Attention and prediction modulations in expected and unexpected visuospatial trajectories.

Authors: Kristen S. Baker[1], Alan J. Pegna[2], Naohide Yamamoto[1], & Patrick Johnston[1]

[1] School of Psychology and Counselling, Faculty of Health, Queensland University of Technology, Brisbane, QLD, Australia

[2] School of Psychology, Faculty of Health and Behavioural Sciences, University of Queensland, Brisbane, QLD, Australia

Corresponding author

E-mail: kristen.baker@hdr.qut.edu.au (KB)

Abstract

Humans are constantly exposed to a rich tapestry of visual information in a potentially changing environment. To cope with the computational burden this engenders, our perceptual system must use prior context to simultaneously prioritise stimuli of importance and suppress irrelevant surroundings. This study investigated the influence of prediction and attention in visual perception by investigating event-related potentials (ERPs) often associated with these processes, N170 and N2pc for prediction and attention respectively. A contextual trajectory paradigm was used which violated visual predictions and neglected to predetermine areas of spatial interest, to account for the potentially unpredictable nature of a real-life visual scene. Participants (*N*=36) viewed a visual display of cued and non-cued shapes rotating in a five-step predictable trajectory, with the fifth and final position of either the cued or non-cued shape occurring in a predictable or unpredictable spatial location. Results showed both enhanced N170 and N2pc amplitudes to unpredictable compared to predictable stimuli, and furthermore the N170 was larger to cued than non-cued stimuli. In accordance with previous research these results suggest the N170 is in part a visual prediction error response with respect to higher-level visual processes, and furthermore the N2pc may index attention reorientation. The results demonstrate prior context influences the sensitivity of the N170 and N2pc electrophysiological responses. The findings suggest attention boosts the precision of prediction error signals, furthering our understanding of how expectation can modulate prediction in selective visuospatial attention. Implications of this research provide insight into how prior context in visuospatial motion guides attention in a visual scene.

Introduction

Humans perceive their visual surroundings as a complete picture of the environment. Yet, the cognitive processes involved in correctly and rapidly processing all incoming stimuli in the context of prior knowledge continues to be debated. Two key characteristics of the visual environment are considered to influence successful visual perception. Attention involves enhancing task-relevant information in the environment, whilst simultaneously suppressing irrelevant information. In vision, the direction of attention refers to the prioritisation of visual objects, features or regions of space which are relevant to the viewers' internal and external goals. Prediction is another key component in visual orientation. The term prediction in cognition refers to the increased probability of a stimulus appearing based on prior context. Predictive coding models of perception stress the interplay of top-down and bottom-up signals in resolving percepts. Such models suggest incoming stimulus input is constantly checked against predicted inputs; where a mismatch occurs, prediction error signals inform the updating of future predictions [1, 2]. In visual processing, this theory proposes an internal model of a scene is generated in higher order visual cortical areas, which receive feedback from actual visual input, turning the incorrect predictions into error signals. Subsequently, this leads to continuously updated predictions in a recursive hierarchical fashion [1, 3].

The relationship between prediction, attention, and prioritisation of information continues to be debated. As described by Jiang and colleagues [4], two differing models propose attention either increases or filters out prediction errors. The model whereby attention increases prediction errors proposes the brain seeks to enhance statistical learning by increasing associations in stimuli relationships, and hence attention acts to enhance the distinction between expected and unexpected stimuli (i.e. through prediction error signals)

[4]. By this model attention functions by increasing the association between stimuli, with the intention of reducing the future occurrence of prediction error [4]. Attention operates to direct resources towards minimising future prediction error signals so the brain can preserve resources by reducing surprise when faced with similar situations in future. This is supported by studies involving multivariate pattern classifiers in fMRI [4], surprising visual stimuli using EEG [5], as well as in auditory stimuli using EEG scalp and source data [6]. An alternative model whereby prediction errors are filtered out proposes the primary function of attention is to enhance relevant information and simultaneously suppress irrelevant information, hence task irrelevant and unpredictable information is suppressed [4]. According to this model if expected and relevant information is presented it elicits the largest amount of neural activity as attention functions by increasing the precision of predictions, rather than enhancing prediction errors. The distinction between predictable and unpredictable stimuli is dampened irrespective of the predictability of the stimuli (i.e. reduced prediction error signals) as attention reverts attenuation of predictable stimuli [7]. If unexpected and irrelevant information was presented, attention functions by suppressing this information in order to continue enhancing processing of the task-relevant stimuli. Furthermore, if unexpected but relevant information is presented, attention suppresses prediction errors in order to continue increasing focus on the task relevance of the stimuli, as this outweighs the unpredictable status of the stimuli. This theory is supported by evidence of greater activity in the visual cortex to predictable compared to unpredictable stimuli [7], a greater N1 to predictable attended compared to unpredictable attended and unattended auditory stimuli [8], and a simulation model demonstrating attention enhances expected featured-tuned neuronal firing [9].

A prominent approach to investigate cognitive mechanisms is to measure electrophysiological recordings time-locked to stimulus onset, termed event-related potentials

(ERPs). Here we consider two widely studied visual ERPs – the N170 and the N2pc. The N170 has been of interest with respect to the processing of faces, and as the first ERP component indexing "higher-level" vision [10]. Recent evidence has shown the N170 may be strongly modulated by violated expectations [11-14]. The N2pc, a lateralised difference wave potential occurring slightly later than the N170, has been traditionally associated with spatially selective attention, and is thought to index processes relating to prioritised processing of attended stimuli. Since recent work has shown the earlier occurring N170 is strongly modulated by predictions, here we address the question of whether the attention relevant N2pc might show similar sensitivity.

