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Camouflage properties modulate neural markers of attention and decision making

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Author Contributions

J.B. Designed the experiment, performed data collection and analysis and wrote the manuscript. C.H. Contributed to experiment conception and writing of the manuscript. M.C. contributed to EEG statistical analysis.

Key words: Camouflage, attention, decision making, neural, EEG

28 Abstract

29

30 Many animals rely on visual camouflage as an effective means of avoiding detection and,

31 consequently, increasing their chances of survival. Edge disruption is commonly seen in the natural

32 world, with animals using high contrast markings which are incongruent with their real body outline

33 in order to avoid recognition. Whilst many studies have investigated how camouflage properties

34 influence performance and eye-movement in predation search tasks, researchers in the field have

35 yet to consider how camouflage may directly modulate attention and target processing. To examine

36 how disruptive colouration modulates attention, we use a computational model of visual processing

37 to quantify target saliency and determine if this is predictive of human behavioural performance and

38 subjective certainty, as well as physiological markers of attention and decision making. We show that

39 increasing edge disruption not only reduced detection rates, but was also associated with a

40 dampening of neurophysiological markers of attentional filtering. Increased self-reported certainty

41 regarding decisions corresponded with neurophysiological markers of evidence accumulation and

42 decision making.

43

44

Introduction

Over the last century, a great deal of progress has been made in studying the principles that underlie animal signalling. This body of work has defined a number of evolutionary traits by which species can avoid detection. Visual camouflage is a common means of avoiding detection, including; background matching (e.g. blending into the background on the basis of colour, contrast, texture frequency (1)); disruptive camouflage (e.g. the use of visual patterning to prevent easy recognition of prominent features (2, 3)); and self-shadow concealment (an animal disguises its three dimensional structure by exhibiting a darker upper surface and a lighter lower surface (4)). Edge disruption is a particular form of disruptive camouflage in which marking orientations are incongruous with the animal's bodily outline and, thus, act to prevent detection and recognition. In recent years, quantification of edge disruption has been useful in exploring how such markers impair search performance. In simple search predation paradigms, a greater number of edge intersecting patches on prey stimuli has been found to lengthen the search time before detection and increase prey survival rates (3, 5). Approaches to quantification have also been more directly inspired by what is known about the neural architecture of the visual system. Troscianko et al. (6) devised a measure ("GabRat") which utilises Gabor filters to mimic processing early in the visual cortex in order to measure the ratio of perceived false edges to real edges within a target's outline. This measure was optimal in predicting search times for targets in comparison to existing measures, and provides a more flexible means of measuring edge disruption in species with more elaborate markings and in varying scenarios. This study highlights the importance of considering the neural underpinnings of visual attention in the pursuit of understanding the means by which camouflage operates.

A small number of eye-tracking studies have also proven useful in further elucidating the mechanisms by which camouflage markings act to foil the observer. Such studies have shown that prey with more intersecting patches are passed over more during search (i.e. gaze lands on the target but does not linger) and looked at for longer prior to active recognition and capture (3). Camouflage markings also modulate known observable markers of attention, such as the speed and amplitude of the first saccade (eye-movement to the target) (7). By moving beyond simple reaction times and capture rates, these studies more directly point to a mechanism by which disruptive markers act to both evade attentional capture and hamper object recognition. However, whilst eye-tracking can inform us about overt visual attention to camouflage targets (8), nothing is known about how cryptic patterning modulates early attentional orientation mechanisms which are a precursor to overt eye-movements during visual search and attack. Further, covert attention can be orientated to a target, and a decision made regarding the targets properties, without any observable eye-movements (9). Thus, within the approaches to measuring the effects of camouflage so far, there is potentially a considerable amount of informative data being lost, purely because it is beyond the measurement limits of the tools being used.

If we are to truly understand how camouflage markings modulate attention and target processing we need the finer grained temporal resolution afforded to us with neurophysiological approaches. Detecting a camouflage object could be broadly said to require two processes. Firstly, detecting where the object is and, secondly, demarcating the edges of the object in order to make a decision regarding its orientation. This leads us to hypothesise that variation in the level of edge disruption should lead to discernible differences in neurophysiological markers of attention, object recognition

88 and decision making. Attention in humans has been well studied in the field of psychology using
89 electroencephalogram (EEG) paradigms which enable 1000Hz+ sampling resolution of electrical
90 signals produced by the brain. The well documented N2pc (Negative 200 Posterior Contralateral) is
91 an early lateralised negative deflection occurring in occipital regions around 150-300msec after
92 stimulus presentation. It is at a greater amplitude (more negative) contralateral to the stimulus
93 which is drawing attention (10). It is purported to arise during early covert attentional selection
94 processes, prior to (or in the absence of) overt saccadic eye-movement (11). The exact role of N2pc
95 has long been a source of debate (12), although it can be elicited by discontinuities in the visual scene
96 (13), it is more persistent in paradigms with distracting items which must be suppressed in order to
97 respond to a target (10). Thus, it is thought to reflect both a discriminative filtering process
98 (suppressing non-relevant distractors and selecting relevant information) (10) and the process of
99 converting of raw sensory input into a coherent representation for identification (9, 14). Failure to
100 detect a camouflage object in the visual scene in a naturalistic setting could plausibly reflect the
101 failure of both these processes and we therefore hypothesise that N2pc will be modulated by
102 camouflage properties.

104 Research regarding perceptual decision making has indicated that a central parietal positivity (CPP)
105 neural signature scales with the accumulation of sensory evidence (15). This phenomenon is
106 observed with both time-varying stimulus in continuous monitoring paradigms (15) as well as static
107 stimulus which vary in detectability (e.g. via luminance manipulation) (16). N2pc has been found to
108 influence the development of CPP following the onset of a target stimulus (17, 18), suggesting a
109 coupled (but perhaps distinct) process. It has been observed that CPP is mediated by the subjective
110 certainty in the decision response and therefore may also represent ‘conscious experience’ during
111 the evidence accumulation process as opposed to a pure reflection of the physical stimulus
112 characteristics (16). This may arise due to the influence of internal neural noise during the
113 accumulation process and it is a finding that accounts for erroneous responses (i.e. false positives),
114 particularly in paradigms with hard to detect stimulus (16). The finding that observers can spend a
115 relatively extended amount time looking directly at a stimulus before deciding to make an attack (3)
116 may be a reflection of the role of camouflage in slowing the decision making process in addition to,
117 or instead of, failing to attract attention in the first place. This is an interesting notion and it may
118 provide an explanation for why some hypothesized camouflage features appear to be imperfect, such
119 at the white ‘comma’ on the wings of the comma butterfly (*Polygonia c-album*) which has caused
120 considerable debate as to its specificity as a cryptic marking per se (19, 20).

