Cognition does not automatically influence perception:

Evidence from neural encoding of colours belonging to different categories

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Abstract

The firmest evidence in favour of models that posit early high-level influences of cognition on perception comes from electroencephalography (EEG). Enhanced early, pre-attentive processing of light and dark blue feature changes compared to light and dark green changes was reported in Greek speakers, who have two basic terms for 'blue' (*ghalazio/ble*). In the present three-experiment study, we systematically re-evaluate this evidence and test an alternative model that the early difference waves in the human EEG instead mainly reflect contrast adaptation phenomena. We use the same classical oddball paradigm presenting alternating light or dark standards and deviants that systematically differ in colour and/or luminance and chromatic contrast. We then calculate the visual mismatch negativity (vMMN), a putative index of pre-attentive feature change processing and predictive coding derived from EEG data, by subtracting the activity elicited by standards from that elicited by task-irrelevant deviants. Our experiments demonstrate the following: 1) vMMN is driven by contrast adaptation, being observable only in the presence of contrast differences between the stimuli and not reliably observed for different hues of equal contrast; 2) there is no reliable difference between green- and blue-related difference waves in speakers with two basic blue colour categories, the difference waves again driven by contrast rather than their categorical content. Our findings are highly significant for the debate concerning the interface between perception and cognition, as the absence of early categorical effects speaks against models that predict Whorfian-type cognitive influences.

Significance statement

The tide is turning on Whorfian effects of language on colour perception. For a long time, it was accepted that basic language terms alter one's perception of the world in a fundamental manner. The evidence came from electrophysiological responses that indicated early differences between speakers of languages with different basic colour terms. The brain response taken as an indicator of these differences was considered to be a robust marker of early, pre-attentive processing and predictive coding. In this multi-experiment study, we present evidence that early electrophysiological differences to colour index signatures of hue, saturation and luminance contrast and their adaptation, rather than categories. This means that evidence in favour of early, pre-attentive categorical colour perception has been significantly eroded.

Introduction

With its fast temporal resolution, EEG has the potential to provide the most definitive answers to questions that concern an early interplay between perception and cognition. It is therefore not surprising that EEG has been frequently used to study how colour cognition affects colour perception. However, a recent critical review of EEG studies on colour categorisation between speakers of different languages raises some major problems with this body of work and asks for a methodologically sound re-evaluation of the evidence base(1). These concerns are further compounded by specific issues with validity of early electrophysiological markers of visual feature-change detection and their robustness to contrast-adaptation effects(2).

The evidence for early colour category effects is highly significant in relation to the debate on cognitive penetrability of perception (3, 4). As discussed in the keynote dialogue of Ahissar and Scholl on the topic of cognitive penetrability of perception at the European Conference of Visual Perception in 2018, the most robust and direct evidence in favour of penetrability remains the EEG study by Thierry and colleagues on Greek 'blues'(5). This was a classical visual mismatch negativity (vMMN) study, which reported greater vMMN resulting from light and dark blue series of standards and deviants compared to light and dark green series in Greek speakers, who have two basic terms for 'blue' (*ghalazio/ble*). Since vMMN is an electroencephalographic (EEG) component taken to be an early, pre-attentive marker of feature change detection (6), Thierry et al.'s study is considered to provide strong evidence in favour of models that posit high-level, top-down categorical effects on early processing of colour (7) and goes against the more recent categorical facilitation model, which argues that effects of colour categories on perceptual processing are late and mediated by attention(8, 9).

Recently, the vMMN's status as a marker of pre-attentive processing and predictive coding was challenged by Male et al.(2), who demonstrated that the classic vMMN elicited by elementary visual features is driven by adaptation to the repeated, standard stimulus. After experimentally controlling for the effects of adaptation, these authors failed to find a genuine vMMN response to orientation, contrast, phase, and spatial frequency features of Gabor patches. They did, however, identify an early deviant-related positivity (~100 ms) and proposed that, instead of the vMMN, this positive deflection might in fact be the neural marker of early predictive processing of elementary visual feature values. Previously, in the auditory domain, rapid and stimulus-specific adaptation had already been proposed as the underlying mechanism for a similar, standard-stimulus driven build-up in early positivity in evoked activity, related to echoic memory traces(10) and considered as the foundation of predictive coding(6).

Considering this fundamental challenge to the validity of the vMMN as the index of early pre-attentive feature change processing, it is important to re-evaluate Thierry et al.'s findings and provide more robust evidence for theories of colour cognition, and, more generally, for models of the perception/cognition interface. Here, we do that in three experiments, whose key aspects are depicted in Figure 1:

(1) A direct replication of Thierry et al.'s(5) key comparison of light and dark greens and blues with Russian speakers, who, too, have two basic terms for 'blue' (*goluboj/sinij*).
(2) An indirect replication with English speakers, with standards and deviants in the 'cool' and 'warm' regions of colour space, respectively: light/dark blue and light/dark green, which are non-basic terms, and pink/red and yellow/brown, which are basic terms.

(3) A definitive, pre-registered follow-up experiment, in which we test whether the vMMN can be reliably observed for feature changes along three perceptual dimensions of colour: hue, lightness, and saturation (colourfulness). Only hue changes should elicit robust categorical differences.

