300 amplitude would function as a measure of processing resources allotted for detecting onsets and offsets.

The present study used this postulation to test the default mode hypothesis. This hypothesis posits that perceiving onsets is prioritised in the system of visual change detection in its initial state. One way of implementing this prioritisation is to assign a greater amount of processing resources for detecting onsets by default. Thus, if a larger amplitude of P300 was

observed when participants detected onsets as compared to when they detected offsets, it would support the default mode hypothesis by showing that more resources are indeed allocated to detection of onsets. It is important to note that, as shown in the method section below, onsets and offsets were equal in the present experiment in that both were to-be-detected targets and they occurred in the same frequency and in the same spatial locations across trials. Therefore, participants did not have any particular reasons to pay more attention to one type of change than the other. If onsets were still detected more efficiently and if it was accompanied with a larger P300, it would indicate that allocation of processing resources is biased in favour of onset detection in the default mode of the system.

P100

The P100, also known as the P1, is a positive ERP component that peaks around 70–150 ms after the appearance of a visual or auditory stimulus (Di Russo, Martínez, Sereno, Pitzalis, & Hillyard, 2001; Mangun, 1995; Martínez et al., 1999). The P100 is ubiquitous in tasks that involve visual stimuli, suggesting that this ERP is elicited in part by bottom-up processing of sensory information that occurs regardless of observers' intention to perceive the stimuli (Luck & Kappenman, 2012). However, the P100 is also the earliest visually evoked ERP that is robustly affected by attention (Pratt, 2012). For example, as observers shift the focus of attention to the left and right of their visual field, the amplitude of the P100 increases at electrodes contralateral to the attended hemifield (Mangun, Hopfinger, Kussmaul, Fletcher, & Heinze, 1997; Martínez et al., 1999). Unlike the P300 that is distributed across the scalp surface over the temporal, parietal, and occipital cortices (Eimer & Mazza, 2005; Koivisto & Revonsuo, 2003; Polich, 2007), the visual P100 tends to be localised to posterior electrodes over the extrastriate and occipito-temporal cortices, suggesting that the attentional modulation of the P100 reflects the effects of top-down signals on feedforward sensory processing in early visual areas (Di Russo et al., 2001; Gomez

Gonzalez, Clark, Fan, Luck, & Hillyard, 1994; Mangun et al., 1997; Martínez et al., 1999).

The P100 was chosen as an additional target for investigation because it can potentially offer insights into the debate about the origin of onset primacy. As the visual properties of a stimulus, such as its luminance, shape, or motion compared to its surroundings, can influence attentional capture, it is argued that the primacy of onset detection can be attributed to these sensory transients created by an appearing object, rather than the appearance of the object itself (Franconeri, Hollingworth, & Simons, 2005; Hollingworth, Simons, & Franconeri, 2010; Miller, 1989; Theeuwes, 1994). An alternative view is that object onset engages higher-order cognitive processes such as creation of a new mental representation of the object, and these cognitive operations constitute a primary source of onset primacy (Boot, Kramer, & Peterson, 2005; Cole et al., 2004; Davoli, Suszko, & Abrams, 2007; Yantis, 1993). If the sensory account were true, then early sensory ERP components should reveal clear differences between onset and offset conditions. Given that the P100 is the earliest visual ERP in which the amplitude reliably alters with the way the stimulus is attended, it was deemed a good candidate for showing amplitude variation between onset detection and offset detection. On the other hand, if the cognitive account were true, then onsets and offsets should evoke similar responses in the early components, and begin to differ in later components that represent the cognitive processes (e.g., the P300). Although the primary focus of the present study was on the P300, examining the P100 provided an opportunity to shed some new light on the mechanisms that give rise to onset primacy.

The Objectives of the Present Study

In summary, the goal of the present study was to seek neural evidence for the default mode hypothesis of onset primacy (Donaldson & Yamamoto, 2016). To this end, an experiment was conducted to measure P300 amplitude while participants were presented with

onsets and offsets. It was predicted that the P300 would appear in a larger amplitude for onset than offset conditions in electrodes over temporal, parietal, and occipital regions of the brain. Additionally, the P100 was examined to explore whether the pattern of its amplitude could discriminate between the two major accounts of onset primacy. If the P100 amplitude was greater during onset detection than offset detection at electrodes over the extrastriate and occipito-temporal cortices, it would indicate the contribution of early sensory processes to onset primacy. On the other hand, if similar P100s were observed in onset and offset trials, it would suggest that onset primacy mainly stems from cognitive processes involved in object representation.

Method

Participants

Twenty-five students (19 female, 6 male) aged 17–29 years (M = 20.88, SD = 3.25) participated in return for partial credit toward their course. Written informed consent was obtained prior to their participation. All were right-handed with no known history of neurological disorder, and had normal or correct-to-normal vision, as confirmed by a Snellen eye-chart. The experiment was approved by the Human Research Ethics Committee of the Queensland University of Technology.