122 In order to examine how edge disruption modulates attention and decision making, we use a
123 computational model of visual processing (6, 21, 22) to quantify target saliency and determine if this
124 is predictive of behavioural performance and electrophysiological responses to the stimuli in a
125 variation of an attention cueing paradigm. We also collect self-reported subjective decision certainty
126 following response in order to determine if this was correlated with edge disruption and whether this
127 had a mediating effect on neurophysiological responses associated with decision making.

129 Methods

130 Participants

Twenty-one adult participants were recruited from the local community. Two participants were removed immediately following data collection; one could not complete the task as they could not see the camouflage stimuli and (due to an equipment failure) one did not have any recorded behavioural data. Participants were screened and all had corrected to normal vision and an absence of neurological conditions. Remaining participants comprised 9 males and 10 females with a mean age of 32.1 (range: 19-60). Ethical approval was gain from the local research ethics committee prior to study commencement (School of Psychology Research Ethics Committee: PSYC-288, 17/08/2021).

EEG Task

We used an electroencephalogram (EEG) experimental cuing paradigm (Figure 1A) in which two stimuli were presented in sequence within a trial (referred to as **cue** and **target** hereafter), with the location cue being in the same location as the subsequent target on ~85% of trials (*valid cue*). In the remaining ~15% of trials, the target was presented in the opposite visual field but on the same horizontal plane (*invalid cue*). Based on a more traditional type of cueing paradigm (23) the heightened probability of the target being in the same position as the cue means that participants should covertly attend to the target location in advance of the target appearing (**if** they see the camouflaged cue). In traditional paradigms this results in faster reaction times (RT) for cue valid trials as well as neurophysiological evidence of attention being directed to the cued side before the onset of the target (23, 24). Thus, comparing valid to invalid trials can inform us about covert attentional deployment across different value of edge disruption (EdgeDis).

The **cue stimuli** comprised a camouflaged triangle presented on tree bark like background (Figure 1B and Supplementary Materials 3). The cue stimulus varied in the level of EdgeDis and texture rotation (TexRot) compared to background. The degree of EdgeDis was quantified as a ratio of orthogonal to parallel orientations within edge zones, computationally determined using a visual object recognition model (21, 22) (Figure 1B & 1C and Supplementary Materials 2). TextRot could either be 0° (i.e. matched with background texture orientation) or 45° or 90° (i.e. both unmatched with background texture orientation). Cue stimuli were presented with an equal probability of the triangle apex pointing up or down for the purpose of the discrimination task. The **target stimuli** were greyscale triangles, all identical aside from orientation (with ~50% match to cue orientation). The uniformity of the targets across trials firmly places the variations in trial difficulty with the variations in the initial cue camouflage properties.

A total of 348 trials were presenting during the laboratory EEG study using Psychtoolbox (25). On each trial camouflage cue stimuli could be presented on one of four bark locations (Figure 1A). Stimuli were presented in the central 23.1 x 22.0 ° visual angle, with each individual bark patch being presented at 10.0 x 9.0 ° visual angle in a square configuration. Following a cross hair presentation for 600 msec, the cue was presented for 600 msec in one of four locations. The target (in the same location as the cue stimuli on 85% of trials) was a uniform grey colour (50 percentile of grey scale of the original bark image) and presented for 100 msec following a 1000 msec crosshair presentation (+/-50 msec jitter). Participants were asked to indicate whether the two moths presented in sequence were of the *same* orientation (e.g. both with vertex up) or of a *different* orientation (i.e one vertex up and one down). They were given 2500 msec to respond following the presentation of the target, after which a null-response was recorded if no answer was given. After a response (or 2500 msec

timeout) participants were asked to give a subjective indication of how sure they were of their response as either *guess* (0% certainty), *fairly sure* (more than 0% but not 100%) and *certain* (100% certain of answer). They were not given a restricted time to make this response, but were asked not to think too much about this answer. The next trial continued once they had made this response, this in itself provided some variation in inter-stimulus interval to prevent anticipation and reduce EEG artefacts. Trials were presented over 5 blocks, with self-paced rests in between each block.

Whilst technically a cueing paradigm, the nature of the cue presentation emulated a visual search paradigm in that the cue could be located in one of four locations. Such an approach allowed for fixation to be maintained throughout (which would have been difficult in ‘free’ visual search paradigms used in previous ecology studies (3, 6)) and, thus, mitigates eye-movement related EEG artefacts as a result of the task itself. Further, the restricted nature of our cue visual search (to four locations) would reduce the reaction time (RT) variability which can result from randomness in the search path trajectory as opposed to the attention capturing properties of the stimuli themselves (8). By presenting two stimuli in sequence and only requiring a motor response following the second stimulus, event related potentials (ERP) responses to the cue properties could be more reliably dissociated from ERP responses associated with action initiation (26).