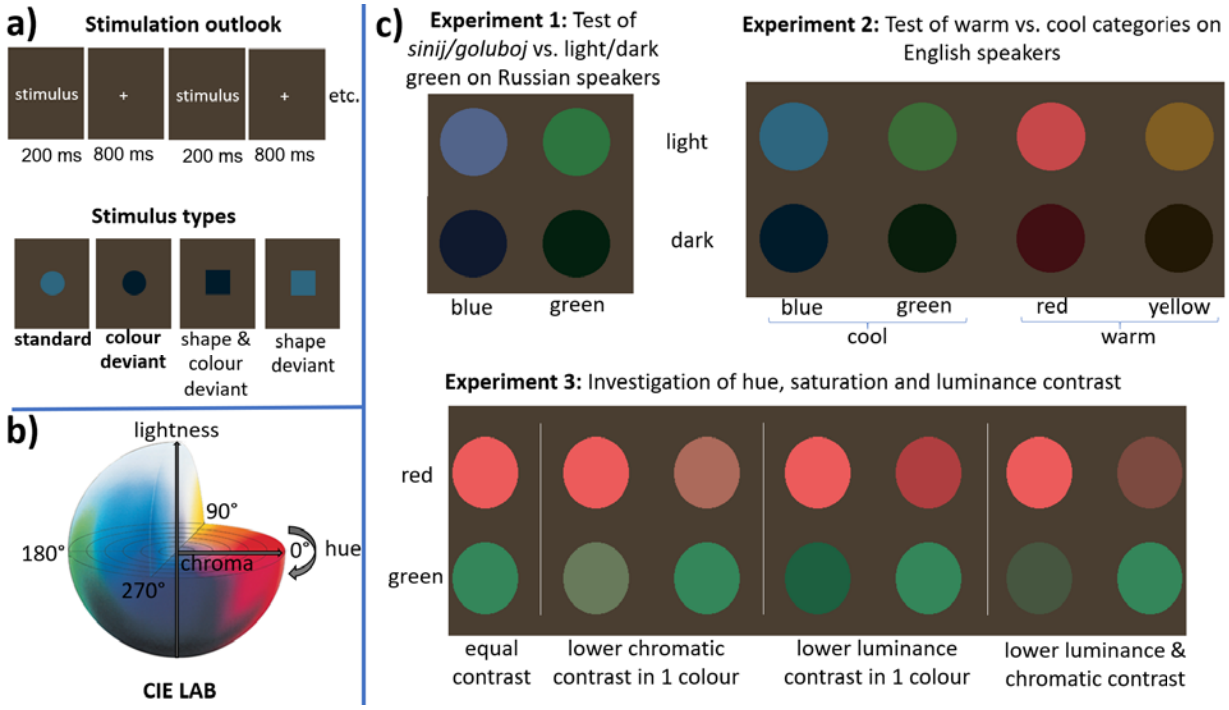

Figure 1. Experimental stimuli and the oddball paradigm*. A) Stimuli are presented in pseudorandom sequences of 3-5 standard stimuli of circular shape, followed by an oddball that is either a deviant only in colour, and thus task-irrelevant, or is also a target (i.e., square) shape. The example stimulus types are taken from a block in which light blue is the standard colour and dark blue the deviant colour. B) CIE LAB colour space, with lightness (L; range 0-100) as its vertical dimension, chroma (C; zero being achromatic) as the distance from the central lightness axis which defines the colourfulness of the stimulus, and hue as the angle of rotation on any of the horizontal planes within the space. Red and green are on the opposite ends of the 0º-180º axis, while blue and yellow lie along the 90º-270º axis. C) Examples of stimulus appearance taken from each of the experiments. Appearance of the stimuli has been simulated to correspond as closely as possible to their appearance in the experiment, within the gamut available on a standard monitor. Note the increased chromaticness and the slight shift towards purple in the blue sample from Experiment 1, which replicates the samples used by Thierry et al. (2009). Note also that in the third experiment, the two colours consistently belong to two different basic colour categories, but are otherwise either equal in chromatic or luminance contrast, different along one of these dimensions only, or different along both dimensions.*

Foreshadowing our findings, we observe that EEG difference waves in the early time-window corresponding to the vMMN are driven by contrast adaptation, rather than presence or absence of colour categories. We fail to replicate Thierry et al.'s(5) observation of enhanced vMMN in speakers with two basic colour terms in the 'blue' region of colour space, their outcome likely stemming from

the fact that the original observation had an effect size whose 95% confidence interval was very close to zero and thus imprecisely estimated (μ_p^2 = 0.112, with a 95% CI of 0.004–0.273, estimated using the non-central F distribution(11)). Instead, we observe a series of robust, well-powered findings that consistently reflect effects of adaptation to chromatic contrast, luminance contrast, or both.

Results

As can be seen from Figures 2-4, our stimuli elicit event-related potential (ERP) patterns similar to those observed in the control participants in the Thierry et al.(5) study. The difference waves in all our experiments, however, appear very dissimilar – in fact, these three experiments provide consistent evidence that negativities in the difference wave in the time window of the vMMN are driven by contrast adaptation, rather than categorical colour properties.

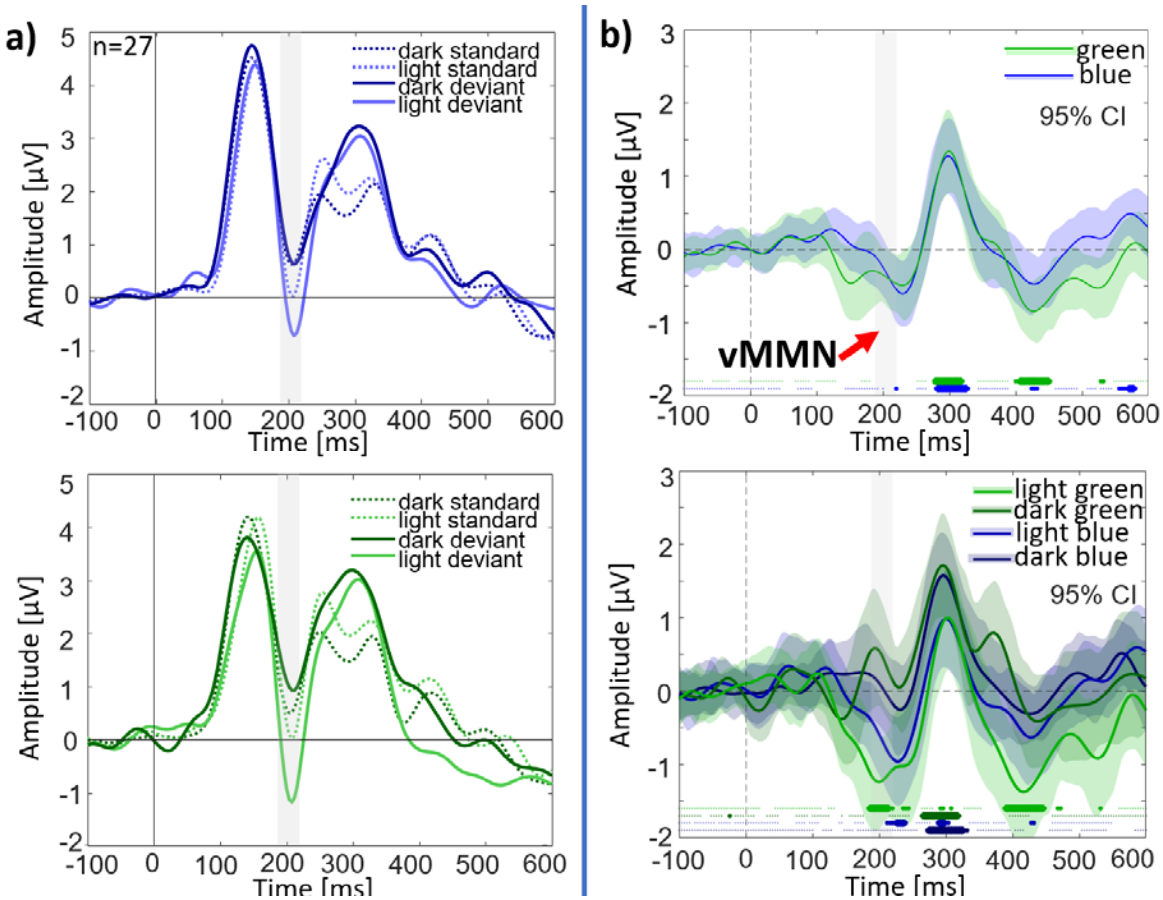

Figure 2. ERPs and difference waves from the experiment on Russian speakers, who are expected to exhibit a higher vMMN for blue due to two basic colour categories for dark and light blue, sinij/goluboj. *(a) this panel depicts the grand-mean waveforms elicited by light and dark standards and deviants for blue (top) and green (bottom panel). Note that during the windows characteristic of the N1 and vMMN components (shaded in grey) it is the light standards and deviants that appear to elicit higher activity, and this is particularly the case with the light deviant, which would follow a set of repeated dark standards. (b) Difference waves, created by subtraction of light and dark standards*

from their respective deviants. The top panel depicts the difference wave averaged across lightness, while the bottom panel depicts the difference waves separately for each hue/lightness combination. Bayes factor values are indicated above the x axis, with smallest dots indicating lack of significant differences from zero (BF < 0.33), medium-sized dots indicating moderate evidence for a significant difference (10 > BF > 3) and large dots indicating strong evidence of a deflection in the difference wave (BF > 10). Two things are of note: (1) the difference wave between blue and green is highly similar and small when averaging across lightness (top panel); (2) averaging across lightness levels however conceals that for dark greens and blues, there is no robust vMMN present, with the component only being notable for light colours. Note: the key ERP components elicited in each top panel are denoted with red arrows and labels, these are P1, N1 and P300 in the ERPs in panel (a) and vMMN in the difference wave in panel (b). The time window of the N1 component is highlighted with a grey overlay.

In the first, near-exact replication on Russian participants (Figure 2), we fail to see a difference between *sinij/goluboj* and light/dark green vMMNs (BF_{10} = 0.301), but observe a modulation by lightness and deviance, which interact: ERP responses in the N1 time-window are more negative for light deviants (-0.96 µV [95%CI -1.33 – -0.60 µV], t(182)=5.206, p<.001, 81% variance explained by the linear mixed effect model; for full model details, see Supplementary Information 1). As noted in Figure 1, light and dark colours differ in chroma (i.e., colourfulness; corresponding to chromatic contrast) as the stimuli were selected from the Munsell Colour System which does not equate different hues in these terms(12). For lighter colours, which also happen to be higher in chroma, we see moderate to extremely strong evidence of a robust difference wave negativity (light blue BF_{10} = 4.491, light green BF_{10} = 218.993), but there is anecdotal to strong evidence of absence of a vMMN-type negativity for darker colours (dark blue BF_{10} = 0.444; dark green BF_{10} = 0.250). Bayesian t-tests conducted across the timecourse of the ERP (see Fig. 2b) corroborate these statistical analyses.