Materials

This experiment used Donaldson and Yamamoto's (2012) change detection task, who modelled it from the one-shot flicker paradigm developed by Cole, Kentridge, Gellatly, and Heywood (2003). Stimuli depicted visual scenes, each of which included a small circular table-top (30 cm diameter) with a single supporting leg (38 cm height). A range of objects of approximately equal size (4 cm width, 3 cm height, 2 cm depth) were placed onto the table in 16 different arrangements. The number of objects on the table was varied, ranging from six to nine, to minimise the potential to predict patterns of change. Images were presented at a

central fixation point, with visual angle subtending approximately 7° horizontally and 4° vertically. Participants viewed the stimuli from an approximate distance of 60 cm on a monitor with a screen resolution of 1920 × 1080 pixels, via PsychoPy software (version 1.86; Peirce, 2007, 2009).

Design and Procedure

Participants were informed that they were going to view a series of paired photographs, and that a change would be identifiable on the appearance of the second image. They were instructed to indicate whether they observed the change on the left or right side of the stimulus by pressing either F or J on their keyboard, respectively. Participants were asked to keep their index fingers resting on the response keys throughout the experiment and to respond as quickly and accurately as possible. Participants were not informed of the nature of change (onset or offset) across trials and received no performance feedback throughout.

The paired photographs were presented across a single block of trials. In onset trials, the second image contained one additional object on the tabletop; in offset trials, the second image removed one object from the tabletop (see Figure 1 for an example). The change occurred on each side of the table (left and right) an equal number of times and was counterbalanced across onset and offset conditions. To control for the potential influence of object properties, such as colour, location, or semantic salience, the same paired photographs were used for both onset and offset trials, in reversed order. Each photograph in the pair had either seven or eight objects on the tabletop, with each object acting as the change target an equal number of times. There were 64 trials for each change type, making a total of 128 experimental trials.

Additional 32 photograph pairs were created as filler trials. Across 16 filler onset trials, an eight-object display was followed by a nine-object display. Across 16 filler offset trails, a seven-object display was followed by a six-object display. These filler trials were

included to discourage participants from anticipating the type of an upcoming trial on the basis of the first photograph alone. Without the filler trials, having a seven-object display in the first photograph could mean for certain that it would be an onset trial; similarly, having an eight-object display in the first photograph could mean that it would be an offset trial. The filler trials were randomly intermixed with experimental trials, creating a total of 80 onset and 80 offset trials. Each participant performed all of these trials (i.e., a within-participant design). Data from the filler trials were not included in the analysis. Participants also completed 16 practice trials (8 onset and 8 offset, randomised) to familiarise themselves with the task. Practice trials consisted of new photograph pairs that were not used in the filler or experimental trials.

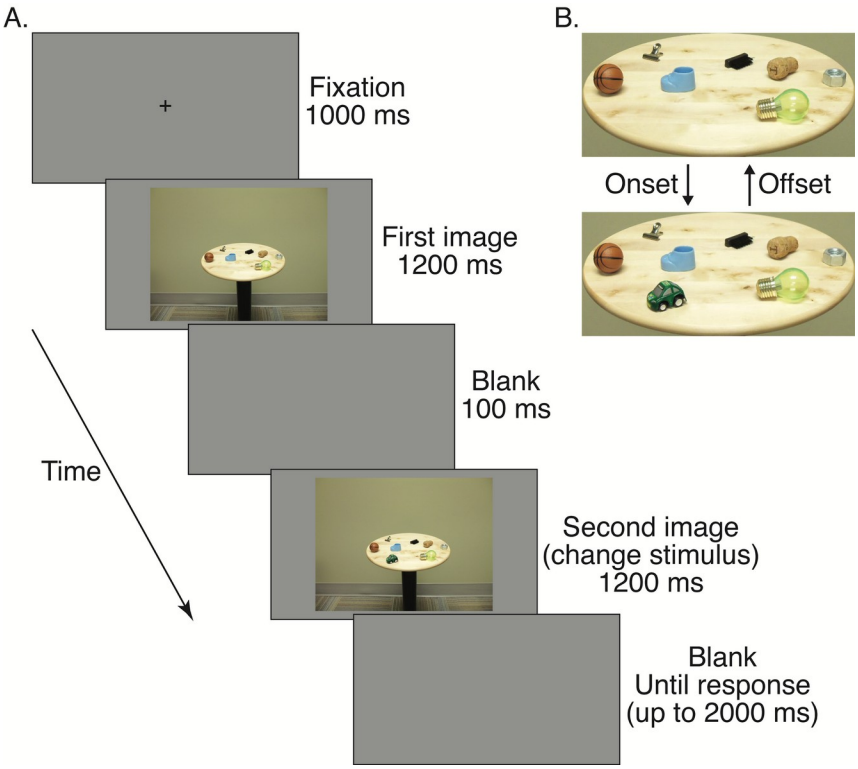

Figure 1. Experimental stimuli (adapted from Donaldson & Yamamoto, 2012). (A) Sequence of trials. (B) A closer view, demonstrating how the paired images changed in onset and offset trials. Here, the green car is the object of change. A coloured version of the figure is available online.