N170

The N170 is a negative deflection of the ERP response observed post stimulus onset at approximately 150 to 200 milliseconds (ms) in the lateral occipital region [15]. Earlier research examines the N170 in indexing the encoding of faces, demonstrated by studies investigating processing of facial category, configuration and emotional expression [16-19]. Other researchers have argued the N170 is not exclusively face-specific [20], with recent evidence using face stimuli in addition to shapes, bodies, and nude statuettes demonstrating the N170 could be an index of mismatches between prior expectations and actual stimulus input in higher-level vision [12, 13]. Johnston and colleagues [12] demonstrated this in experiments whereby participants observed sequences of images in either predictable or unpredictable conditions, with the final step of unpredictable conditions violating the established order of the sequence of preceding stimuli. Investigating both EEG and magnetoencephalography (MEG) responses, the N170 and M170 were larger in amplitude for unpredictable versus predictable stimulus onsets, irrespective of object category. Furthermore, N170 amplitudes to unexpected stimuli have been found to be enhanced in a

dose dependent manner, based on the strength of accumulated evidence for the predicted outcome, and the degree to which the observed stimulus differs from that outcome [13]. These studies support the idea the N170 is in part a visual prediction error signal reflecting a conflict between internally generated predictions and actual sensory input [12, 13]. In light of the recent findings of the N170 modulated by prediction error processes, and given the close proximity in electrode sites (N170 often P7 and P8, N2pc often PO7 and PO8), and time windows (N170- peaks at 170ms, N2pc generally varies between 180-300ms) of the components, ERPs are an appropriate choice investigating prediction and attention in visual stimuli.

N2pc

The N2pc is a component considered to index attentional processes. The N2pc has been observed to salient lateralised targets in competition with distractors, in the cerebral hemisphere contralateral to the visual field of the target. It is calculated as a contralateral-minus-ipsilateral difference waveform, with the resultant difference waveform indicative of the lateralised cognitive activity [21]. Initial evidence for the N2pc elicited to targets came from studies which used different combinations of simple visual objects (such as letters, shapes and colours) with a target and distractor in opposing visual fields. Despite the presence or absence of distractors the N2pc was elicited contralateral to target stimuli (e.g. [22-24]. This suggested the N2pc is more dependent on target characteristics. Whilst the N2pc was initially investigated in basic visual processing [21, 22, 25], more recently the N2pc has been identified in studies of individual differences in attention as broad as rejection cues in low self-esteem [26], detection of threat in social anxiety [27, 28], face processing after exposure to violent video games [29], and fear related phobias [30].

Since the discovery of the N2pc a prominent view is this component reflects suppression of neighbouring distractors in favour of enhancing identification of the target. This is analogous to the spotlight metaphor of spatial attention where information in the 'beam' of the spotlight receives enhanced processing [31]. The N2pc component is thought to index the operations of a spatial filter enhancing processing of a particular location in space whilst inhibiting the interference of surrounding distractors. This is supported by studies in which the N2pc was elicited to prospective cues of targets [32], larger to repeated rather than novel arrays [33], and expected target locations marked by placeholder objects [34]. According to this idea, it would be expected the N2pc would be larger to a cued stimulus landing in a predictable region as a filter has pre-emptively been set up to accommodate expected processing in this location.

A contrasting view considers the N2pc to reflect the reorientation of attention. In one study [35], two targets were shown in quick succession with the second target (T2) appearing in the same or opposite visual field of the first target (T1). An attenuated N2pc was found to T2 when it followed the same visual field as T1, however when T2 was in the opposite field a second N2pc occurred. The N2pc has also recently been found to be elicited to orientation singletons which swap as target and distractor between trials [36]. This evidence suggests the N2pc is reflective of the reorientation of attention rather than an enhancement of sustained target processing in a predetermined spatial location. The overall evidence demonstrates the N2pc is dependent upon varying characteristics wherein attention is aimed.

The present study

The present study was designed to determine the influence of expectancy violations on modulation of prediction and attention in visual processing by analysing responses of the N170 (prediction) and N2pc (attention). To accurately measure discrete early visual temporal

processes, our paradigm combined predictable and unpredictable visuospatial trajectories. Participants viewed a five-step sequential trajectory of a cued shape and non-cued shape, which concluded in a predictable or unpredictable spatial location. This allowed an extrapolation of processes indexed by separable ERPs- the N170 as a prediction error signal and the N2pc as a marker of predictive spatial filtering or attention reorientation.

It was expected enhanced N170 amplitudes would exist for unpredictable compared to predictable conditions. In addition, if enhanced spatial filtering elicits the N2pc component enhanced amplitudes would be observed to predictable cued shapes compared to unpredictable cued shapes. On the other hand, if the N2pc is modulated by attention reorientation elicited by expectancy violations enhanced N2pc amplitudes would exist for unpredictable compared to predictable conditions.

Method

Participants

Data were initially collected from 40 participants; however, four participants were excluded from further analyses due to artefacts in the overall recording or in the electrodes of interest. Thus, 36 participants remained in the sample aged from 17-60 years (*M* = 25.25, *SD* = 9.29, 26 females, 29 right-handed). Participants received a gift card or university course credits for participation. All participants had normal or corrected-to-normal vision, and no history of neurological conditions. Ethical approval was granted by Queensland University of Technology's Research Ethics Committee.

Stimuli and paradigm

For each trial participants viewed a visual display of three stimuli of three black two-dimensional shapes (circle, square, and arrow), on a HP monitor with screen resolution of 1920x1080 pixels. The visual display consisted of an arrow positioned in the centre, pointing at one of the simultaneously presented shapes. The stimuli were arranged such that the circle and square were displayed in one of 12 different possible positions in a circular array. The arrow was always centrally fixed but varied in orientation in 30-degree increments, dependent on the shape it was pointing to. The arrow stimuli were presented centrally subtending approximately 1.9° of visual angle, with circle and square stimuli subtending 3°, offset by approximately 1.8° from the central fixation point. The square stimuli measured 225 x 225 pixels, the circle circumference 225 pixels, and the arrow stimuli 50 (length) x 24 (width) pixels. Each sequence was made up of five trials whereby the first trial began with the cued shape and non-cued shape appearing at any of the 12 possible positions, followed by four additional steps in a clockwise or anticlockwise trajectory circling around the arrow. The orientation of the arrow varied such that it always pointed at the position of the cued shape for each of the five steps in the sequence, except for the fifth step in unpredictable conditions whereby the arrow continued in the expected trajectory and the cued shape or non-cued shape moved back one position. Arrows cues have been found to automatically orient attention, even when being uninformative or incongruent to the correct location of cues [37, 38]. Hence, the cued shape in each sequence was considered the shape the arrow was pointing to, whereas the non-cued shape was the opposing shape the arrow was not pointing to. When the circle was the cued shape, the square was the non-cued shape and vice versa. As such there were equal presentations of circles and squares as both cued and non-cued shapes. Visual stimuli at the final step was situated with the cued shapes in the vertical midline and the non-cued shapes laterally, or vice versa (cued lateral, non-cued midline). A duplicate set of

images with red dots placed in the centre of the arrow were produced for red dot trials, which were to ensure participant's gaze was maintained centrally. These trials appeared randomly in approximately 10% of all trials, constituting 48 trials out of 480 trials overall. Any participant who did not respond correctly to over 90% of red dot trials was excluded as indication of insufficient attention to the task. Red dot trials were separately coded and then subsequently discarded during EEG pre-processing.