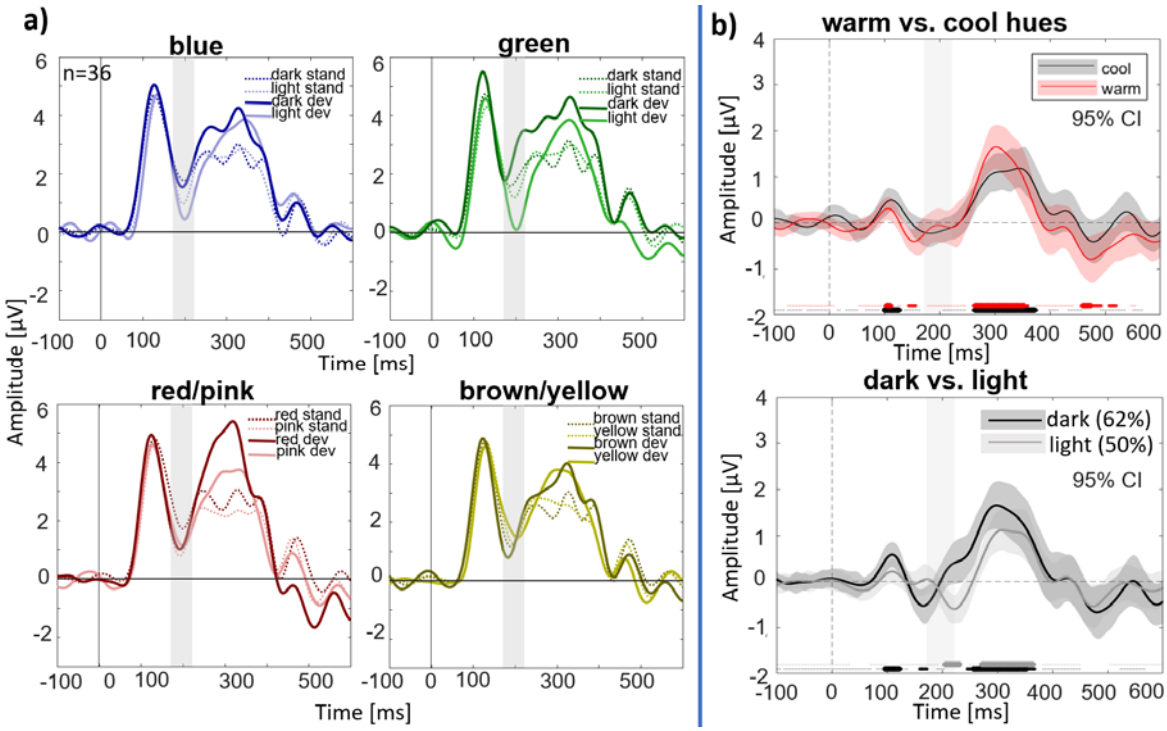

Figure 3. ***ERPs and difference waves from the experiment on English speakers, who are expected to exhibit a higher vMMN for 'warm' hues due to multiple basic colour categories occupying that region of colour space (i.e., red/pink, or yellow/brown), as opposed to the more categorically uniform green and blue ('cool' hue) regions.*** *(a) This panel depicts the grand-mean waveforms elicited by light and dark standards and deviants for light/dark blue and green (top panels) and red/pink and brown/yellow (bottom panel). The overall waveforms are similar to those in Figure 2, with P1, N1 and P300 components being most prominent. Note, however, the apparent differences in the latency of the N1 response in the grey shaded window between dark and light green and yellow, with the N1 peak appearing earlier for darker shades. (b) Difference waves, created by subtraction of warm and cool (top) or light and dark (bottom panel) standards from their respective deviants. Bayes factor values are indicated above the x axis, with smallest dots indicating lack of significant differences from zero (BF < 0.33), medium-sized dots indicating moderate evidence for a significant difference (10 > BF > 3) and large dots indicating strong evidence of a deflection in the difference wave (BF > 10). Two things are of note: (1) The difference wave for warm and cool hues does not exhibit a significant deflection in the N1 window, but there appears to be an earlier positive deflection at ~110 ms, coinciding with the P1 window of the ERP; (2) As in Fig. 2b, averaging hues across lightness levels conceals differences between dark and light colours. We see evidence for a positive deflection at ~110 ms and an earlier subsequent vMMN for dark colours, which also happen to be higher in luminance contrast against background. The effects of contrast on vMMN for dark vs. light colours with an absence of a reliable effect of category for warm vs. cool hues is again inconsistent with an interpretation of early evoked differences in the EEG as a signature of categorical processing. The time window of the N1 component is highlighted with a grey overlay.*

In the second, conceptual replication on English speakers (Figure 3; for Bayesian stats across the difference wave timecourse, see panel B), we fail to observe a reliable vMMN driven by 'warm' (BF_{10} = 0.134) or 'cool' colours (BF_{10} = 0.436), despite the fact that 'warm' colours are denoted by basic colour terms across their light and dark variants, unlike 'cool' colours, which are denoted only by hyponyms or modified terms (for names provided by our participants, see Supplementary Information 2). In this experiment, we removed the difference in chroma between light and dark colours by selecting our colours from CIE LAB space. Instead, we introduced a small difference (12%) in luminance contrast between them. The luminance contrast difference is too small to alter categorical or relative (dark or light) belongingness, but is expected to elicit different degrees of adaptation of ON (light) and OFF (dark) luminance mechanisms (13). In line with this experimental manipulation, we observe difference wave modulations by luminance contrast, with a significant vMMN for lighter (BF_{10} = 2.340) but not darker colours (BF_{10} = 0.142) in the 170-220 ms time window. Figure 3b reveals that this is due to the delay in the vMMN component driven by the less contrasty lighter colours. This time, we do observe a three-way interaction in the linear mixed effect model of ERP amplitudes – there is a significant difference between standards and deviants only for light 'cool' colours, driving the vMMN (-0.762 µV, 95% CI: 0.407 – 1.117 µV; t(519) = 4.210, p<.001; see Supplementary Information 2 for more detail). Thus, instead of the predicted vMMN enhancement for warm colours, we find the opposite pattern, although simulated power analysis (14) demonstrates we have only just enough power to observe this small effect (marginal R^2 = 0.026, conditional R^2 = 0.814; see Supplementary Materials 2 for further details). It can be seen in Figure 3 that the negative ERP difference is shifted forward in time for dark colours. The subsequent P300 deflection in the difference wave then also appears earlier, resulting in the average amplitude being approximately zero in the N1 time window. There is also an early positive component in the difference wave, which is robustly present for darker colours only (BF_{10}=2.03, compared to light

colours BF_{10}=0.21; see also Fig. 3b). The enhanced P1 for darker colours is in line with earlier and stronger luminance OFF responses(15), again conforming with an explanation of early evoked differences as a signature of contrast and its adaptation, rather than categorical processing.

Finally, to verify the observed effects of hue, saturation and luminance contrast on the vMMN, we conducted the third, pre-registered experiment, in which we modulate all three attributes systematically. Consistent with the findings from our first two experiments, vMMN responses were primarily driven by contrast-based properties (see Figure 4). Bayesian hypothesis testing revealed no reliable effect of hue on the vMMN (BF_{10} = 0.197). Changes in saturation elicited asymmetrical responses, with a more negative deflection observed only for saturated deviants relative to standards (see Figure 4b), while desaturated colours showed no such effect, yielding a non-significant overall vMMN for saturation (BF_{10} = 0.238). In comparison, for lightness, we found strong evidence supporting the presence of the vMMN (BF(d<0) = 10.059). This suggests that luminance contrast modulates vMMN amplitude, again, consistent with its explanation by the contrast-adaptation mechanisms rather than categorical colour processing.