The sequence of each trial is demonstrated in Figure 1. First, participants viewed a central fixation cross for 1000 ms. The first image then appeared for 1200 ms, followed by a blank grey screen for 100 ms. The second image, depicting the change (change stimulus), then appeared for 1200 ms, before a final grey screen lasting 2000 ms. Participants were able to provide a response any time after the appearance of the change stimulus. When a response was provided, or when the final grey screen timed out, the fixation cross would reappear to indicate the start of the next trial.

EEG Data Acquisition and Analysis

Electrical activity was recorded across 64 channels, aligning with the International 10–20 system of electrode placement. Data were collected using a sampling rate of 1024 Hz and electrode impedance values were kept below 25 kΩ throughout the recording. EEG data were recorded using the BioSemi ActiveTwo 64-channel amplifier and the ActiView software (version 7.06). Pre-processing was completed using BrainVision Analyzer (version 2.1, Brain Products GmbH). Amplitude data were analysed using MATLAB (version R2019a, MathWorks) and the statistical program R (version 4.0.2, R Foundation for Statistical Computing).

During pre-processing, data were re-referenced to a common average based on all electrodes. A bandpass filter (0.1–30 Hz, slope = 24 dB/octave) was applied with a notch filter as per Australia mains frequency (50 Hz). BrainVision Analyzer's automated ocular correction procedure using independent component analysis was used to identify and reject blink components on the basis of the Fp1 electrode. This electrode was selected because of its proximity to the eye. Each participant's data were visually inspected, and electrodes containing excessive noise were rejected and interpolated by spherical spline interpolation (splines = 4; polynomials = 10 degrees; $\lambda = 10^{-5}$). An automatic raw data inspection was then applied, which was set to identify steep changes in voltage (a time-step slope smaller than

−50 μV/ms or greater than 50 μV/ms) and large voltage drifts (the difference in neighbouring 300-ms intervals larger than 300 μV). Time intervals including the instances of these artefacts, beginning 100 ms before a given instance and ending 100 ms after the instance, were excluded. These processes resulted in exclusion of one participant from all analyses because data from more than 14% of trials were lost due to the artefacts. In the remaining participants, on average, 1.36% of onset trials and 1.19% of offset trials were removed from each participant's data. Subsequently, data were epoched into segments spanning from 100 ms preceding the appearance of the change stimulus to 1000 ms after. Average ERPs were computed during the time window for onset and offset conditions separately within each participant for further analysis. Activity during the inter-stimulus period (−100–0 ms) was used to baseline the data.

Outcome Measures

Behavioural Measures. Reaction time was measured as the time that elapsed between the appearance of the change stimulus and the participant's response. Accuracy of the change location judgement, as indicated by the keyboard button press, was also measured. Trials where participants failed to provide a response before the end of the final grey screen were considered incorrect. When incorrect responses were made, associated reaction time data were excluded from analysis.

P300. The region of interest (ROI) for the P300 included electrodes over the cortical surface of the temporal, parietal, and occipital lobes (Eimer & Mazza, 2005; Koivisto & Revonsuo, 2003; Polich, 2007). They were grouped into clusters corresponding to their topographic location (Figure 2): left (CP1, CP3, CP5, TP7, P1, P3, P5, P7, PO3, PO7, and O1), centre (CPz, Pz, POz, and Oz), and right (CP2, CP4, CP6, TP8, P2, P4, P6, P8, PO4, PO8, and O2). Peak amplitude measures were derived from the largest positive amplitude peaks within the time window of 275–500 ms after the appearance of the change stimulus.

In all EEG analyses reported in this article, mean amplitude measures were also computed and analysed using the same ROI and the time window as in corresponding peak amplitude analyses. However, results from the mean amplitude analyses are not reported below because they were consistent with those from the peak amplitude analyses. Both peak and mean amplitude data are available on the Open Science Framework at https://osf.io/jnq27. The EEG measures were calculated using correctly performed trials only.

P100. For measuring the P100, electrodes over the surface of the extrastriate cortex were targeted because of its presumed origin in this region (Di Russo et al., 2001; Gomez Gonzalez et al., 1994; Martínez et al., 1999; Mangun et al., 1997). Specifically, the P100 was measured at P7 and PO7 in the left hemisphere as well as at P8 and PO8 in the right hemisphere (Figure 3) using the time window of 75–150 ms after the appearance of the change stimulus. The two electrode clusters were selected on the basis of previous studies in which this ERP was evoked at these electrodes in response to appearing and disappearing visual stimuli (Di Russo et al., 2001; Hopfinger & Mangun, 1998, 2001; Hopfinger & Maxwell, 2005; Mangun & Hillyard, 1991). Peak amplitude measures were derived from the largest positive amplitude peaks within the time window of interest.