ERP data pre-processing

EEG data was recorded continuously using a BioSemi ActiveTwo EEG system (BioSemi©) with 64 electrodes at a 1024Hz sampling rate; data was down sampled to 512Hz in the initial stage of pre-processing. Eye-movements were recorded by placing an electrooculogram (EOG) lateral to each eye, and one both above and below the left eye. Two reference electrodes were also placed on the mastoid bone. EEG recording took place over one continuous ~30 minute period, with recording continuing during the self-paced rest breaks. All data pre-processing was carried out using EEGLab (27) and Fieldtrip (28) on a Matlab2019b (29) platform (see Supplementary Materials 1 for further details). Exceptionally bad channels visibly evident during recording were removed (4 participants – 1 channel, 1 participant – 2 channels: all occipital) before the continuous data was re-referenced to the average of all 64 (-removed) channels. Using EEGLab, data was high-pass finite impulse response (FIR) filtered using 1Hz cut-off for data used to identify artefact components, and a 0.1Hz cut-off for data destined for ERP statistical analysis. Independent component analysis (ICA) using the extended infomax algorithm (30) was used to identify eye-movement and other artefact components in the 1Hz cut-off data set. These identified components were used to remove artefacts from both the 1Hz cut-off and 0.1Hz cut-off datasets. Data the 0.1Hz data sets were used for ERP analysis. Sets were divided into epochs (-0.6 - 5.9s for cue locked epochs, and -1.5 - 0.2s for response locked epochs). The Fully Automated Statistical Thresholding for EEG Artefact Rejection (FASTER) toolbox (31) was used to detect and interpolate bad channels and remove trials with remaining noise artefacts. Data was then exported to FieldTrip for further statistical analysis. A priori regions of interest (ROI) were used for statistical analysis. For occipital ERPs O1, O2, PO3, PO4, PO7 and PO8 were used to calculate average waveforms for each hemisphere and a Laterality Index (LatIndex = Contralateral-Ipsilateral to stimulus). Central Parietal Positive (CPP) was calculated from the average of electrodes CPZ and Pz. One participant was removed at the pre-processing stage due to a high number of exceptionally noisy channels.

Statistical analysis

Behavioural data was only considered for trials included in the EEG result presentation (i.e. RTs, accuracy and subjective certainty was removed from data analysis for noisy, excluded, EEG trials). Data from 5767 trials across all participants remained (i.e. an average of ~27 trials removed per participant). Pre-processing of behavioural data consisted of removing response times (RTs) <100ms, under the presumption that these were too fast to be valid responses. RTs were positively skewed (as is typical on RT experimental paradigms) and, thus, log RT time data was used for subsequent analysis. When analysing RTs, only correct response trials were used. For the purpose of analyses the degrees of texture rotation (0,45,90,135,225,270,305°) were categorised into three TexRot values: 0° (matched), 45° (oblique [45,135,225,305°]), and 90° (perpendicular [90, 270°]). Statistical analysis of both behavioural data and ERP ROI data was carried out using R packages 'lmerTest' (lmer, glmer) (32) and 'nnet' (multinom) (33); and model comparisons to the maximal model (including both random slopes and random intercepts) were carried out in order to assess the overall fit of the models (34). Akaike information criterion (AIC) values were compared for models, and reduced models with random intercepts only provided a better fit for all analysis. Mediation analysis was carried out using the mediation toolbox in R (35). Model code and output is available via the University of Leeds research repository (indexed in Supplementary Materials 1).

The time series analysis comprised testing significance across the time series from stimulus onset (0 msec) with data averaged across a 50 msec window, with 50 msec increments within the region of interest electrodes. In order to avoid false positives resulting from multiple comparisons when running timeseries analysis, a cluster level thresholding procedure (ClusterP) was put in place. Monte Carlo simulations (36) (1000 repetitions for each of 33 increments) were carried out on data sets with randomised independent variable labels. Clusters ≥ 2 were >95% confidence interval, clusters ≥ 3 were >99% confidence interval, and clusters ≥ 4 were $\geq 99.99\%$ confidence interval.

249 Results and Discussion

250 *Edge disruption predicts accuracy and certainty of decisions*

251 Overall, accuracy on the task was 77.3%, with 15.5% of responses being incorrect, and a remaining
 252 7.3% of trials eliciting no response (coded as incorrect for the purpose of statistical analysis as these
 253 were interpreted as not seeing the cue stimulus). For cue valid trials (i.e. location of the target
 254 matched the location of the cue), accuracy was 78.7%, with an average RT of 952 msec (sd = 391)
 255 for correct responses and 1205 msec (sd = 536) for incorrect responses. Accuracy for cue invalid trials
 256 (i.e. location of the target was in the opposite visual field to the cue) was 69.4% with an average RT
 257 of 1027 msec (sd = 398) for correct responses and 1165 msec (sd = 467) for incorrect responses.

258 For all behavioural outcome variables models were estimated with stimulus properties (EdgeDis
 259 *TexRot) and cue validity (cueV) as predictors (R pseudocode: outcome = cueV + EdgeDis*TexRot +
 260 (1|participant)). Linear mixed effects models (LMMs) were used to predict RT. Cue validity was the
 261 largest significant predictor of RTs ($F_{(1,4418)} = 53.083$, $p < 0.001$), with slope estimates ($b = 0.104$, $se =$
 262 0.014 , $CI[0.076 - 0.132]$) indicating faster RTs for valid cues, as would be expected in a standard cuing
 263 paradigm (23). There was an interactive effect of EdgeDis*TexRot ($F_{(2, 4417)} = 3.921$, $p < 0.05$), with
 264 negative estimates (EdgeDis*TexRot.45: $b = -0.006$, $se = 0.016$, $CI[-0.037 - 0.026]$;
 265 EdgeDis*TexRot.90: $b = -0.040$, $se = 0.019$, $CI[-0.077 - 0.004]$) reflecting that the increase in RT with
 266 increasing EdgeDis was reduced in non-0° TexRot stimulus compared to 0° TexRot and this reduction
 267 was stronger for 90°. The main effects of EdgeDis ($F_{(1,4417)} = 0.4870$, $p = 0.485$) and TexRot ($F_{(2,4417)} =$
 268 2.293 , $p = 0.101$) on RT were non-significant. Overall this suggests that increasing EdgeDis results in
 269 participants taking a longer time to respond to the matching task, but that this effect is smaller when
 270 the targets texture orientation is unmatched to the background.

271
 272 Generalised linear mixed effect models (GLMM) were used for predicting accuracy. Cue validity ($\chi^2_{(1)} =$
 273 34.687 , $p < 0.001$) and EdgeDis ($\chi^2_{(1)} = 91.862$, $p < 0.001$) were predictors of accuracy, with odds
 274 ratios (OR) indicating that both an invalid cue and increasing EdgeDis resulted in lower accuracy (cue:
 275 $OR = 0.606$, $se = 0.052$, $CI[0.513 - 0.716]$; EdgeDis: $OR = 0.713$, $se = 0.033$, $CI[0.651 - 0.780]$). Neither
 276 the EdgeDis*TexRot interaction ($\chi^2_{(2)} = 5.270$, $p = 0.072$) or the main effect of TexRot ($\chi^2_{(2)} = 2.114$,
 277 $p = 0.348$) were significant in predicting accuracy. Again, these findings are in line with typical cuing
 278 paradigms (23) in showing that cue-target location compatibility increases task performance. These
 279 results also indicate that EdgeDis does have a distinguishable effect on the ability to determine the
 280 shape of the cue for future matching to the target.