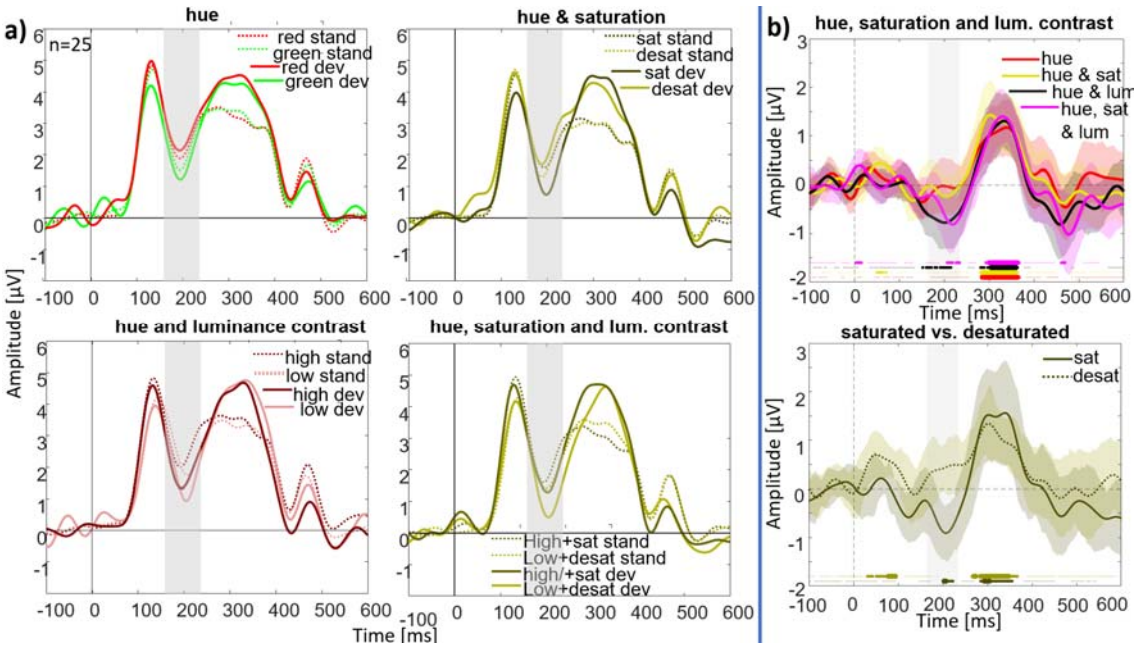

Figure 4. ***ERPs and difference waves from the pre-registered experiment examining the effects of hue, saturation and lightness.*** *As stimuli are defined in CIE LCh space, lightness is equivalent to luminance contrast and chroma (i.e., colourfulness) corresponds to saturation, with higher chromatic contrast for more saturated stimuli. (a) This panel depicts the grand-mean waveforms elicited by standards and deviants differing in hue (red and green; top left), hue and saturation (top right), hue and lightness/luminance contrast (bottom left) or all three (i.e., hue, saturation and lightness; bottom right). The overall waveforms are similar to those in Figures 2 and 3, with P1, N1 and P300 components. Note, however, the differences in the amplitudes and latencies in the P1/N1 complex, with P1 amplitude appearing to be higher and latency faster for higher luminance contrasts. As expected, red also appears to elicit a higher P1 then green(16). (b) Difference waves, created by subtraction of deviants and standards in the four panels of Figure 4A (reflecting differences in hue alone, or hue together with saturation, luminance, or combined contrast differences) or separated between saturated and desaturated hues (bottom panel). Bayes factor values are indicated above*

the x axis, with smallest dots indicating lack of significant differences from zero (BF < 0.33), medium-sized dots indicating moderate evidence for a significant difference (10 > BF > 3) and large dots indicating strong evidence of a deflection in the difference wave (BF > 10). Two things are of note: (1) The difference waves only exhibit a significant deflection in the N1 window when differences in luminance contrast are present. These differences are less robust across time for a combination of saturation and luminance contrast changes. (2) Averaging hues across saturation levels conceals differences between saturated and desaturated colours. This may be the reason why combined effects of saturation and luminance contrast are less robust than for luminance contrast alone. The driver of these differences appears to be in an early appearing positivity for desaturated colours. In Supplementary Materials, we show a summation analysis of chromatic and luminance contrast combinations, depicted in bottom right panel of Figure 4b. This summation is not linear(17). Note that the time window of the N1 component is highlighted with a grey overlay in all subplots.

Discussion

Our findings consistently and robustly demonstrate that colour categories do not automatically influence early neural markers of colour feature processing. We first perform a close replication of Thierry et al.'s(5) authoritative study with Russian participants, who also have two basic terms for blue. Although the two shades fall into different 'blue' categories for both Greek and Russian participants(18), we fail to observe any categorical modulations. In fact, through two further experiments that systematically examine the factors that modulate EEG activity in the time-window of the early, perception-related processing of colour, we observe a series of consistent modulations by adaptation to luminance and colour contrast, with no modulations by basic colour terms. Our findings do not only challenge psychological models that posit an early, automatic influence of cognition on perception(7), but also raise questions that concern models of predictive coding(6), which propose some of the same visual contrast-driven EEG components as neural correlates of prediction.

How can we re-interpret the original finding of Thierry et al.(5) in light of our failed replication? Their study failed to consider that the vMMN could be driven by factors other than categorical stimulus properties, e.g., lightness of a colour. If lightness was included in their statistical models, the authors would have observed that it appears to be the critical factor in eliciting the vMMN. This is not consistent with categorical effects and implies a more basic explanation for drivers of EEG differences. In the Munsell Color System, from which they have drawn their stimuli, lighter colours have higher chromatic contrast (12). Our third experiment, manipulating hue, chromatic or luminance contrast, demonstrates that the vMMN is not robustly present for red vs. green, which is a highly salient categorical difference, but, rather, depends on chromatic and luminance contrast. Notably, while stimuli differing in luminance contrast elicit a robust vMMN, irrespective of whether the deviant or the standard has higher luminance contrast, for chromatic contrast the vMMN is elicited only for the higher-contrast deviant with lower-contrast standards. Chromatic contrast is associated with negative deflections in the early ERP and lacks an initial positive peak(19). The asymmetric effect of refractory activity following adaptation that we report here, to our knowledge, has not been previously reported.

In addition, we fail to observe a difference in 'green' and 'blue' elicited activities in Greek participants, while Thierry et al.(5) do. One possible explanation for this is that the Thierry et al.(5) study was not fully powered for observing a mixed-effect (i.e., between/within-participants) three-way interaction. This is hinted at by the fact that their effect size has very large 95% confidence

intervals that are close to zero (μ_p^2 = 0.112, 95% CI: 0.004–0.273), implying that estimation of the effect was less than fully precise. In our experiment on 'warm' and 'cool' hues, power simulations show that we have just about enough power to observe a conceptually similar three-way within-subject interaction with 36 participants, which is almost twice their sample size of 20.

Returning to the positive aspects of our findings, an even more significant implication of the high susceptibility of vMMN to contrast-adaptation effects concerns models of predictive coding. These models take MMN to be a signature of prediction across all sensory modalities (6). Male et al.(2) argue that the positive difference at ~100 ms may be the signature of prediction for basic featural changes, instead of the vMMN. However, we demonstrate that even this positive deflection is contrast-related, since it is observed reliably only when stimuli vary in contrast and luminance polarity, and that its modulations are not independent of the subsequent modulations in the N1 window (see Supplementary Figure S.3). In fact, one could even argue that the oddball task, as employed by Thierry and colleagues(5), cannot elicit a genuine vMMN since the stimuli are all in the focus of attention. This would be corroborated by large P300 deflections that appear enhanced for deviants as opposed to standards (see Figures 2-4). Future studies will need to perform systematic tests of contrast vs. feature responsiveness at different retinal locations to establish whether foveal vMMN exists independently of contrast(20, 21).