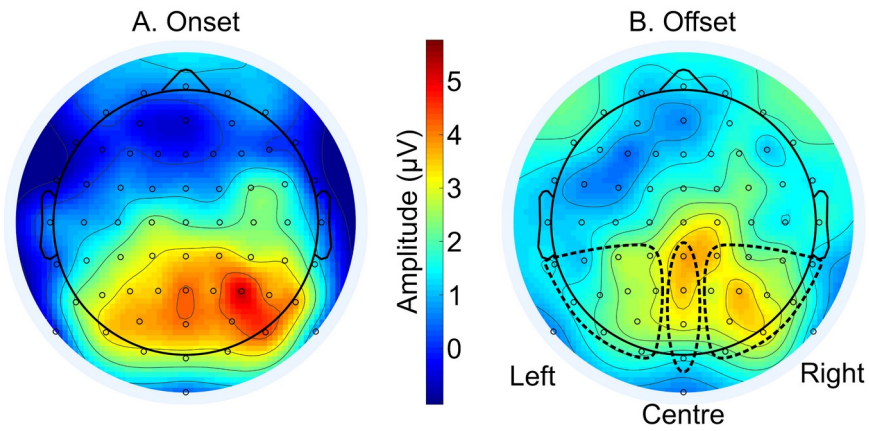

Figure 2. Grand average topographic plots collapsed over participants (*N* = 21), showing the distributions of the peak voltage in the P300 time window (275–500 ms post change stimulus) separately for each change type (A: onset; B: offset). Circles represent EEG electrodes. Broken lines indicate electrode clusters that constituted the region of interest (ROI): left (CP1, CP3, CP5, TP7, P1, P3, P5, P7, PO3, PO7, and O1), centre (CPz, Pz, POz, and Oz), and right (CP2, CP4, CP6, TP8, P2, P4, P6, P8, PO4, PO8, and O2). A coloured version of the figure is available online.

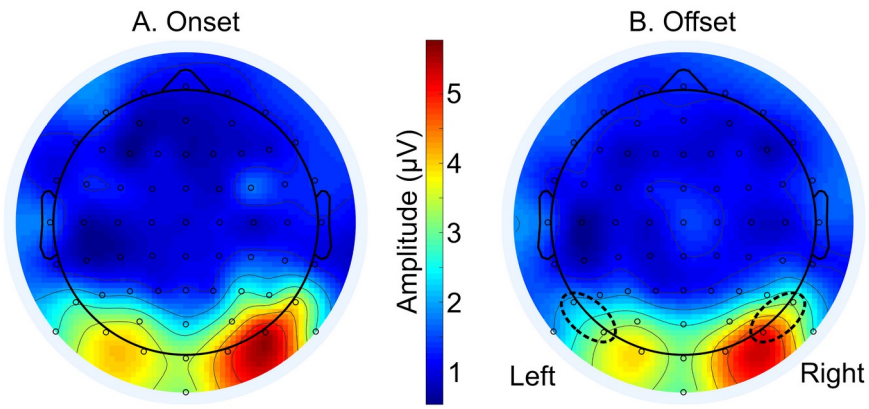

Figure 3. Grand average topographic plots collapsed over participants (*N* = 21), showing the distributions of the peak voltage in the P100 time window (75–150 ms post change stimulus) separately for each change type (A: onset; B: offset). Circles represent EEG electrodes. Broken lines indicate electrode clusters that constituted the ROI: left (P7 and PO7) and right (P8 and PO8). A coloured version of the figure is available online.

Results

Behavioural Results

Accuracy. Accuracy scores were defined as outliers if they were more than two standard deviations away from the mean of all participants, considering onset and offset conditions separately. This resulted in the exclusion of three participants from all further analyses (adjusted $N = 21$). The mean accuracy scores of the excluded participants were 78.65% ($SD = 5.49\%$, onset) and 77.08% ($SD = 10.40\%$, offset). The mean accuracy scores of the remaining participants were 95.61% ($SD = 3.58\%$, onset) and 94.20% ($SD = 3.28\%$, offset). Although participants detected onsets with slightly greater accuracy, this difference was not statistically meaningful, $t(20) = 1.49$, $p = 0.153$, $d_{rm} = 0.41$ (for the definition of d_{rm}, see Lakens, 2013). This is not contrary to prediction, as previous studies demonstrated that accuracy is not as sensitive to onset primacy as reaction time (Donaldson & Yamamoto, 2012, 2016). The similarly high accuracy in onset and offset detection ensured that EEG results were derived from equivalent numbers of trials in onset and offset conditions.

Reaction time. The mean reaction times across trials were 571 ms ($SD = 78$ ms, onset) and 630 ms ($SD = 54$ ms, offset), indicating that participants detected onsets faster than offsets, $t(20) = 4.79$, $p < 0.001$, $d_{rm} = 0.83$. These data align with prediction and show that onset primacy was present.

EEG Results

P300. The peak P300 amplitude values were derived from each participant, at each electrode in the ROI, for onset and offset trials separately. They were analysed by a 2 (onset, offset) × 3 (left, centre, right) repeated measures analysis of variance (ANOVA).

Descriptive statistics for the peak amplitude data are displayed in Table 1. Consistent with prediction, the P300 amplitude was higher in onset than offset conditions. The amplitude values also suggest that amplitude varied with electrode location, with the amplitude being

larger in the centre and right clusters than in the left cluster on average. These patterns can be seen in Figure 2 that shows the topographic distributions of the peak P300 amplitude, which also reveals that the highest peak amplitude occurred in the right cluster (at P4 in the onset condition; $M = 5.21$ μV, $SD = 5.24$ μV). Figure 4 displays mean ERP waveforms from each cluster that demonstrate the expected pattern of the P300, where the amplitude was consistently higher in onset trials than in offset trials.