There were four conditions termed predictable cued, unpredictable cued, predictable non-cued, and unpredictable non-cued. These were named with respect to whether the final location of one of the shapes in the sequence was in a lateralised predicted or unpredicted position. Each condition was equally divided on rotation direction (clockwise or anti-clockwise), lateralised endpoint shape status (cued or non-cued), and endpoint position (left or right visual field). The four conditions were equated in low-level visual properties of the two shapes in the critical final trial, such that any differences in ERPs could be attributed to the preceding steps. There were 480 five-trial sequences in total, consisting of 108 sequences per condition and 48 red dot sequences. All conditions were presented randomly per participant. Each trial in the sequence was presented for 500 ms, 0 ms intertrial interval, and a 500 ms intersequence interval. Refer to Fig 1 for a visual depiction of each of the conditions.

Fig 1. Examples of all conditions.

Example of one sequence for each of the four conditions. Stimulus duration as indicated, 0 ms intertrial interval, 500ms intersequence interval. Conditions are named with respect to lateralised shape status in the fifth trial, as outlined in red. All conditions were equal in low-level visual properties of the two shapes (excluding the arrow) in the critical final trial.

Procedure

Participants were seated approximately 60cm in front of the computer screen, fitted with the EEG cap and instructed to watch the sequence of images appearing on the screen. EEG data were recorded from 64 channels, using the international 10-10 system for electrode placement. Participants viewed a display of 480 sequences with each sequence consisting of the presentation of five shape trials. Participants viewed four blocks of 120 trials each, with a break in between each block whereby they initiated the next block via button press. To ensure gaze was fixated centrally, participants were informed to fixate on the centre of the computer screen and respond via button press if a red dot appeared in the centre of the arrow.

Data analysis

A Biosemi 64 channel amplifier recorded electrophysiological data at a sampling rate of 1024 Hz, using a common reference (CMS/DRL). EEG data was displayed to the experimenter on the BioSemi acquisition program, Actiview [39]. Electrode offset was maintained below 20 mV. Pre-processing of EEG data was performed with the software BrainVision Analyzer 2 [40]. Following this, ERP waveform processing was undertaken with MATLAB [41] and descriptive/inferential statistics with SPSS software [42].

Pre-processing

A band-pass filter between 0.1 to 30 Hz (24db/octave slope) with a notch filter of 50Hz was applied. Artefact rejection was performed by applying criterion of Min-Max fluctuations of >500µv in 100ms intervals, marking 100ms before and 100ms after the event. Visual inspection of the raw EEG data was carried out and noisy electrodes were interpolated using the spherical spline interpolation method. Due to excessive noise and EEG recording artefacts, the aforementioned four participants were excluded at this stage with 36 remaining participants. Eye-blinks were identified and rejected with BrainVision Analyzer's automated

ocular correction procedure using independent components analysis. Data were re-referenced to an average electrode. Next, data were segmented into 2600ms time-locked epochs, beginning 100ms pre the first stimulus onset in the sequence and ending 500ms post final stimulus onset. Separate epochs were created for each condition as to whether the final stimuli were predictable or unpredictable, cued or non-cued, and lateralised shape ending in the left or right visual field. Next, an average of each epoch was generated. Due to the absence of an interstimulus interval final averaged waveforms were baseline corrected to the time period of stimulus onset of -150ms to 0ms of the average of both the fourth and fifth step in the sequence [12]. Grand average ERP waveforms were then generated from activity at electrode clusters for each of the four conditions, also divided by visual field, resulting in eight separate grand averages. Electrode clusters consisted of channels P5, P7, PO3, and PO7 for the left hemisphere (LH), and electrodes P6, P8, PO4, and PO8 for the right hemisphere (RH). These electrodes were chosen based on a review of previous literature of typical sites of maximal N170 and N2pc responses [12, 15, 28, 43, 44]. N170 responses were measured by pooling activity for both visual fields irrespective of the location of the final stimuli, for each condition. N2pc components were generated by subtracting activity in the electrode cluster of the corresponding ipsilateral hemisphere to stimulus presentation from activity in the contralateral hemisphere, resulting in a difference waveform.

Results

Participants were included if they correctly identified >90% of red dot sequences. No participants were excluded on this basis, thus 36 participants remained. The remaining 36 participants achieved an accuracy rate of 98.43% correctly identifying red dot trials, with a mean reaction time of 497.64ms (*SD* = 12.97ms). EEG data were comprised of ERP waveforms at the fifth and final trial in each sequence, for each of the four conditions. The

N170 peak-to-peak amplitude was measured by subtracting the N170 inflection points maxima from the P1 inflection points minima, as per previous studies [11, 13]. The peak-to-peak measure provides a valid reference to measure the N170, unencumbered by differences attributed to another peak when there is no difference in P1 [45]. N170 amplitudes were measured in the time window 140ms to 210ms, and the P1 80ms to 130ms. The N2pc component was measured as the average amplitude between 200ms to 300ms post final stimulus onsets, as the difference wave (contralateral electrode cluster minus ipsilateral electrode cluster). All amplitudes reported herein were measured in microvolts (μV).

To investigate the hypotheses two omnibus ANOVAs were performed to investigate the N170 (main effect of expectation), and the attention reorientation hypothesis of N2pc (main effect of expectation). For investigating the hypothesis of enhanced spatial filtering, if a significant expectation and shape status interaction occurred in the hypothesized direction (increased N2pc amplitudes for predictable compared to unpredictable conditions), then planned comparisons would occur. However, this follow-up would only be necessary if the interaction is significant in the N2pc ANOVA, and in the direction proposed by the filtering hypothesis. Cook's distance was calculated to identify potential outliers, with no outliers identified. The assumption of sphericity was met for both ANOVAs.