In conclusion, our results reliably, consistently and systematically confirm the crucial role of contrast and contrast adaptation, rather than categorical basicness, in driving early event-related activity in the EEG in the first 200 ms of processing. This refutes some of the strongest evidence in favour of models that propose a high degree of cognitive penetrability of perception(5, 7). Indeed, further studies of cognitive penetrability of perception could benefit from testing their predictions in the colour vision domain, where much is already known about the low-level drivers of visual evoked potentials(22) and therefore potential low-level confounds are easier to predict and account for. This also applies to the search for neural markers of predictive coding. In fact, it would be highly interesting if in the visual domain they were built upon the probabilistic read-out of other, more basic and general biological mechanisms such as contrast adaptation(23). Having contrast adaptation at the root of prediction is not inconsistent with computational models of adaptation that involve 'unaware' read-outs(24). Indeed, examining the contributions of sensory adaptation to prediction anomalies would be a highly fruitful avenue for future research, of particular relevance for clinical applications of the model, which presume aberrant predictive coding in psychosis and often rely on MMN measures (25, 26).

Methods

Participants. *27 native Russian participants recruited from a university student population (10 male; all right-handed; mean age 23, range 19-25) completed the exact replication of experiment 1. Three further participants were removed from the sample: the first did not complete the experiment, the second had an excessive miss rate (56%) and the third produced insufficient artifact-free trials. All participants had normal or corrected-to-normal vision and showed normal colour vision assessed by the Farnsworth-Munsell 100 Hue test. Before participating, they gave written informed consent. The experiment was approved by the Ethics Committee of Smolensk State University.*

The next two experiments were conducted at the University of Edinburgh, with study protocols approved by the Psychology Ethics Committee. In the conceptual replication with English speakers (experiment 2), 36 participants (6 male, 1 non-binary; 4 left-handed; mean age 25, range 19-36) were

kept in the final sample, with 5 participants removed due to technical issues during the recording. Our final, pre-registered follow-up experiment on colour feature determinants of the vMMN (experiment 3; https://osf.io/ymk9u/) included 25 participants (9 male, 2 left-handed, mean age 26, range 18-59) in the final sample, with 1 further participant removed due to an incomplete EEG session. All participants were recruited through posters around the university campus and word-of-mouth. They reported normal or corrected-to-normal visual acuity and had adequate colour vision, as assessed with the diagnostic plates from the City University test(27). Participants gave written informed consent and were reimbursed for their participation.

All three studies were conducted in line with the Declaration of Helsinki (1964).

Apparatus, stimuli and procedure. *Experimental stimuli and procedures were aligned as much as possible between the two experimental sites (Smolensk and Edinburgh), despite the reliance on different types of apparatus and EEG recording systems.*

Experiment 1 (Smolensk) was run on an X-Rite™ Pantone® certified factory calibrated AERO 15 OLED 15.6-inch monitor with a screen resolution of 3840 x 2160 pixels at a refresh rate of 144 Hz viewed from a distance of 70 cm in a dark room with no other light source. Accuracy of colour reproduction on the monitor during the experiment was controlled with the help of the The Calibrite ColorChecker Display Pro device and software. The experiment was run using Psychophysics Toolbox Version 3 (PTB-3) software that extends Matlab (Mathworks, USA) with functions for research-grade stimulus presentation and response collection (28, 29). A VOROTEX K03 Red Switch (Vorotex, China) response pad with a simplified 3-key layout was used to collect behavioural data.

Experiments 2 and 3 (Edinburgh) were conducted using a calibrated Display++ screen (Cambridge Research Systems [CRS], UK) controlled by a ViSaGe visual stimulus generator (CRS, UK). The experiments were run using the CRS toolbox and CRS colour toolbox (30) for Matlab (Mathworks, USA). Measurements of monitor spectra were obtained using a SpectroCAL (CRS, UK) spectroradiometer. Participants were seated at a 70-cm distance from the display, which was positioned in a dark room with no other light source. They provided responses using a Cedrus-RB530 button box (Cedrus, USA).

Stimulus colours are depicted in Figure 1. Stimuli subtended 2° visual angle enabling use of 2° colour matching functions for calculating colour coordinates via the Optprop toolbox for Matlab(31). As in Thierry et al.(5), a grey background was set to CIE 1931 coordinates 0.3128, 0.3290, 26.2 cd/m^2.

In experiment 1, colours were identical to those used by Thierry et al. (CIE 1931 dark blue: 0.234, 0.230, 10.7 cd/m^2, light blue: 0.259, 0.264, 41.5 cd/m^2, dark green: 0.259, 0.397, 10.7 cd/m^2, light green: 0.279, 0.377, 41.7 cd/m^2). Luminance contrast against the background amounts to 59%, with LCh transformation of CIE LAB coordinates for lightness (L), chroma (C) and hue (h) equal to L=39 for dark colours, L=71 for light colours, and C=41, h=255° for dark blue, C=46, h=253° for light blue, C=31, h=156° for dark green, and C=39, h=154° for light green. The differences in chroma and hue between Munsell colours of different lightness result from the fact that this colour system is not designed to be perceptually uniform across its three different dimensions, unlike CIE LAB(12).

In experiment 2, colour coordinates were defined in CIE LAB with two aims in mind: 1) to ensure equal saturation and hue, by setting all colours to have equal chroma (C = 27) and hue angles (green h=155°, blue h=254°, red h=0° and yellow h=101°), while keeping colour appearance of green and blue broadly similar to that in the Thierry et al.(5) study; 2) to introduce a small difference in luminance contrast (with luminance of 10.08 cd/m^2 for dark and 39.34 cd/m^2 for light colours, equal to 62% and 50% contrast, respectively): whilst insufficient to alter the relational (light or dark) or

categorical status (yellow or pink), such luminance contrast would still be sufficient to affect the EEG response systematically due to varying response properties for luminance ON and luminance OFF neurons(15). CIE LAB was chosen as it accounts for differences in saturation effectively(32).

We verified that colours indeed belonged to the same or different categories by asking participants to free name all colour samples at the end of the experiment. Colour circles were presented on the screen in a randomised order; we report frequency and percentage of basic colour terms assigned to them, as well as of hyponyms, modified, compounded, or 'fancy' terms that could be allocated to those same categories (e.g., periwinkle for light blue; see Supplementary Materials for the full list of names). Light and dark blue stimuli were named blue by 21 (58%) and 29 (81%) participants, respectively, with the remaining participants generally using non-basic terms that would fall under light or dark blue. A similar picture emerged for light and dark green, which were named green by 16 (44%) and 28 (78%) participants, respectively. Pink was labelled as such by 27 (75%) of observers, while in naming of the red sample both pink (10 participants, 28%) and red (8 participants, 22%) were prominent (for similar patterns of pink naming, see Rosenthal et al., 2021). Yellow was named as such by 30 (79%) participants, while naming of the brown stimulus was split across two basic terms, with 11 participants (31%) opting for green and the same number opting for brown. An increase of greenness in yellow colours with reduction of luminance was to be expected(33).

In experiment 3, we selected our colours so as to manipulate hue, saturation and luminance contrast selectively – either in isolation or in combination with each other – to test the effects observed in the first two experiments in a principled manner. These manipulations were preregistered prior to data collection on the Open Science Framework (OSF; https://osf.io/ymk9u/). Colours – red and green – were specified using CIE LAB LCh coordinates, which allowed us to systematically vary perceptual properties across blocks. Red was always set to h=0° and green to h=180° in CIE LCh. The experiment consisted of 16 blocks, organised into 8 block pairs, with standard and deviant roles reversed within each pair. Blocks 1-2 and 3-4 had stimuli of fixed lightness and chroma (L=75, C=27 for both red and green). In blocks 5-6 and 7-8, both hue and chroma were manipulated - in blocks 5-6 green was desaturated (L=75, C=27 for red and L=75, C=10 for green), while in blocks 7-8 red was desaturated (L=75, C=10 for red and L=75, C=27 for green). Blocks 9–10 and 11–12 manipulated hue in combination with luminance contrast, lowering lightness while keeping chroma constant (L = 75, C = 27, h = 0° vs. L = 65, C = 27, h = 180°; and L = 65, C = 27, h = 0° vs. L = 75, C = 27, h = 180° respectively). Finally, blocks 13–14 and 15–16 introduced combined changes in all three dimensions—hue, chroma, and lightness. In blocks 13–14, both chroma and lightness were reduced for one hue (L = 75, C = 27, h = 0° vs. L = 65, C = 10, h = 180°), and in blocks 15–16, the asymmetry was reversed (L = 65, C = 10, h = 0° vs. L = 75, C = 27, h = 180°). Each block comprised 225 trials, of which 45 were deviant (either by colour, or shape, or combination of both).