The ANOVA examining the amplitude data revealed a significant main effect of change type, $F(1, 20) = 12.64$, $p = 0.002$, $\eta_G^2 = 0.050$, where onsets ($M = 3.30$ μV, $SD = 1.39$ μV) were greater than offsets ($M = 2.60$ μV, $SD = 1.11$ μV). There was also a significant main effect of electrode location, $F(2, 40) = 4.53$, $p = 0.017$, $\eta_G^2 = 0.061$. Follow-up pairwise comparisons (each with a Bonferroni-corrected α of 0.016) indicated that this main effect was primarily driven by the centre cluster ($M = 3.29$ μV, $SD = 1.68$ μV), which yielded significantly larger amplitude than the left cluster ($M = 2.40$ μV, $SD = 1.12$ μV), $t(20) = 2.88$, $p = 0.009$, $d_{rm} = 0.59$. The right cluster ($M = 3.16$ μV, $SD = 1.47$ μV) showed equally large amplitude to the centre cluster, $t(20) = 0.45$, $p = 0.661$, $d_{rm} = 0.08$, but the amplitude difference between the right and left clusters did not reach statistical significance, $t(20) = 2.20$, $p = 0.039$, $d_{rm} = 0.57$. The interaction between change type and electrode location was not significant in the ANOVA, $F(2, 40) = 0.37$, $p = 0.692$, $\eta_G^2 = 0.002$, suggesting that the effects of change type on peak amplitude similarly appeared in all three clusters of the electrodes.

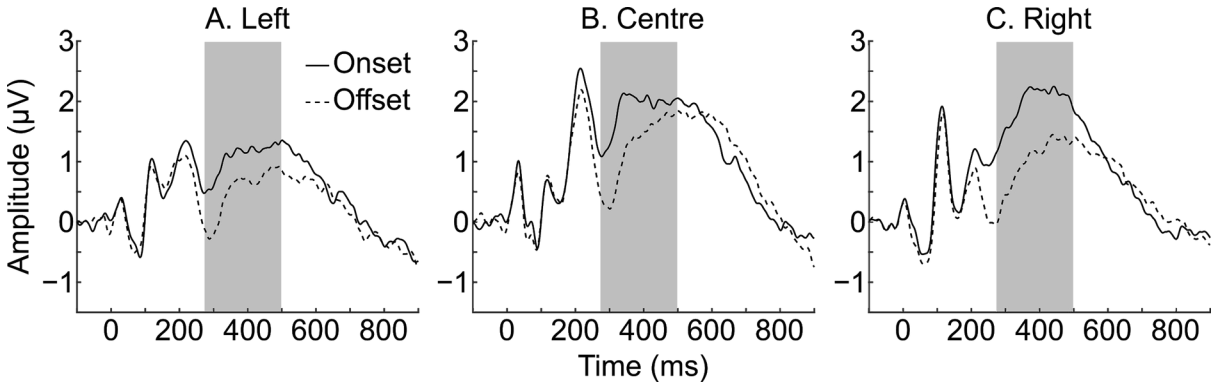

Figure 4. Mean P300 amplitude time series collapsed over participants (*N* = 21), displayed separately for each change type and each electrode cluster (A: left; B: centre; C: right). The shaded area indicates the time window from which peak amplitude was extracted for analysis (275–500 ms post change stimulus).

Table 1

Peak Amplitude of the P300 as a Function of Change Type and Electrode Location Collapsed over Participants (N = 21)

	Amplitude (μV)			
	Onset		Offset	
Location	*M* (*SD*)	95% CI	*M* (*SD*)	95% CI
Left	2.69 (1.45)	[2.03, 3.35]	2.11 (1.06)	[1.63, 2.60]
Centre	3.62 (2.03)	[2.70, 4.54]	2.96 (1.70)	[2.19, 3.74]
Right	3.59 (1.74)	[2.80, 4.38]	2.72 (1.28)	[2.14, 3.30]

Note. The following electrodes formed clusters in each location—left: CP1, CP3, CP5, TP7, P1, P3, P5, P7, PO3, PO7, and O1; centre: CPz, Pz, POz, and Oz; right: CP2, CP4, CP6, TP8, P2, P4, P6, P8, PO4, PO8, and O2.

ERP waveforms shown in Figure 4 suggest that the difference between onset and offset conditions in P300 amplitude might have sustained beyond the time window of interest (275–500 ms post change stimulus) that was set a priori on the basis of previous studies (Hopfinger & Mangun, 1998; Hopfinger & Maxwell, 2005; Koivisto & Revonsuo, 2003). To ensure that results were not biased by truncating the time window at 500 ms, the same analysis was run by computing amplitude measures using an extended time window (275–600 ms). The outcomes of this additional analysis did not differ from those reported above.