N170

A 2 x 2 repeated measures ANOVA was conducted with factors of expectation (predictable and unpredictable), and shape status (cued and non-cued). There was a significant main effect of expectation, $F(1,35) = 8.62$, $p = .006$, $\eta_p^2 = .198$. The N170 amplitude was significantly larger (i.e. more negative) to unpredictable trials ($M = -2.29$, $SE = .24$) compared to predictable trials ($M = -2.02$, $SE = .20$). There was a significant main effect of shape status, $F(1,35) = 7.70$, $p = .009$, $\eta_p^2 = .180$, with cued trials eliciting a larger

N170 amplitude (M = -2.26, SE = .23) compared to non-cued trials (M = -2.05, SE = .21). The interaction effect was not significant, $F(1,35) = 0.37$, $p = .548$, $\eta_p^2 = .010$. These results indicate a larger N170 was elicited by lateralised cued shapes than lateralised non-cued shapes, and by unpredictable trials than predictable trials, however the effect of (un)predictability on N170 was not greater when it was a cued than non-cued shape. Fig 2 illustrates the grand averaged N170 scalp topographies and grand averaged waveform amplitudes.

Fig 2. Grand average N170 topographies and amplitudes.

A) Scalp topographies across all electrodes during the N170 time window for all conditions. From top to bottom: top, right, left, and back view. Heat map scales were set at -1μV minimum and 1μV maximum for display purposes. B) Grand averaged mean N170 amplitudes (μV) for all conditions pooled across left and right hemisphere electrode clusters. Error-bars denote 95% Confidence Intervals calculated for repeated measures using the Cousineau-Morey Method [46]. C) Grand averaged waveforms pooled across hemispheres for all four conditions. PN= predictable non-cued, PC= predictable cued, UN= unpredictable non-cued, and UC= unpredictable cued trials.

N2pc

A 2 x 2 repeated measures ANOVA of the N2pc component was conducted with factors of expectation (predictable and unpredictable), and shape status (cued and non-cued). There was a significant main effect of expectation, $F(1, 35) = 4.98$, $p = .032$, $\eta_p^2 = .125$. The N2pc amplitude was significantly larger (i.e. more negative) to unpredictable trials (M = -.10, SE = .08) compared to predictable trials (M = .19, SE = .12).There was no significant main effect of shape status, $F(1, 35) = 0.023$, $p = .881$, $\eta_p^2 = .001$, and no significant interaction effect $F(1, 35) = 1.48$, $p = .232$, $\eta_p^2 = .041$. These results demonstrate larger N2pc

components occur to unpredictable conditions, but this is not contingent upon cued or non-cued status. Overall, these results suggest unpredictable shapes elicit a larger N2pc response, indicating the N2pc is modulated by reorientation of spatial attention, rather than pre-emptive spatial allocation. Refer to Fig 3 for visual depictions of grand averaged ERP difference waveforms of the N2pc for all conditions.

Fig 3. Grand average N2pc amplitudes.

A) Grand averaged N2pc amplitudes pooled across hemispheres for all conditions (pooled contralateral activity minus pooled ipsilateral activity). B) Grand averaged ERP amplitudes (μV) of N2pc difference waves for all four conditions. Error-bars denote 95% Confidence Intervals calculated for repeated measures using the Cousineau-Morey Method [46]. PN= predictable non-cued, PC= predictable cued, UN= unpredictable non-cued, and UC= unpredictable cued trials.

Discussion

The aim of the present study was to investigate modulations of prediction and attention in visual processing using expectancy violations by analysing responses of the N170 (prediction) and N2pc (attention). We investigated the relationship between non-cued and cued stimuli using ERPs considered responsible for indexing these cognitive processes. It was expected the N170 would be larger for unpredictable cued and non-cued trials compared to predictable cued and non-cued trials, indicative of a higher-level prediction error neural response. It was also hypothesised if the N2pc was reflective of predictive spatial enhancing then a larger N2pc amplitude would be observed to predictable cued conditions compared to unpredictable cued conditions, indicative of setting up a pre-emptive attention filter. However, if the N2pc was reflective of attention reorientation then a larger N2pc would be

found to unpredictable conditions compared to predictable conditions. The hypothesis for the N170 was supported as larger amplitudes were identified for unpredictable stimuli compared to predictable stimuli. Furthermore, the N2pc, like the N170, was found to be larger to unpredictable stimuli compared to their predictable equivalents as primed by prior motion trajectories, supporting the attention reorientation view of the N2pc.

The results of the N170 being larger in unpredictable conditions compared to predictable conditions supports the view the N170 is reflective of a prediction error signal [12]. This study also demonstrates the N170 is attention dependent too, with the larger N170 found to cued stimuli and the smaller to non-cued stimuli. It must be noted there was only a single identifying feature in our study (spatial region) as opposed to multiple features (e.g. colour, orientation, or size) which could influence the sensitivity of the amplitude. Hence, a possible direction for future research would be to further investigate the amount of violations dependent on features on the N170 response, to lend support to the view of the N170 as a higher-level visual prediction error signal.

The results of this study for the N170 lend support to the notion attention promotes prediction errors [4, 5, 6]. The N170 was greater when stimuli were attended to, demonstrated by a significant main effect of shape status indicating in this study attention has promoted neural processing. Also, the N170 was enhanced to unpredictable compared to predictable stimuli which further supports the notion the brain seeks to enhance awareness of prediction errors by strengthening signals which indicate the presence of the errors to facilitate a reduction in surprise in future similar situations. Although recent research has examined the relationship among prediction and attention, further research is necessary to examine various subcomponents of attention such as spatial attention, and its influence by established neural expectations. This is necessary to further investigate the predictive coding theory proposed of the brain.