Our experimental procedure followed closely the template provided by Thierry et al.(5). Stimuli were presented for 200 ms with an interstimulus interval of 800 ms. Streams of 3, 4 or 5 standard stimuli were followed by a randomly selected oddball stimulus resulting in stimulus streams with 6.67% oddballs of each type (shape only oddball, luminance and shape oddball, luminance only oddball; in Thierry et al. paper, oddball proportions were incorrectly reported as 10%, as personally communicated to us by that study's co-authors Benjamin Dering and Jan-Rouke Kuipers). Participants were instructed to respond to shape oddballs (i.e., squares) and ignore circles. The stream contained the following total numbers of stimuli: 2700 in four blocks of 675 trials, which included 540 standards and 135 deviants (45 of each type) in experiment 1; 3600 in eight blocks in experiment 2, with 450 standards and 90 deviants of each colour (30 of each type; thus 60 non-target deviants, when collapsed across 'warm' and 'cool' hues) in experiment 2; and 3600 in experiment 3, separated into

16 blocks. Block order was randomised across participants. One participant from experiment 1 was rejected due to low hit rate (<75%). Participants remaining in the sample performed the task with a high degree of accuracy (experiment 1: 86.0% correct rejections, 0.7% false alarms, 13.0% hits, 0.3% misses, reported as a percentage out of a total of 100%, with average reaction time (RT) and standard deviation 600 ± 115 ms; experiment 2: 86.5% correct rejections, 0.2% false alarms, 12.9% hits, 0.4% misses, RT 423 ± 95 ms; experiment 3: 86.49% correct rejections, 0.18% false alarms, 13.06% of hits and 0.27% misses, RT 444 ± 98 ms).

EEG recording and pre-processing. *In Smolensk (experiment 1), electrophysiological data were recorded continuously using an eego mylab 64-channel amplifier and waveguard original EEG caps, with 64 Ag/AgCl electrodes placed according to the extended 10–20 system. Data was sampled at 250 Hz. Bipolar horizontal and vertical electrooculograms were recorded simultaneously to monitor eye movements. Impedance of all electrodes was kept below 10 kΩ. Stim Tracker (Cedrus, San Pedro, CA, USA) was used to synchronise stimuli with the EEG data, bypass delays associated with operating systems, and accurately record true onset time of the stimuli. In Edinburgh (experiments 2 and 3), continuous EEG was recorded using a 64-channel BioSemi Active-Two (Biosemi, Netherlands) amplifier system, digitising the signal at a 1024 Hz sampling rate. 64 Ag-AgCl electrodes were mounted in an elastic, tight-fitting cap. In addition, we also recorded horizontal (HEOG) and vertical (VEOG) electrooculograms and two mastoid references. Stimulus triggers were sent from the Display++ device, synchronised to stimulus onset using Visage Framestore cycling functions.*

Data from both sites were analysed in Matlab (Mathworks, US) using the EEGLAB toolbox(34). FASTER(35) and ADJUST(36) toolboxes were used for artifact rejection and correction. Initially the data were average-referenced and filtered using a 40 Hz low-pass and 0.1 Hz high-pass Hamming windowed sinc Finite Impulse Response (FIR) filters, as implemented in EEGlab(34). Recordings were then separated into epochs representing individual trials, 1000 ms in duration. This consisted of a 200-ms period before the stimulus onset and 800 ms thereafter. We also applied a baseline correction between -100 and 0 ms. Contaminated trials were identified and rejected using the FASTER toolbox. This is done by characterising global channel properties using statistical parameters of the data and applying a metric of ±3 z-score as a marker for contaminated data. Independent component analysis (ICA) was then performed using the default runica algorithm; the ADJUST toolbox was used to identify specific components driven by blinks, eye movements and local discontinuities. These were removed from the data. Following artifact rejection, FASTER was used to identify any contaminated channels and interpolate them from neighbouring channels. A threshold of ±3 was applied to the F-score parameter to define these outliers, which were removed and interpolated. A manual check was then performed on the data to verify quality of the artifact rejection procedure. In experiment 1, percentage of rejected trials ranged between 1% and 5%; in experiment 2, this was between 1% and 7% and in experiment 3 between 1% and 5%. As in Thierry et al., the vMMN was quantified over parieto-occipital electrodes: in experiment 1, these were O1, O2, Oz, PO7 and PO8, while in experiments 2 and 3, Iz was also available in the electrode montage and, thus, added to this electrode cluster. Time-windows for statistical analyses were selected to encompass the N1 peak from the grand-mean ERP plots: 188-220 ms in experiment 1, 172-223 ms in experiment 2, and 164-234 ms in experiment 3. The slight differences in the time-windows stem from the need to encompass the N1 component of the ERP, which varied in latency in those experiments that manipulated contrast along expected lines(19, 37).

Statistical Data analysis. *We fitted linear mixed effects models (LMEMs) to our data, with random by-participant intercepts to model overall differences in amplitude between observers and fixed effects of deviancy, hue and lightness (in experiment 3, there was an additional fixed effect of*

saturation) to model our experimental manipulations, with simple coding of effects. To evaluate whether the ERP difference wave manifested a reliable difference from zero, we used Bayesian t-tests(38). Other statistical analyses were implemented in R 4.3.1(39) using the following packages: lmerTest 3.1-3(40), emmeans 1.10(41), DHARMa 0.4.6(42), simr 1.0.7(43), and BayesFactor 0.9.12(44). For further details of statistical analysis, see Supplementary Materials, where we also report statistical sensitivity/power analyses and all the properties of best fitting models.

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Supplementary Materials

Colour perception and cognition: Revisiting classical findings of categorical influences

by Martinovic et al.

1 – Effect of additional basic colour categories in the 'blue' region of the colour space (Experiment 1)

Best fitting linear mixed effect model: Fixed effects of deviancy (standard - reference level, or deviant) and lightness (dark – reference level, or light) and random by-participant intercepts only.

Model: amplitude ~ deviancy*lightness + 1|participant

	Amplitude (μV)		
Predictors	Estimates	95% CI	p
(Intercept)	-0.12	-0.86 – 0.61	0.742
Deviancy	-0.49	-0.75 – -0.23	**<0.001**
Lightness	-0.81	-1.07 – -0.56	**<0.001**
Deviancy × Lightness	-0.95	-1.46 – -0.43	**0.001**
Random Effects			
σ^2	0.87		
$\tau_{00\ participant}$	3.51		
ICC	0.80		
$N_{participant}$	26		
Observations	205		
Marginal R^2 / Conditional R^2	0.061 / 0.814		

Prior to statistical analyses, we rejected any datapoints that were outliers – this resulted in a rejection of 11 datapoints, which included all the datapoints from one participant (as can be seen from N and Observation rows in the table above).

Assumption checks were performed using the DHARMa R package and confirmed that the data was appropriate for the fitted model. We also verified that the predictors were not correlated by fitting an additive model and evaluating it with the *check_collinearity* function from the performance R package.