281
 282 Overall, 23.5% of trials were reported as *guess* responses, 26.8% as *fairly sure* and 49.7% as *certain*.
 283 Accordingly, accuracy within these categories of certainty was 45.2%, 75.2%, and 94.1% respectively.
 284 A multinomial Logit Model (MLM) was used to determine if stimulus properties predicted decision
 285 certainty. There was a significant main effect of cue validity ($\chi^2_{(2)} = 19.044$, $p < 0.001$) with estimates
 286 (*fairly sure*: $b = -0.170$, $se = 0.099$, $CI[-0.365 - 0.025]$; *certain*: $b = -0.397$, $se = 0.091$, $CI[-0.576 -$
 287 $0.218]$) indicating that in trials with valid cues, participants were likely to report higher levels of
 288 certainty. There was also an EdgeDis*TexRot interaction ($\chi^2_{(4)} = 10.175$, $p < 0.05$) and a main effect
 289 of EdgeDis ($\chi^2_{(2)} = 223.040$, $p < 0.001$). Although there was an overall decrease in certainty with an
 290 increasing amount of EdgeDis (*fairly sure*: $b = -0.168$, $se = 0.120$, $CI[-0.403 - 0.067]$; *certain*: $b = -$
 291 0.535 , $se = 0.106$, $CI[-0.742 - -0.327]$), this effect was slightly less pronounced for non-0° TexRot
 292 stimulus (EdgeDis*TexRot.45 - *fairly sure*: $b = -0.172$, $se = 0.129$, $CI[-0.425 - 0.082]$; *certain*: $b = -$
 293 0.031 , $se = 0.115$, $CI[-0.204 - 0.386]$; EdgeDis*TexRot.90 - *fairly sure*: $b = 0.091$, $se = 0.150$, $CI[-0.256$

– 0.194]: *certain*: $b = 0.223$, $se = 0.135$, $CI[-0.041 - 0.486]$), reflecting the RT results. There was no significant main effect of TexRot ($\chi^2_{(4)} = 3.578$, $p = 0.466$).

Overall, these results are in line with previous studies which have shown edge disruption to influence predation performance. Previous studies have reported decreases in time to capture with increased target edge disruption (3, 6) within naturalistic search paradigms in which RT was the primary outcome metric. Larger variations in time to decision (regarding orientation of target) are likely to have occurred following the presentation of the earlier camouflaged cue (for which no observable response was required) rather than following the target (in which all stimuli were matched in terms of visual properties). Accordingly, cue properties were relatively stronger model predictors when determining accuracy as opposed to RT. We have also uniquely shown that EdgeDis can also influence subjective decision certainty, a factor that, in itself, is likely to heighten performance in a standard search paradigm and predation success in ecological settings. It is important to note that on *guess* trials, participants were not asked to distinguish whether they had failed to see the cue, or, had seen the cue, but not discerned its orientation; it is likely that both scenarios occurred within this subset of trials. Finally, these results provide further validation that neurophysiologically derived computational metrics of edge disruption are reflected human behavioural performance in visual search task (6), thus provide a good proxy for understanding how camouflage disrupts object detection and identification.

Edge disruption drives ERP markers of attentional filtering

Figure 2A depicts contralateral and ipsilateral occipital ERP waveforms following cue onset for categorised low, medium and high EdgeDis values over time. N2 was defined as the negative deflection at 300-400 msec following clear P1, N1 and P2 components. Although slightly later than reported in some studies, we speculate this is a result of the reduced distinguishability of the cue from background. N2pc was defined as the contralateral N2 (N2c) relative to the ipsilateral N2 (N2i) wave form. The scalp distribution of N2pc at 300-400msec post cue onset is displayed in Figure 2B for low, medium and high EdgeDis values (see also Figure Supplementary 4A for overall averages). LMMs were fitted in order to test whether stimulus properties determined N2pc response (R pseudocode: $N2pc_{Cue} = EdgeDis * TexRot + (1 | participant)$). In predicting N2pc, there was no significant interaction between EdgeDis and TexRot ($F_{(2,5751)} = 0.509$, $p = 0.601$), nor was there a main effect of TexRot ($F_{(2,5750)} = 0.224$, $p = 0.799$). EdgeDis significantly predicted N2pc elicited following the cue ($F_{(1,5749)} = 4.136$, $p < 0.05$, $b = 0.049$, $se = 0.041$, $CI[-0.030 - -0.129]$).

We also explored whether the N2pc electrophysiological response to the cue could be predicted by accuracy and certainty and found no relationship (interaction ($F_{(2,5766)} = 0.4922$, $p = 0.611$; certainty: $F_{(2,5516)} = 2.53$, $p = 0.08$; accuracy: $F_{(1,5738)} = 0.283$, $p = 0.594$). This strengthens the premise that N2pc is driven by stimulus properties and not subjective judgement or general focus on the task. Whilst N2c was greater than N2i across all cue stimulus, this effect was more pronounced for cues with lower EdgeDis values. The N2pc response is likely to have been modulated by suppression of distracting non-cue panels; however, these distractors were luminance matched across panels and uniform across all EdgeDis values. This leaves the interpretation that variations in N2pc were a reflection of the selection of task relevant features (the outline edge) and feature conversion to a coherent sensory representation and that this process is muted in high EdgeDis cue stimulus.

The cue determined target location on ~85% of trials and successful attentional orientation to cues should result in sustained attention to the target hemi-field, if the cue was detected. Thus, N2pc following the target should be modulated differently on cue valid versus invalid trials. Specifically, we would expect the opposite effect in invalid cue trials, again, only if the cue was detected. LMMs were fitted with both EdgeDis and cue validity as an interaction term (R pseudocode: $N2pcTarget = CueV * EdgeDis + (1|participant)$). There was a significant interaction between EdgeDis and cue validity ($F_{(1,5759)} = 5.762$, $p < 0.05$; $b = 0.007$, $se = 0.039$, $CI[-0.172 - -0.017]$) and there was a main effect of EdgeDis ($F_{(1,5750)} = 4.101$, $p < 0.05$; $b = 0.095$, $se = 0.014$, $CI[-0.020 - 0.035]$), but no main effect of cue validity ($F_{(1,5750)} = 1.433$, $p = 0.231$). N2pc was greater in low EdgeDis trials when the target location was congruent with the cue location, and vice versa for invalid cues (Figure 2C & D and Figure Supplementary 4B). This suggests that if cue camouflage was poor, attention was more likely to be orientated to the incorrect target hemifield in invalid trials and, therefore, N2pc responses to the target were attenuated in comparison to trials with high cue camouflage efficiency.