P100. The peak P100 amplitude values were analysed in the same manner as the P300 data. The topographic distributions of the peak P100 amplitude shown in Figure 3 suggest that while the difference between left and right electrode clusters was evident, onset and offset trials yielded a similar pattern of amplitude overall. However, descriptive statistics summarised in Table 2 show that the P100 amplitude was higher in onset than offset conditions, and in the right cluster than the left cluster. This can also be seen in Figure 5 that displays mean ERP waveforms from each cluster: Within the P100 time window (indicated by the grey shade), the onset and offset conditions differed subtly but consistently such that onsets evoked larger P100s in both clusters.

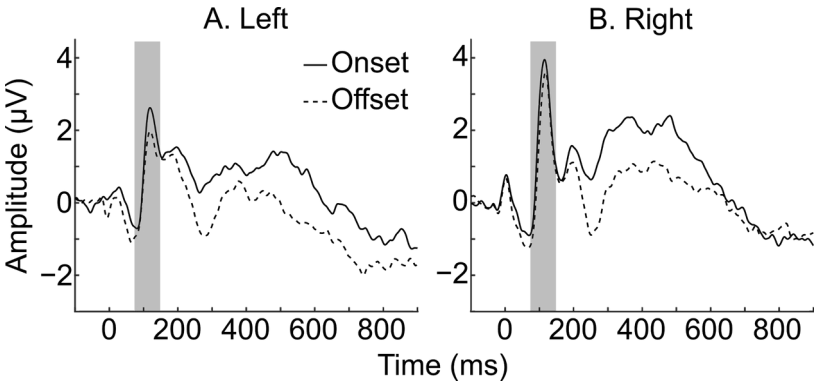

Figure 5. Mean P100 amplitude time series collapsed over participants ($N = 21$), displayed separately for each change type and each electrode cluster (A: left; B: right). The shaded area indicates the time window from which peak amplitude was extracted for analysis (75–150 ms post change stimulus).

Table 2

Peak Amplitude of the P100 as a Function of Change Type and Electrode Location Collapsed over Participants (N = 21)

	Amplitude (μV)			
	Onset		Offset	
Location	*M* (*SD*)	95% CI	*M* (*SD*)	95% CI
Left	3.22 (2.12)	[2.26, 4.19]	2.65 (1.89)	[1.79, 3.51]
Right	4.62 (2.50)	[3.48, 5.76]	4.12 (2.39)	[3.03, 5.21]

Note. The following electrodes formed clusters in each location—left: P7 and PO7; right: P8 and PO8.

The ANOVA examining the amplitude data did yield a significant main effect of change type, $F(1, 20) = 9.41$, $p = 0.006$, $\eta_G^2 = 0.015$, where onsets ($M = 3.92$ µV, $SD = 1.85$ µV) were greater than offsets ($M = 3.38$ µV, $SD = 1.90$ µV), suggesting that although the overall difference between onset and offset conditions was small, it consistently appeared across participants and electrodes. There was also a significant main effect of electrode location, $F(1, 20) = 9.46$, $p = 0.006$, $\eta_G^2 = 0.097$, showing that amplitude was greater in the right cluster ($M = 4.37$ µV, $SD = 2.37$ µV) than in the left cluster ($M = 2.93$ µV, $SD = 1.84$ µV). The interaction between change type and electrode location was virtually non-existent, $F(1, 20) = 0.02$, $p = 0.887$, $\eta_G^2 < 0.001$, which is in line with the above observation that the P100 was consistently larger during onset detection than offset detection in both electrode clusters.

Discussion

The current study aimed to test the default mode hypothesis (Donaldson & Yamamoto, 2016) by examining whether behavioural findings of onset primacy were reflected on a neural level, as indicated by EEG recordings during a change detection task. The default mode hypothesis postulates that a larger amount of processing resources is allocated to onset detection than offset detection under the initial mode of attention, leading unbiased observers to perform trials involving the detection of onsets with greater neural efficiency than trials involving the detection of offsets. On the basis of previous studies of dual-task performance (Isreal et al., 1980; Mangun & Hillyard, 1990; Nash & Fernandez, 1996; Sirevaag et al., 1989; Strayer & Kramer, 1990; Wickens et al., 1983), the amplitude of the P300 ERP was hypothesised to be an index of this efficiency. Specifically, it was predicted that the P300 would have a higher amplitude in onset trials compared to offset trails, across the specified time-window (275–500 ms post change stimulus) and ROI (temporal, parietal, and occipital regions), reflecting the relative abundance of processing

resources for detecting onsets in the change detection task.

The prediction was confirmed, as peak amplitude of the P300 was larger in onset than offset conditions, while participants detected onsets more quickly than offsets. Accuracy of change detection was equivalent in onset and offset trials, indicating that the quicker detection of onsets was not a mere consequence of speed-accuracy trade-offs. It should be noted that these findings were obtained when the onset and offset trials were well equated—that is, onsets and offsets occurred equally often on the same objects and at the same locations across the trials, and the participants were instructed to respond to the location of a change, not to the type of change. Given the design of the task, it was very likely that the participants carried out the trials without shifting their attentional priority to specifically detecting onsets or offsets. Nevertheless, onsets were still detected faster and this behavioural performance was associated with the greater P300 amplitude, strengthening the interpretation that onset primacy is a result of the attentional system's default mode in which the allocation of processing resources is biased in favour of onset detection.