Initially, we fitted a model with the full set of fixed effects (deviancy*colour*lightness), but the step function from lmerTest R package indicated that colour (with two levels: blue and green) did not contribute significantly to the model, individually or in interaction with the other two factors:

Deviancy:Colour:Lightness, $F(1, 171.98) = 3.4135$, $p = 0.066$

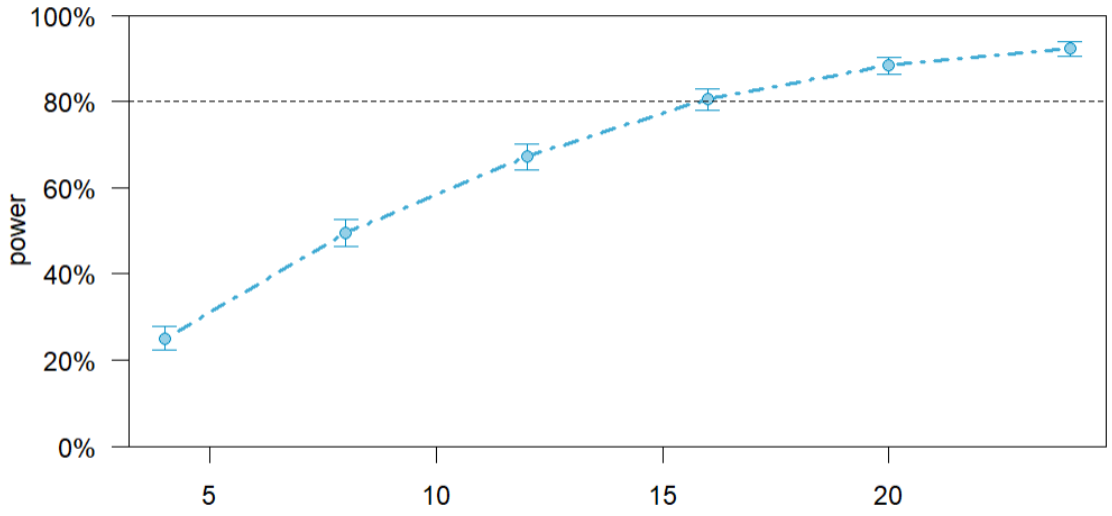
Deviancy:Colour, $F(1, 172.98) = 0.0339$, $p = 0.854$

Colour:Lightness, $F(1, 173.98) = 0.631$, $p = 0.428$

Colour, $F(1, 174.98) = 0.0436$, $p = 0.835$

On the other hand, deviancy and lightness interacted significantly and therefore could not be removed from the model ($F(1,175.98)=12.963$, $p<.001$).

Power analysis: Sensitivity analyses were performed by resampling the number of participants (1000 simulations) and evaluating the observed power for obtaining the statistically significant fixed effects in the best fitting model, using the R package *simr*. Sufficient power is reached within 16 participants for the interaction of deviancy and lightness (see Figure below, plotting simulated power on the y axis against number of participants on the x axis). We also evaluated the power to detect the observed effects if they were reduced by 15%, as advised by Kumle and colleagues ((14)), and found that this was 91.70% (95% CI: 89.81% - 93.34%).



S1. Supplementary Figure 1. Power analysis for Experiment 1: deviancy by lightness interaction.

2 – Differences between 'warm' and 'cool' colours, which differ in lightness-based basic colour terms (Experiment 2)

Best fitting linear mixed effect model: Fixed effects of deviancy (standard - reference level, or deviant), colour (cool – reference level, or warm) and lightness (dark – reference level, or light) and random by-participant intercepts only.

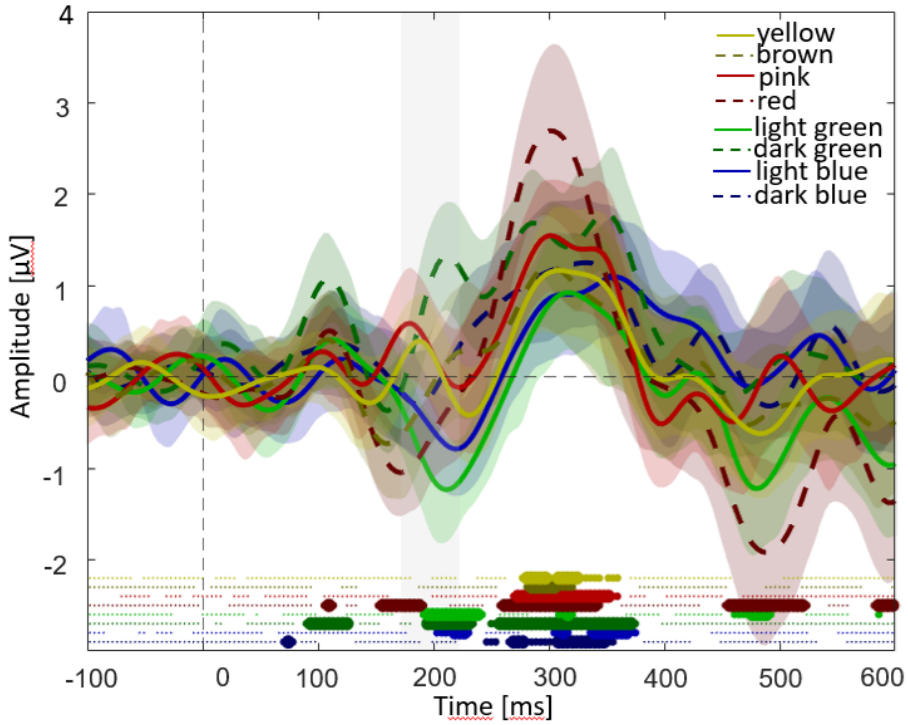
Model: amplitude ~ deviancy*lightness*colour + 1|participant

	Amplitude (μV)		
Predictors	Estimates	95% CI	P
(Intercept)	1.56	0.83 – 2.28	**<0.001**
Deviancy	-0.20	-0.38 – -0.02	**0.029**
Colour	-0.04	-0.21 – 0.14	0.689
Lightness	-0.50	-0.68 – -0.32	**<0.001**
Deviancy × Colour	0.11	-0.24 – 0.47	0.525
Deviancy × Lightness	-0.24	-0.59 – 0.12	0.193
Colour × Lightness	0.87	0.51 – 1.22	**<0.001**
Deviancy × Colour × Lightness	1.56	0.85 – 2.27	**<0.001**
Random Effects			
σ^2	1.14		
$\tau_{00\ participant}$	4.86		
ICC	0.81		
$N_{participant}$	36		
Observations	562		
Marginal R^2 / Conditional R^2	0.026 / 0.814		

Prior to statistical analyses, we rejected any datapoints that were outliers – this resulted in a rejection of 14 datapoints (as can be seen from Observations row in the table above).

Assumption checks were performed using the DHARMa R package and these confirmed that the data was appropriate for the fitted model. We also verified that the predictors were not correlated by fitting an additive model and evaluating it with the *check_collinearity* function from the performance R package.

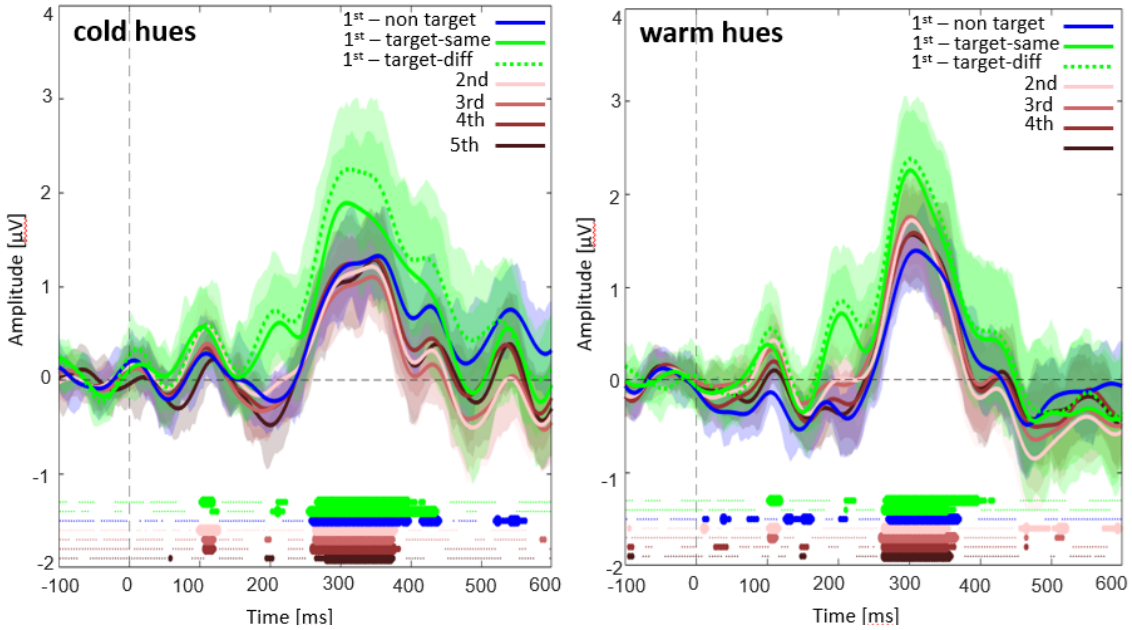
The best fitting model is identical to the full model we initially fitted, as there was a significant 3-way interaction between colour, lightness and deviancy ($F(1,518.58)=18.506$, $p<.001$). For a Figure depicting this interaction, see below, with Bayesian stats delineated (smallest dot – evidence of absence, BF<1; medium dot - moderate evidence for a significant difference (10 > BF > 3); large dot - strong evidence of a deflection in the difference wave, BF > 10):