For the N2pc results, the larger N2pc component to unpredictable conditions compared to their predictable counterparts indicates the N2pc is responsible for the reorientation of attention rather than pre-allocation of spatial attention. The N2pc component was attenuated in predictable conditions primed by four prior steps. This counteracts the notion the N2pc is modulated as an expectancy filter where pre-emptive strategies elucidate a prioritisation of an upcoming spatial location. These findings are consistent with other studies which found attenuation of the N2pc in a primed location [35], and reorientation to stimuli of alternating salience status between target and distractor [36]. This demonstrates prediction plays an important role in the elicitation of the N2pc, which should be taken into consideration in future studies. This reiterates the importance of controlling the prior context and priming existent in paradigms which could influence the electrophysiological activity in cued and non-cued shapes recognition. Future research could also investigate dosage of prediction violations on the N2pc component, as previously found to vary for the N170 component [13]

It could be argued the non-significant main effect of shape status between cued and non-cued trials at the N2pc component suggest the stimuli were not differentiated by attentional relevance. However, there was a main effect of shape status with the N170 which demonstrates differences were noticed between cued and non-cued stimuli. Differences in cued and non-cued trial processing were observed as early as the N170. Some research has found a positivity (P_D) occurs for suppressing task irrelevant stimuli which follows on from the N2pc [47] that has been observed from around 200ms onwards [47-49]. This contrasts to our findings whereby the differences in attention relevance were observed to be modulated by the N170 which peaks earlier in time at 170ms [12, 15] compared to the P_D.

The present study used stimuli which stepped back one position, as opposed to forward one position or appearing at random in any position aside from the expected one. Previous research has shown an ‘inhibition of return’ phenomenon where attention is

suppressed to a previously attended spatial region [50], of which could be operating in this study in unpredictable conditions where the stimuli returns to the previous position. However, if this phenomenon was evident in this case then one would observe the distractor suppressive component (P_D) demonstrated by a positive ERP waveform to unpredictable conditions as suppression of the previously attended area occurs. In this study a positive component was not observed to previously attended areas (i.e. unpredictable conditions), thus indicating the stimuli was not being suppressed in these instances.

Conclusion

This study demonstrates prediction by prior context should be considered when investigating attention processes of the N170 and N2pc. The findings of this study reiterate the need to continue to control for prediction in attention components, as confirmed expectations demonstrated a dampening in N170 and N2pc responses evidenced by reduced amplitudes in predictable conditions. This research indicates the value of prior context in influencing the elicitation of the N2pc component. Whilst the complicated nature of a conjunction of features and combination of attention and prediction factors encountered in daily life must be acknowledged, this research has demonstrated investigating visual perception using singleton feature stimuli assists by improving our knowledge of how attention and prediction direct processing of visual information, and why some stimuli may capture attention more so than others.

Acknowledgments

We would like to thank all the research participants for generously donating their time to participate in this research, without whom this study would not be possible.

References

1. Friston K. A theory of cortical responses. Philosophical transactions of the Royal Society of London Series B, Biological sciences. 2005;360(1456):815-36. Epub 04/29. doi: 10.1098/rstb.2005.1622. PubMed PMID: 15937014.
2. Rao RPN, Ballard DH. Predictive coding in the visual cortex: a functional interpretation of some extra-classical receptive-field effects. Nature Neuroscience. 1999;2:79. doi: 10.1038/4580.
3. Friston K. The free-energy principle: a unified brain theory? Nature Reviews Neuroscience. 2010;11:127. doi: 10.1038/nrn2787
4. Jiang J, Summerfield C, Egner T. Attention sharpens the distinction between expected and unexpected percepts in the visual brain. The Journal of Neuroscience. 2013;33(47):18438. doi: 10.1523/JNEUROSCI.3308-13.2013.
5. Smout CA, Tang MF, Garrido MI, Mattingley JB. Attention promotes the neural encoding of prediction errors. PLoS Biol. 2019;17(2):e2006812-e. doi: 10.1371/journal.pbio.2006812. PubMed PMID: 30811381.
6. Garrido MI, Rowe EG, Halász V, Mattingley JB. Bayesian mapping reveals that attention boosts neural responses to predicted and unpredicted stimuli. Cerebral Cortex. 2018;28(5):1771-82. doi: 10.1093/cercor/bhx087.
7. Kok P, Rahnev D, Jehee JFM, Lau HC, de Lange FP. Attention reverses the effect of prediction in silencing sensory signals. Cerebral Cortex. 2012;22(9):2197-206. doi: 10.1093/cercor/bhr310.
8. Hsu Y-F, Hamalainen J, Waszak F. Both attention and prediction are necessary for adaptive neuronal tuning in sensory processing. Frontiers in Human Neuroscience. 2014;8(152). doi: 10.3389/fnhum.2014.00152.
9. Spratling MW. Predictive coding as a model of biased competition in visual attention. Vision Research. 2008;48(12):1391-408. doi: 10.1016/j.visres.2008.03.009.
10. Rossion B, Caharel S. ERP evidence for the speed of face categorization in the human brain: Disentangling the contribution of low-level visual cues from face perception. Vision Research. 2011;51(12):1297-311. doi: 10.1016/j.visres.2011.04.003.
11. Johnston P, Overell A, Kaufman J, Robinson J, Young AW. Expectations about person identity modulate the face-sensitive N170. Cortex. 2016;85:54-64. doi: 10.1016/j.cortex.2016.10.002.
12. Johnston P, Robinson J, Kokkinakis A, Ridgeway S, Simpson M, Johnson S, et al. Temporal and spatial localization of prediction-error signals in the visual brain. Biological Psychology. 2017;125:45-57. doi: 10.1016/j.biopsycho.2017.02.004.
13. Robinson JE, Breakspear M, Young AW, Johnston PJ. Dose-dependent modulation of the visually evoked N1/N170 by perceptual surprise: a clear demonstration of prediction-error signalling. European Journal of Neuroscience. 2018;0(0). doi: 10.1111/ejn.13920.