Response locked CPP is driven by subjective decision certainty

In paradigms where a manual response is required, CPP tends to show a classical rise with a peak at the time of response. It should be noted that CPP shares many properties with the classical P300 component (15, 37). However, given that P300 is generally considered in terms of stimulus locked ERPs (15), here we shall use the term CPP in our consideration of response locked CPP. We used the *same/different* response locked (0msec) CPP averaged over +/- 100 msec as our model outcome variable. There was no significant influence of cue validity on CPP ($F_{(1,5170)} = 0.015$, $p = 0.902$), therefore all trials (cue valid and invalid) were included in the model. Given that CPP is influenced by reaction time (15) and, potentially, accuracy (16), these were added to the model in addition to certainty (R pseudocode: $CPP = Accuracy + Certainty + RT + (1|participant)$). Both certainty and RT predicted CPP amplitude at the time of response, accuracy did not (certainty: $F_{(2,5172)} = 4.501$, $p < 0.05$; RT: $F_{(1, 5164)} = 6.086$, $p < 0.01$; accuracy: $F_{(2,5163)} = 0.681$, $p = 0.409$). The CPP component was evident as a typical focal peak over Pz for *certain* and *fairly sure* responses, but was not evident for *guess* responses (Figure 3A and B). Estimates for certainty (*fairly sure*: $b = 0.102$, $se = 0.035$, $CI[0.033 - 0.171]$; *certain*: $b = 0.086$, $se = 0.035$, $CI[0.018 - 0.155]$) represent the lack of the typical cumulative response for *guess* and the more typical peaks for not *guess* trials (Figure 3B). Estimates for RT ($b = -0.180$, $se = 0.073$, $CI[-0.323 - -0.037]$) reflect the increased peak amplitude of CPP as RTs get shorter. Such a covariation between RT and CPP has been found in previous studies (37). There was no indication that the physical properties of the initial cue stimulus (R pseudocode: $CPP = EdgeDis * TexRot + (1|participant)$) predicted CPP following the target (EdgeDis: $F_{(2,5170)} = 2.876$, $p = 0.09$; TexRot: $F_{(1, 5170)} = 0.279$, $p = 0.757$; interaction: $F_{(2,5170)} = 1.197$, $p = 0.302$), therefore CPP seems to represent the conscious experience of the stimulus, which may be influenced by internal neural noise.

Whilst there was a build-up within the central parietal ROI following the cue which could be a direct reflection of evidence accumulation in relation to camouflage properties, it was evident from the topography of the cue locked central parietal development that it was not typical of those seen in evidence accumulation tasks (15, 16), where a more focal and distinct central parietal peak is evident. The early central parietal rise in amplitude was influenced by early occipital positivity and the peak amplitude was associated with a developing right dorsolateral peak (Supplementary Materials 5). The timing and location of this frontal peak corresponds with slow wave frontal components seen in memory encoding paradigms (38). The lack of distinct CPP following the cue but clear CPP following

the target (when a match response was required) gives more weight to the interpretation that, in our paradigm, CPP was driven by subjective certainty or ‘conscious experience’ as opposed to an accumulation of stimulus features per se. Together these results suggest that the cue-target match response CPP peak is driven by the subjective self-reported confidence in the decision and not by the cue visual properties.

Subjective rating as a mediator of ERP responses

We reported earlier that EdgeDis, but not N2pc, predicted subsequent accuracy and certainty. However, we may expect that if certainty was high on any particular trial, ERP components associated with both attentional allocation and spatial encoding would show a different evolution compared to trials where a *guess* response was reported. In order to discern the relationship between stimulus characteristics, subjective rating of certainty, and ERP response a mediation analysis was run on the ongoing waveform difference between contralateral and ipsilateral occipital responses (Npc), as well as the original N2pc component. The mediation model for N2pc is shown in Figure 4A. Path *a* represents the relationship between the predictor (EdgeDis) and the Mediator (certainty). Path *b* represents the relationship between the mediator and the outcome (N2pc), whilst controlling for the predictor. Path *c* represents the direct (unmediated) relationship between the predictor and the outcome. Whilst EdgeDis directly predicted N2pc and predicted certainty (as reported in the previous sections) there was no mediating effect of certainty for this ERP component ($a*b$; ACME = 0.003, CI[-0.002 - 0.01], $p = 0.204$), Figure 4A.

Timeseries analysis with Monte Carlo correction for multiple comparison identified a later period (800-1050msec) in which certainty both predicted Npc magnitude ($F_{(1,2056)} = 9.979$, $p < 0.01$: $b = -0.044$, $se = 0.014$, CI[-0.071 – - 0.017]) and was a mediating factor between cue EdgeDis and Npc magnitude ($a*b$; ACME = 0.009, CI[0.002 - 0.01], $p < 0.001$, clusterP: $p < 0.001$), Figure 4B. There was no significant direct effect of EdgeDis on Npc during this time period ($F_{(1,5750)} = 0.007$, $p = 0.9336$) suggesting that this was an indirect mediation via the degree of certainty. Figure 4C displays the evolution of Npc following the cue and it is evident that for *fairly sure* and *certain* trials there is a sustained posterior contralateral negativity (SPCN), which is absent in *guess* trials. A SPCN following a distinct N2pc has been found in previous studies which require participants to hold a stimulus in visual short term memory (even if they are not designed as a memory task per se) (39). This SPCN component is most likely a reflection of holding the cue representation in short term working memory, a process which is more likely to be absent or meek in *guess* trials.