In addition to specifically supporting the default mode hypothesis, the present results are more broadly consistent with previous studies on change blindness and detection. Using tasks in which changes were difficult to perceive, these studies found that the P300 was evoked following successful detection of change (Koivisto & Revonsuo, 2003; Niedeggen, Wichmann, & Stoerig, 2001). In the current study, not only onsets but also offsets elicited the P300 when their location was correctly indicated (Figure 4). Because the location judgments were made with very high accuracy, this study alone does not clarify whether the P300 is uniquely associated with correct recognition of change—that is, no reliable EEG data were available as to whether the P300 was absent when the changes were incorrectly localised or entirely missed. However, combined with the previous studies, these findings suggest that the P300 reflects neural processes that have to do with establishing conscious awareness of a

visual stimulus and making decisions about the detected stimulus (Eimer & Mazza, 2005; Turatto, Angrilli, Mazza, Umiltà, & Driver, 2002).

Although this study was carried out without forming any predictions about the effect of electrode location, differences in amplitude did emerge as a function of electrode location for the P300 component. Specifically, the amplitude was overall higher across electrodes in the midline and in the right hemisphere than those in the left hemisphere, regardless of change type. Moreover, there was a distinct peak in the right hemisphere (at the P4 electrode) in the onset condition (Figure 2). These amplitude patterns are consistent with results from previous studies in which the P300 was evoked in midline electrodes by appearing and disappearing visual targets (Eimer & Mazza, 2005; Hopfinger & Mangun, 1998, 2001), and also with the common view that the right hemisphere tends to be dominant in the performance of tasks involving visuospatial attention (Corballis, 2003; Mesulam, 1999; Shulman et al., 2010). This account is supported by EEG studies that examined performance across visuospatial tasks and identified similar P300 lateralisation (Alexander et al., 1995; Makeig et al., 1999).

The present study assessed the P100 in addition to the P300 so that it could inform the debate about the origin of onset primacy. One account is that sensory transients created by a newly appearing object increase its perceptual salience, making the onset particularly noticeable (Franconeri et al., 2005; Hollingworth et al., 2010; Miller, 1989; Theeuwes, 1994). The other account is that the appearance of a new object entails cognitive operations such as formation of a mental representation of the object, which give the onset preferential processing (Boot et al., 2005; Cole et al., 2004; Davoli et al., 2007; Yantis, 1993). Although this study was not designed to perform a strict test of the two accounts, it afforded an opportunity to provide some input into the debate because the sensory account predicts that the P100, as an early sensory ERP component, could be differentially sensitive to onsets and

offsets—namely, its amplitude would be greater during onset detection than offset detection. On the other hand, the cognitive account predicts that the difference between the two types of change should emerge later in cognitive ERPs (e.g., the P300). Data from the experiment showed that P100 amplitude differed between onset and offset conditions in the predicted direction, indicating that early visual processes did contribute to onset primacy as observed in this study. The effect of change type on P100 amplitude was small ($\eta_G^2 = 0.015$), calling for caution in interpreting it as full-fledged support for the sensory account. By contrast, change type exerted a larger effect on P300 amplitude ($\eta_G^2 = 0.050$), suggesting that higher-order cognitive processes played a more prominent role in giving rise to onset primacy in this experiment. Nevertheless, the current results offer a new perspective to the debate by supporting both of the accounts to some extent. That is, they propose a shift in the direction of the debate from pitting the two accounts against each other to developing an understanding of how the sensory and cognitive processes combine to produce onset primacy (Atchley, Kramer, & Hillstrom, 2000).

To elaborate on the role of higher-order cognitive processes in onset primacy, it is important to note that when onsets and offsets were presented as non-informative and task-irrelevant stimuli so that observers had no reason to direct their attention to them (i.e., the onsets and offsets were perceived largely in an exogenous fashion), they did not elicit the P300 at all (Hopfinger & Maxwell, 2005). This finding corroborates the notion that the P300 observed in the present study represented higher-order cognitive processes involved in the change detection task. Given that the P300 waveforms differed in amplitude but resembled in overall shape between onset and offset trials (Figure 4), it was probable that the P300 ERPs were generated from processes that were commonly at play during onset and offset detection, and the two change types only varied in the extent to which these processes were engaged. It then follows that creation of a new mental representation of an appearing object was not the

primary cause of the evoked P300 because only the detection of onsets entailed this operation. Instead, a more likely possibility is that the P300 stemmed from deployment of attention to onsets and offsets, which was necessary for detecting both onsets and offsets, and the P300 amplitude difference reflected the fact that this deployment was more preferentially done for onsets than offsets. In other words, the current results suggest that as a neural correlate of onset primacy, the P300 chiefly captures component processes in which more attention is given to onsets than offsets in an endogenous manner.