14. Robinson JE, Woods W, Leung S, Kaufman J, Breakspear M, Young AW, et al. Prediction-error signals to violated expectations about person identity and head orientation are doubly-dissociated across dorsal and ventral visual stream regions. NeuroImage. 2020;206. doi: 10.1016/j.neuroimage.2019.116325.
15. Luck SJ. Introduction to the Event-Related Potential Technique. Cambridge, United States: MIT Press; 2014.
16. Blau VC, Maurer U, Tottenham N, McCandliss BD. The face-specific N170 component is modulated by emotional facial expression. Behavioral and Brain Functions. 2007;3(1):7. doi: 10.1186/1744-9081-3-7.
17. Itier RJ, Latinus M, Taylor MJ. Face, eye and object early processing: What is the face specificity? NeuroImage. 2006;29(2):667-76. doi: 10.1016/j.neuroimage.2005.07.041.
18. Itier RJ, Taylor MJ. N170 or N1? Spatiotemporal differences between object and face processing using ERPs. Cerebral Cortex. 2004;14(2):132-42. doi: 10.1093/cercor/bhg111.
19. Rossion B, Jacques C. Does physical interstimulus variance account for early electrophysiological face sensitive responses in the human brain? Ten lessons on the N170. NeuroImage. 2008;39(4):1959-79. doi: 10.1016/j.neuroimage.2007.10.011.
20. Thierry G, Martin CD, Downing P, Pegna AJ. Controlling for interstimulus perceptual variance abolishes N170 face selectivity. Nature Neuroscience. 2007;10:505. doi: 10.1038/nn1864.
21. Luck SJ, Hillyard SA. Spatial filtering during visual search: Evidence from human electrophysiology. Journal of Experimental Psychology: Human Perception and Performance. 1994;20(5):1000-14. doi: 10.1037/0096-1523.20.5.1000.
22. Eimer M. The N2pc component as an indicator of attentional selectivity. Electroencephalography and Clinical Neurophysiology. 1996;99(3):225-34. doi: 10.1016/0013-4694(96)95711-9.
23. Li C, Liu Q, Hu Z. Further evidence that N2pc reflects target enhancement rather than distracter suppression. Frontiers in Psychology. 2018;8(JAN). doi: 10.3389/fpsyg.2017.02275.
24. Mazza V, Turatto M, Caramazza A. Attention selection, distractor suppression and N2pc. Cortex. 2009;45(7):879-90. doi: 10.1016/j.cortex.2008.10.009.
25. Luck SJ, Hillyard SA. Electrophysiological correlates of feature analysis during visual search. Psychophysiology. 1994;31(3):291-308.
26. Li H, Zeigler-Hill V, Yang J, Jia L, Xiao X, Luo J, et al. Low self-esteem and the neural basis of attentional bias for social rejection cues: Evidence from the N2pc ERP component. Personality and Individual Differences. 2012;53(8):947-51. doi: 10.1016/j.paid.2012.03.004.
27. Wieser MJ, Hambach A, Weymar M. Neurophysiological correlates of attentional bias for emotional faces in socially anxious individuals – Evidence from a visual search task and N2pc. Biological Psychology. 2018;132:192-201. doi: 10.1016/j.biopsycho.2018.01.004.
28. Reutter M, Hewig J, Wieser MJ, Osinsky R. The N2pc component reliably captures attentional bias in social anxiety. Psychophysiology. 2017;54(4):519-27. doi: 10.1111/psyp.12809. PubMed PMID: 28111770.
29. Liu Y, Lan H, Teng Z, Guo C, Yao D. Facilitation or disengagement? Attention bias in facial affect processing after short-term violent video game exposure. PLoS ONE. 2017;12(3). PubMed PMID: 2017-09901-001.
30. Weymar M, Gerdes ABM, Löw A, Alpers GW, Hamm AO. Specific fear modulates attentional selectivity during visual search: Electrophysiological insights from the N2pc. Psychophysiology. 2013;50(2):139-48. doi: 10.1111/psyp.12008.

31. Posner MI, Snyder CR, Davidson BJ. Attention and the detection of signals. Journal of Experimental Psychology: General. 1980;109(2):160-74. doi: 10.1037/0096-3445.109.2.160.
32. West R, Wymbs N. Is detecting prospective cues the same as selecting targets? An ERP study. Cognitive, Affective, & Behavioral Neuroscience. 2004;4(3):354-63. doi: 10.3758/CABN.4.3.354.
33. Johnson JS, Woodman GF, Braun E, Luck SJ. Implicit memory influences the allocation of attention in visual cortex. Psychonomic Bulletin & Review. 2007;14(5):834-9. doi: 10.3758/BF03194108.
34. Woodman GF, Arita JT, Luck SJ. A cuing study of the N2pc component: An index of attentional deployment to objects rather than spatial locations. Brain Research. 2009;1297:101-11. doi: 10.1016/j.brainres.2009.08.011.
35. Tan M, Wyble B. Understanding how visual attention locks on to a location: Toward a computational model of the N2pc component. Psychophysiology. 2015;52(2):199-213.
36. Tay D, Harms V, Hillyard SA, McDonald JJ. Electrophysiological correlates of visual singleton detection. Psychophysiology. 2019;56(8):n/a-n/a. doi: 10.1111/psyp.13375.
37. Tipples J, Johnston P, Mayes A. Electrophysiological responses to violations of expectation from eye gaze and arrow cues. Social Cognitive and Affective Neuroscience. 2013;8(5):509-14. doi: 10.1093/scan/nss024.
38. Tipples J. Eye gaze is not unique: Automatic orienting in response to uninformative arrows. Psychonomic Bulletin & Review. 2002;9(2):314-8. doi: 10.3758/BF03196287.
39. Biosemi. Actiview. Version 7.07. 2016. Available from https://www.biosemi.com/
40. GmBH BP. BrainVision Analyser 2. Version 2.1 2015. Available from https://www.brainproducts.com/
41. Mathworks. MATLAB. Version 9.1. 2019. Available from https://au.mathworks.com/products/matlab.html
42. SPSS. Version 26. 2019. Available from https://www.ibm.com/au-en/analytics/spss-statistics-software
43. Zhang D, Zhou X, Martens S. The impact of negative attentional set upon target processing in RSVP: An ERP study. Neuropsychologia. 2009;47(12):2604-14. doi: 10.1016/j.neuropsychologia.2009.05.008.
44. Robitaille N, Jolicœur P, Dell'Acqua R, Sessa P. Short-term consolidation of visual patterns interferes with visuo-spatial attention: Converging evidence from human electrophysiology. Brain Research. 2007;1185:158-69. doi: 10.1016/j.brainres.2007.09.004.
45. Event-related potentials: A methods handbook. Handy TC, editor. Camridge, Mass: MIT Press; 2004.
46. Baguley T. Calculating and graphing within-subject confidence intervals for ANOVA. Behavior Research Methods. 2012;44(1):158-75. doi: 10.3758/s13428-011-0123-7.
47. Sawaki R, Geng JJ, Luck SJ. A common neural mechanism for preventing and terminating the allocation of attention. Journal of Neuroscience. 2012;32(31):10725-36. doi: 10.1523/JNEUROSCI.1864-12.2012.
48. Sawaki R, Luck SJ. Active suppression of distractors that match the contents of visual working memory. Visual Cognition. 2011;19(7):956-72. doi: 10.1080/13506285.2011.603709.
49. Hickey C, Di Lollo V, McDonald JJ. Electrophysiological indices of target and distractor processing in visual search. Journal of Cognitive Neuroscience. 2009;21(4):760-75. doi: 10.1162/jocn.2009.21039.
50. Posner M, Cohen Y. Components of visual orienting. Attention and performance X: Control of language processes. 1984;32:531.