Finally we investigated whether certainty mediated the relationship between stimulus properties and response locked CPP peak. There was no significant direct effect of cue EdgeDis on response CPP peak amplitude (as reported above). However, certainty was a mediating factor between EdgeDis and CPP amplitude ($a*b$; ACME = 0.008, CI[-0.01 - 0.00], $p < 0.002$), see Figure 4D. Again, these results are compatible with previous studies that have suggested that it is subjective perceptual experience, rather than stimulus properties per se, that drive the CPP component (16) and that there is a complex relationship between acquiring physical evidence and performance which, is likely influence by internal neural noise. In the natural environment decision confidence, based on evidence accumulation, is likely to influence the speed at which attack is initiated. This is likely to be an influencing factor in the pattern results found in Webster et al. (3) in which participants gazed

lingered longer on more cryptic targets before attack. However, this hypothesis needs more empirical testing with paradigms which influence confidence independent of camouflage markings.

Conclusions

Camouflage properties, particularly edge disruption, directly influenced behavioural measures of detection as well as subjective reports of decision certainty. Further, there was a direct influence on neurophysiological markers of early attentional processes, with increasing edge disruption being associated with a reduced N2pc. We interpret this finding as a failure to assimilate task relevant features (the triangle edge) for conversion into a lucid shape representation. The N2pc occipital response to the cue was correlated with EdgeDis, suggesting that this earlier stage of processing does not reflect an ultimate “detect” or “not detect” binomial outcome but rather a stage where the visual representation of the cue may incrementally gain strength. Adding strength to this hypothesis, it is only following the offset of the camouflage cue that neural signatures diverge and are mediated by subjective reports of certainty (*guess* versus *not-guess*).

In early occipital regions, there is a sustained period of contralateral occipital negativity to the cue location in *fairly sure* and *certain* trials which is absent in *guess* trials and is likely to reflect maintenance of the cue representation (38). A similar dichotomous pattern of activity is apparent in higher order central parietal regions associated with decision making when a match response was made in the latter stages of the trial. This pattern of findings is somewhat comparable to predictions of the “global neuronal workspace model” purported by Dehaene and colleagues with regard to subliminal visual processing in attentional blink and masking paradigms (40, 41). Whilst such paradigms haven’t been employed in the current study, the same principles could readily be applied. Activations in higher order visual areas are linearly related to stimulus clarity (i.e edge disruption) but a certain threshold needs to be exceeded before a “global ignition” occurs, resulting in activation of higher-order parietal and prefrontal areas. Subsequently, reciprocal top-down and bottom-up connections propagate stimulus representation and result in conscious “seen” experience. This could readily account for mock field study findings using eye-tracking in which human participants both pass over camouflaged objects during visual search without detecting them and display longer object visual inspection times before attack (3).

The precise means by which threshold is reached in the visual cortex cannot be determined in the current study. However, it is plausible that this is via a bidirectional hierarchical network in which feedforward and feedback mechanisms serve object delineation (42). This neural framework is an interesting notion with regard to how animals may forage in the field. It is well known that animals can form a “search image” when searching in an environment with multiple prey phenotypes, that is, attention is focussed on one prey type and other prey types may be inhibited (43, 44). Further, it’s been noted that high variation in species phenotype can prevent search image from forming (45). It may be via a top-down enhancement of certain phenotype features within this hierarchical network that a global ignition and conscious experience is reached sooner, a process which would not happen when searching for multiple prey types or when phenotype variation is high. This top-down in enhancement may be consciously driven, or driven by sub-conscious statistical likelihood bias, based on previous experience (46). Investigations which take the predators learning experience into account when considering their interaction with a camouflage prey are vital if we are to understand camouflage in the context of evolutionary ecology, and will be particularly relevant to phenomena such as apostatic selection (47).

481 To the best of our knowledge, this is the first study not only to provide evidence that edge disruption
482 hampers object recognition, but to also provide data to support a plausible neural threshold account
483 as to how camouflage properties result in delayed decision making evasion of capture. We proposed
484 that neurophysiological approaches provide a unique tool for determining how differing camouflage
485 features directly act to manipulate the neural architecture of the observer's visual system and that
486 future studies should prioritise taking contextual learning experiences in to account in order to gain
487 a more nuanced understanding of camouflage in ecological settings.
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Figure Legends: see separate file for figures.

Figure 1: Trial design and stimulus properties

A. Trial sequence (cue in panel 1 is located in the top right bark). **B.** Typical cue stimulus. **C.i.** Dominant edge orientation across stimulus depicted in 1. **B. C.ii.** Dominant edge orientations for a target of the same size and orientation (i.e. greyscale image with no camouflage). **C.iii.** Local EdgeDis (values were averaged to create a global EdgeDis value for each target. EdgeDis was calculated by creating a ratio of parallel (to edge) to orthogonal orientation unit activations (Supplementary Materials 2).

Figure 2: N2pc responses to cue and target as predicted by cue stimulus properties

A: Ipsilateral and contralateral ERP responses for Low Medium and High EdgeDis stimuli (electrodes [PO4, PO8, O2, PO3, PO7, O1]). Stimulus onset and offset at 0 and 0.6 sec respectively. **B:** Topographical plots of Cue N2pc (N2c-N2i) for high, medium and low EdgeDis stimuli. **2C & D.** Spatial distribution of Target N2pc for valid (2C) and invalid (2D) cue trials for high, medium and low EdgeDis stimulus. EdgeDis categorisation is for display purposes only.

Figure 3: Central parietal responses as predicted by certainty

A: Topographic plots of CPP at the point of response (+/- 100msec), distinguished by certainty rating **B:** Cue locked central parietal ERP signature up until the point of response, distinguished by certainty (C=certain, FS=fairly sure, G=gues). ERPs were baseline corrected to the point of stimulus onset on a trial by trial basis. Vertical lines represent mean RT for each level of certainty **C.** Distributions of RTs, displayed as negatives for comparison to 3B. Vertical lines represent mean RTs for each level of certainty.

Figure 4: Mediation analysis with EdgeDis as the independent variable and certainty as the mediating variable.