Given the current findings that the P300 amplitude reflects neural processes underlying onset primacy, future research can utilise this ERP pattern as a neural index of how firmly observers' attentional priority is set to the default onset-detection mode. For example, by measuring this ERP component while observers are being trained to prioritise detection of non-onset events (e.g., offsets), it may be possible to quantify the degree to which this training is effective (Donaldson & Yamamoto, 2016). Similarly, the same approach can be taken for exploring whether the default mode hypothesis persists in populations that may already be well practised in alternate modes of change detection, such as lifeguards or child-care workers. A novel study by Laxton and Crundall (2017) suggests that lifeguards do indeed differ from the general population in their ability to detect change, as indicated by an experiment that required the detection of 'drownings' in a crowded swimming pool. Measuring the P300 while these experts detect offsets can be useful from both theoretical and practical points of view—it not only helps further examine whether the P300 works as a neural marker of onset primacy, but also has a potential for providing an objective measure of how well the experts adopt a non-default attentional mode for performing their professional duties.

Future research could also explore other differences observed between onset and offset conditions, which were not investigated in the present study due to the lack of clear

hypotheses. For instance, the averaged ERP waveforms in Figure 4 show an increased positivity for onsets compared to offsets around 200 ms post change stimulus. The difference between the conditions was statistically significant (Supplementary Results). Given its latency, the positivity may be reminiscent of the P200, or P2, ERP component. However, the visually evoked P200 tends to appear in anterior scalp sites (Luck & Hillyard, 1994; Luck & Kappenman, 2012), whereas the ROI represented in Figure 4 consisted of posterior sites. Figure S1 in Supplementary Results plots topographic distributions of the ERP, clarifying that there was no anterior positivity in this study. Hopfinger and Maxwell (2005) observed a similar posterior positivity centred around the Pz electrode when they presented onsets (but not offsets) as distractors. Since it was absent during offset detection, they suggested that this positivity might be related to creation of the mental representation of a new object. This interpretation is not applicable to the pattern shown in Figure 4 in which offsets also elicited the P200-like ERP to a lesser, but still distinct, extent. Generally, processes underlying positive deflections in this latency range have not been well understood (Luck, 2012; Woodman, 2010), making it difficult to interpret this pattern.

Figure 4 also shows negative deflections that are greater for offsets than onsets around 300 ms post change stimulus. The difference between the conditions was statistically significant (Supplementary Results). It is not uncommon to observe such negatively oriented waves in paradigms that elicit the P300 (Donchin, Ritter, & McCallum, 1978; Folstein & Van Petten, 2008). For example, in oddball paradigms in which deviant targets are presented among a series of standard stimuli, the targets evoke both the P300 and a negative potential that immediately precedes the P300 in parietal, temporal, and occipital electrodes (i.e., N200 or N2; Ritter, Simson, & Vaughan, 1983; Simson, Vaughan, & Ritter, 1977). Although the negative deflections observed in this study did not always go into negative polarity (Figure 4), it is possible that this pattern occurred because the negative waves were overridden by the

subsequent P300 before they fully manifested themselves (Luck, 2012). Notably, the negative potential that co-occurs with the P300 is sensitive to the omission of a stimulus—when the 'target' in these paradigms is created by not presenting any stimuli, it still generates negative potentials at posterior electrodes in a similar latency range (Simson, Vaughan, & Ritter, 1976). Thus, the greater negative deflections in offset trials are possibly related to participants' responding to the absence of an object in these trials. If further differences were established, both theoretically and empirically, between the onset and offset conditions in these other ERPs, they would lead to a deeper understanding of the mechanisms of onset primacy.

Finally, it may be worth noting what steps can be taken to advance this research. Since this was the first study in which Donaldson and Yamamoto's (2012) onset primacy paradigm was combined with EEG, participants' behavioural responses were collected simultaneously with EEG recordings. This was to ensure that any patterns of EEG data were observed while onset primacy was actually taking place. Without the behavioural responses, it would have been necessary to assume that participants were detecting onsets more efficiently than offsets, but it is an open question whether onset primacy occurs in the same way when no overt responses to the changes are required. Thus, in this initial investigation, there was a clear benefit of obtaining the behavioural responses. However, it inevitably came with some drawbacks. Most notably, the EEG data reflected not just perceptual and cognitive processes inherent in onset primacy but also motor processes involved in response preparation and execution. Presumably, these motor processes were commonly engaged in onset and offset trials, and therefore their effects should not have caused a fundamental problem in the comparison between the two types of trials. Nevertheless, to isolate EEG signals that are unique to onset primacy itself, it would be useful to conduct experiments in which participants do not make any behavioural responses while they view onset and offset

stimuli. Such no-response paradigms are now justified because the present study has provided several EEG markers of onset primacy that future experiments can look for—the P300 ERP in particular. These experiments would offer further clarification of how onsets and offsets modulate the EEG signals, thereby delineating onset primacy at both cognitive and neural levels.

Acknowledgements

The authors thank Yasmin Allen-Davidian for cooperation in participant recruitment.

Open Practices Statement

Data from the present study are available at https://osf.io/jnq27. The experiment was not pre-registered.

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