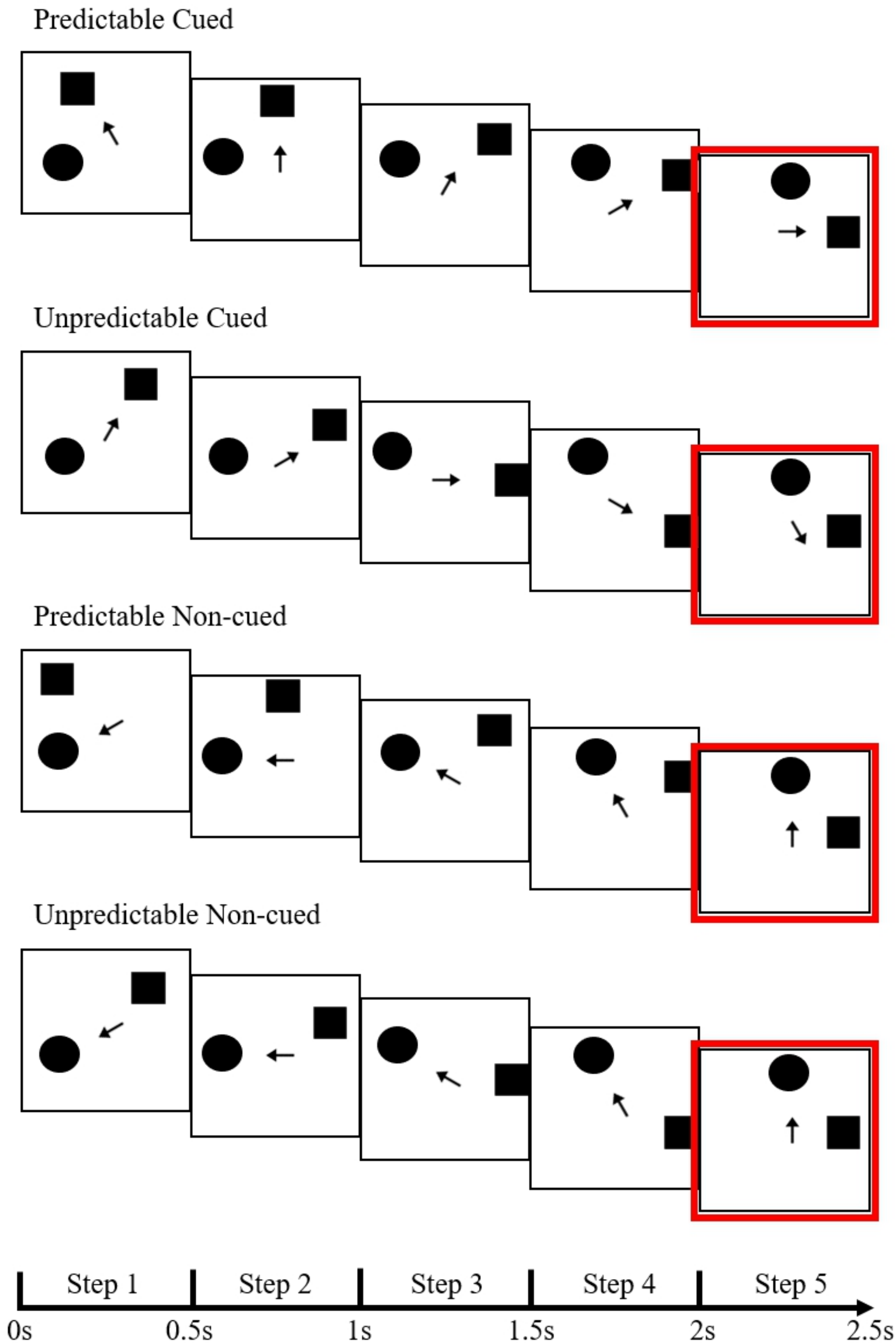
Predictable Cued
Unpredictable Cued
Predictable Non-cued
Unpredictable Non-cued
Step 1
Step 2
Step 3
Step 4
Step 5
0s
0.5s
1s
1.5s
2s
2.5s