A. Mediation model with N2pc as the outcome variable (no significant mediation effect) **B.** Mediation model with Npc (during the 800-1050msec time period) as the outcome variable (significant mediation effect). **C.** Npc timecourse following the presentation of cue distinguished by certainty with significant mediation period highlighted (grey filled rectangle). **D** Mediation model with response locked CPP peak as the outcome variable (significant mediation effect). In A, B and D slope estimates are reported below arrows and significance is denoted as: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

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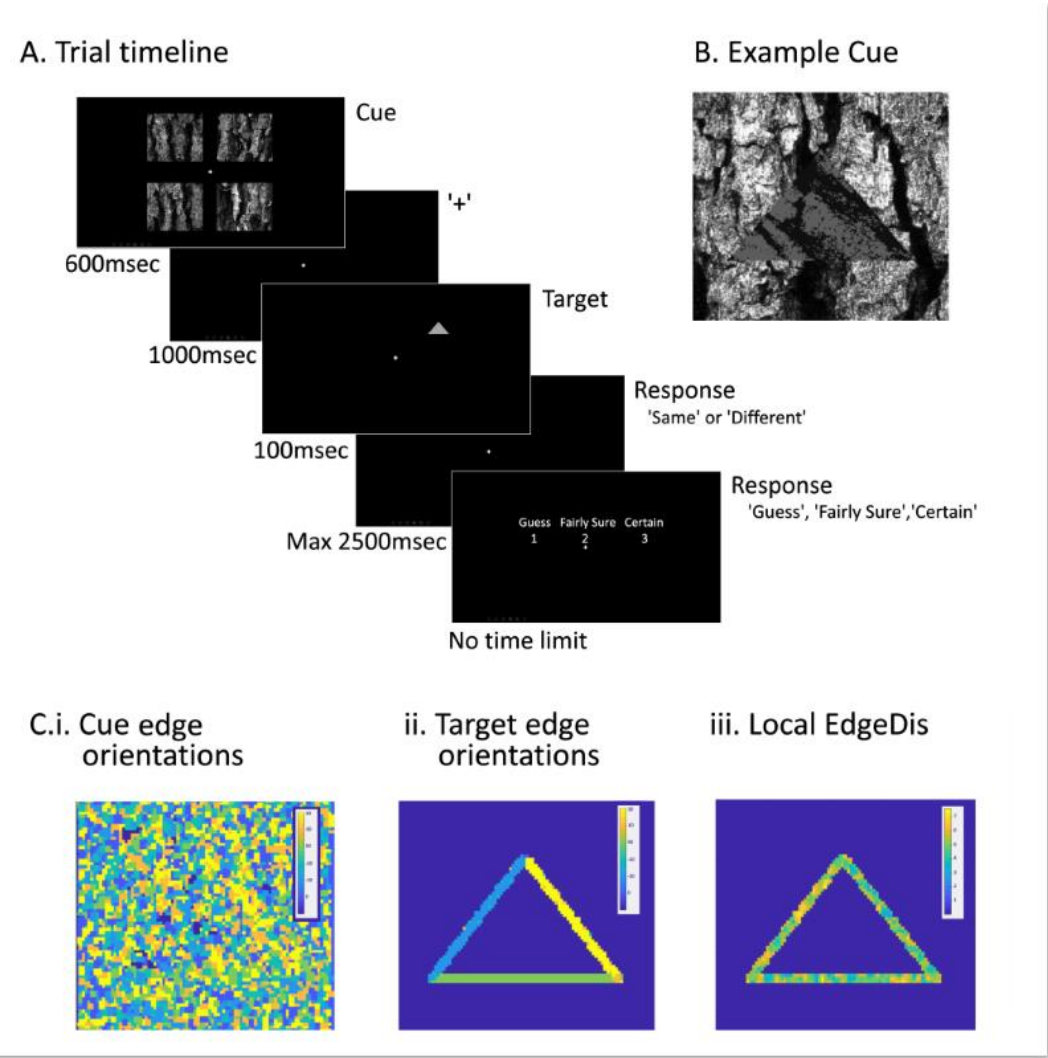
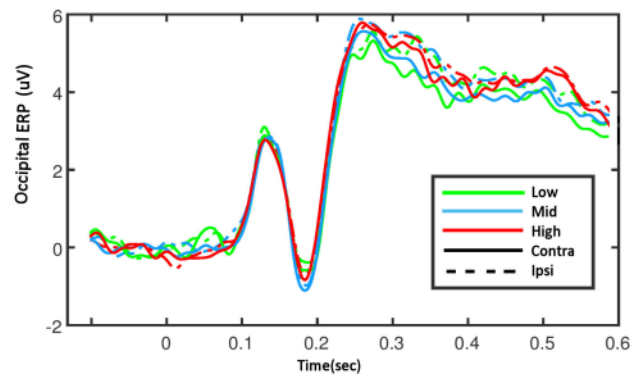


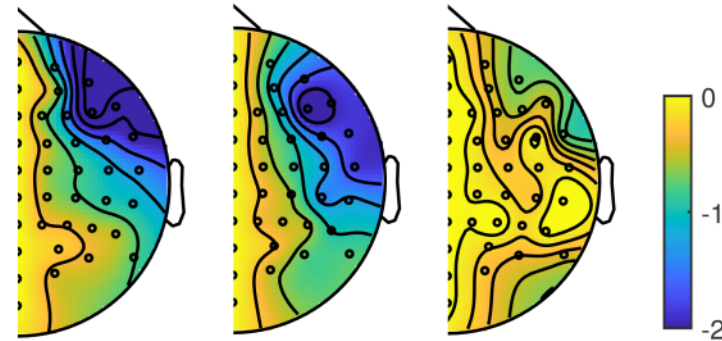
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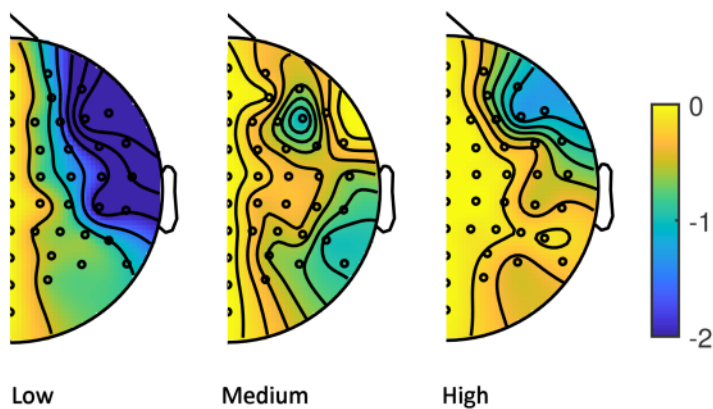
A. Average occipital ERP by EdgeDis