Fig 1

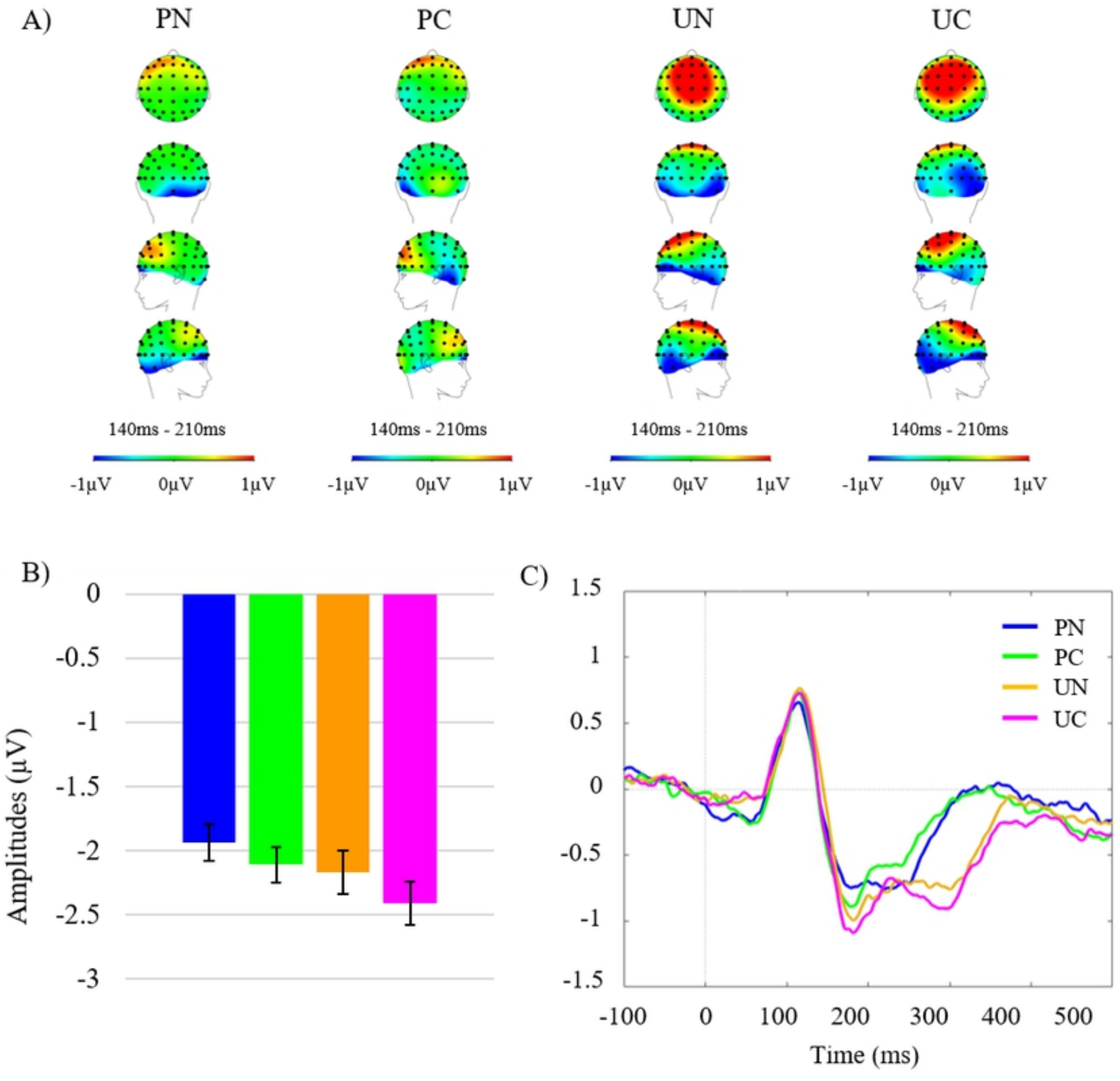
A)
PN
PC
UN
UC
140ms - 210ms
-1μV
0μV
1μV
B)
Amplitudes (μV)
0
-0.5
-1
-1.5
-2
-2.5
-3
C)
1.5
1
0.5
0
-0.5
-1
-1.5
-100
0
100
200
300
400
500
Time (ms)
PN
PC
UN
UC

Fig 2

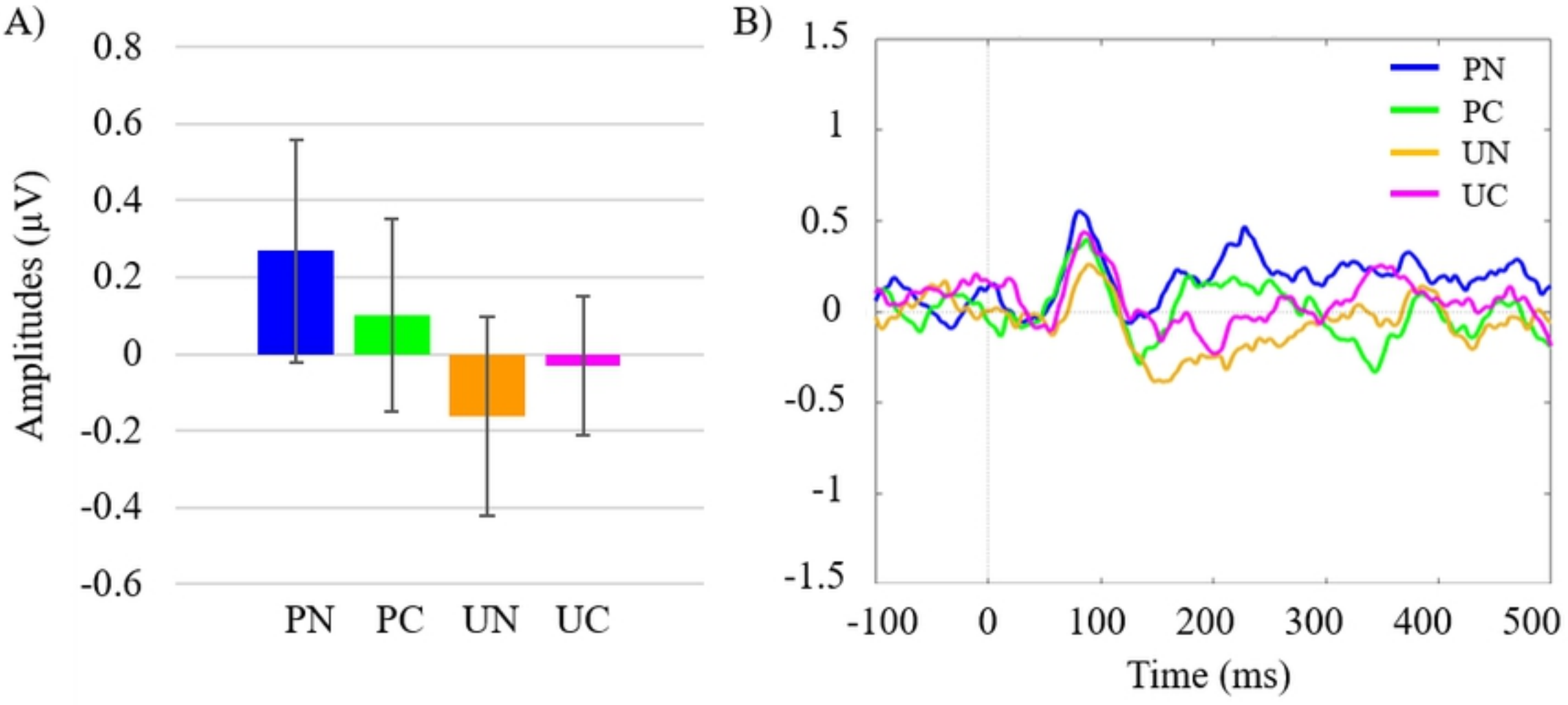
A)
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
Amplitudes (µV)
PN
PC
UN
UC
B)
1.5
1
0.5
0
-0.5
-1
-1.5
-100
0
100
200
300
400
500
Time (ms)
PN
PC
UN
UC

Fig 3