C. Target N2pc by EdgeDis - valid cue



B. Cue N2pc by EdgeDi



D. Target N2pc by EdgeDis -invalid cue

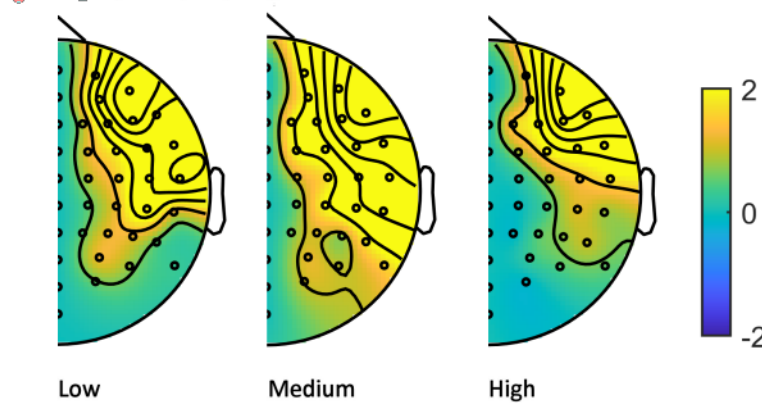


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B: Topographical plots of Cue N2pc (N2c-N2i) for high, medium and low EdgeDis stimuli. 2C & D. Spatial distribution of Target N2pc for valid (2C) and invalid (2D) cue trials for high, medium and low EdgeDis stimulus.

EdgeDis categorisation is for display purposes only.

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A. CPP peak by certainty

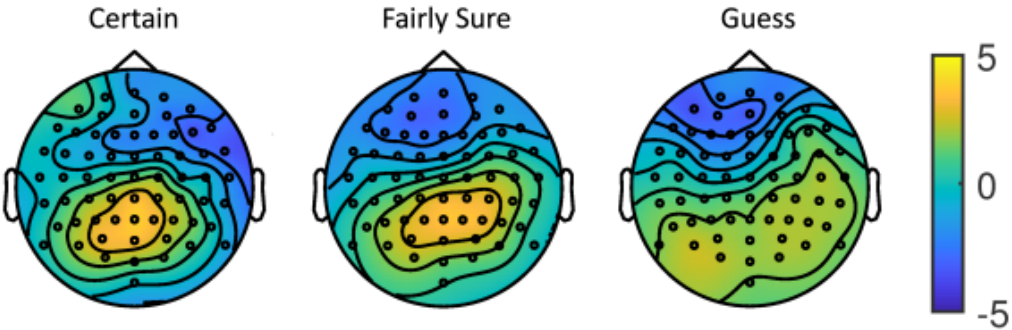
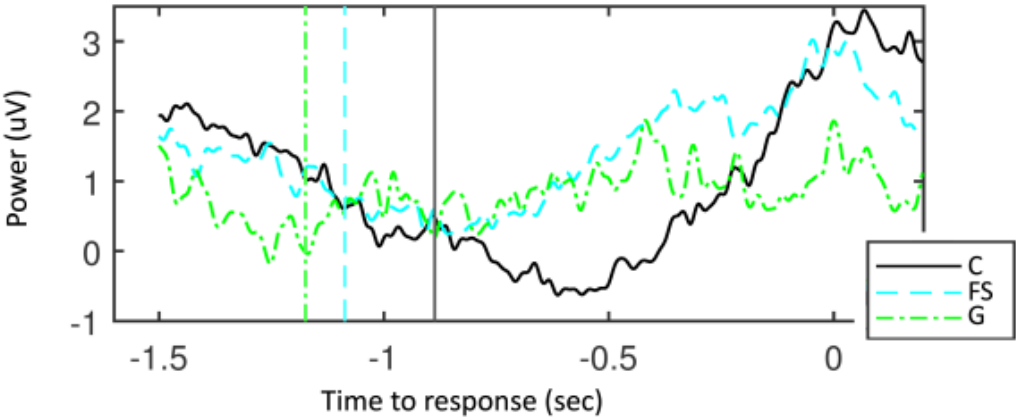
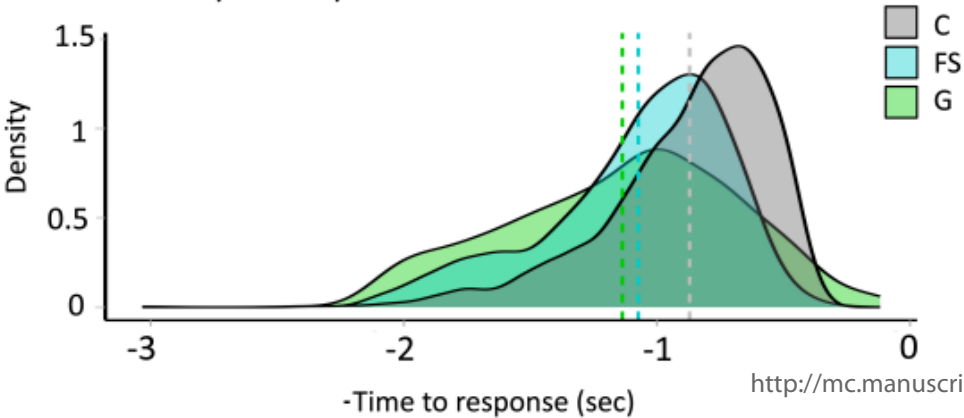


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B. CPP timecourse by certainty



C. RT distribution by certainty



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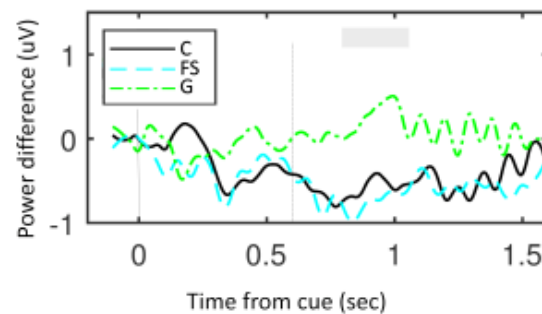
A. N2pc mediation model



B. Npc mediation model



C. Npc timecourse



D. CPP mediation model



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