S2. Supplementary Figure 2. Difference waves elicited by dark and light versions of each colour, with the vMMN window indicated by a shaded grey area around 200 ms. Shaded areas around each wave indicate the 95% between-subject CIs. As in the plots in the main manuscript, Bayes factor values are indicated above the x axis. Smallest dots indicate lack of significant differences from zero (BF < 0.33), medium-sized dots indicate moderate evidence for a significant difference (10 > BF > 3) and large dots indicate strong evidence of a deflection in the difference wave (BF > 10).

The plot reveals that the three-way interaction between colour, lightness and deviancy is likely to be driven by the larger negative deflections for lighter and cooler colours. The difference wave for red also appears to be significantly more negative, but in a slightly earlier time window, while the brown, yellow and pink difference waves did not exhibit an early negativity.

Finally, we also analysed if the difference waves depended on the order of the standard in the stimulus train – as the non-target deviant always followed a stream of 3, 4 or 5 standards. This is depicted in the supplementary figure S.3 below.



S.3 Supplementary Figure. Difference waves for cold (left) and warm (hues) calculated separately for each standard (1st-5th, with standards also separated depending on the preceding deviant). For both types of hues, significant responses in the P1 window are elicited by 1st standards that follow target stimuli (i.e. squares) and 2nd standard – in parallel, strongest negative responses in the N1 window are observed for the 5th standard. On the other hand, 1st standards that follow a target elicit a positive peak in the difference wave in the same time-window.

Power analysis: Sensitivity analyses on the best fitting model were performed by resampling the number of participants (1000 simulations) and evaluating the observed power for obtaining the statistically significant three-way interaction, using the R package *simr*. We evaluated the power to detect the observed 3-way interaction if effect sizes were reduced by 15%, as advised by Kumle and colleagues ((14)), and found that this was 68.50% (95% CI: 65.52% - 71.37%); for effect sizes reduced by 10%, we had 76.10% power (95% CI: 73.33-78.71%) and for effect size reduced by 5% we had 79.20% power (95% CI: 76.55-81.68%).

Free colour naming of colour circles:

1) ***light blue:*** *blue n=21, light blue n=8, sky blue n=3, baby blue n=2, pale blue n=1, periwinkle n=1;*

2) ***dark blue:*** *blue n=29, dark blue n=4, deep blue n=1, royal blue n=1, turquoise n=1;*

3) ***light green:*** *green n=16, light green n=7, mint n=5, turquoise n=3, aquamarine n=1, lime n=1, matcha green n=1, sage green n=1, sage n=1;*

4) ***dark green:*** *green n=28, dark green n=5, forest green n=1, olive green n=1, olive n=1;*

5) ***pink:*** *pink n=27, light pink n=5, red n=2, rose n=1, salmon pink n=1;*

6) ***red:*** *pink n=10, red n=8, dark pink n=4, maroon n=4, magenta n=2, rose n=1, raspberry n=1, burgundy n=1, mauve n=1, purple n=1, purpley pink n=1, brown-red n=1, pinky maroon n=1;*

7) ***yellow:*** *yellow n=30, light yellow n=3, pale yellow n=2, green n=1;*

8) ***brown:*** *green n=11, brown n=11, dark green n=4, olive green n=2, olive n=1, hazel n=1, swamp n=1, taupe n=1, yellow n=1, khaki n=1.*

3 – Early negativities driven by differences in hue, saturation and luminance contrast (Experiment 3)

Initially, we fitted a model with the full set of fixed effects (deviancy*colour*lightness*saturation), but the step function from lmerTest R package indicated that hue (with two levels: red and green) contributed significantly to the model only on its own, rather than in interaction with the other three factors, which also failed to interact in a 3-way fashion with each other:

Deviancy:Hue:Saturation:Lightness, $F(1, 654.99) = 0.0174$, $p = 0.895$

Deviancy:Hue:Saturation, $F(1, 655.99) = 0.0198$, $p = 0.888$

Hue:Saturation:Lightness, $F(1, 656.99) = 0.2164$, $p = 0.642$

Hue:Saturation, $F(1, 657.99) = 0.8408$, $p = 0.359$

Deviancy:Hue:Lightness, $F(1, 658.99) = 1.1350$, $p = 0.287$

Deviancy:Hue, $F(1, 659.99) = 0.1456$, $p = 0.703$

Hue:Lightness, $F(1, 660.99) = 0.6421$, $p = 0.423$

Deviancy:Saturation:Lightness, $F(1, 662.00) = 3.091$, $p = 0.079$

A series of two-way interactions remained in the model, together with the fixed effect of hue:

Hue, $F(1, 663.00) = 9.706$, $p = 0.002$**

Deviancy:Saturation, $F(1, 663.00) = 7.301$, $p = 0.007$**

Deviancy:Lightness, $F(1, 659.99) = 4.994$, $p = 0.026$*

Saturation:Lightness, $F(1, 660.99) = 6.427$, $p = 0.011$*

The best-fitting model properties are listed below:

amplitude ~ deviancy + hue + saturation + lightness + (1 | participant) + deviancy:saturation + deviancy:lightness + saturation:lightness

	Amplitude (μV)		
Predictors	Estimates	95% CI	P
(Intercept)	1.94	1.17 – 2.71	**<0.001**
Deviancy	-0.35	-0.56 – -0.14	**<0.001**

Hue	0.28	0.10 – 0.46	**0.002**
Saturation	-0.17	-0.39 – 0.04	0.109
Lightness	-0.23	-0.45 – -0.02	**0.031**
Deviancy × Saturation	0.57	0.16 – 0.98	**0.007**
Deviancy × Lightness	-0.47	-0.88 – -0.06	**0.026**
Saturation × Lightness	-0.55	-0.97 – -0.12	**0.011**
Random Effects			
σ^2	1.43		
$\tau_{00\ participant}$	3.75		
ICC	0.72		
$N_{participant}$	25		
Observations	695		
Marginal R^2 / Conditional R^2	0.019 / 0.729		

Post-hoc tests via emmeans package (using multivariate t distribution method for correction for multiple comparisons) revealed the following drivers for the observed interactions and the main effect of hue:

<u>For saturation x lightness</u>: Lower lightness was associated with lower amplitudes only when the stimulus was also desaturated (all other ps > 0.872):

higher saturation and lightness vs. desaturated lower lightness: 0.407, 95%CI 0.143-0.672, t(663)= 3.015, p = 0.0139

desaturated of higher lightness vs. desaturated lower lightness: 0.508, 95%CI 0.175-0.841, t(663)= 2.985, p = 0.0151

higher saturation and lower lightness - desaturated lower lightness: 0.4482, 95%CI 0.115-0.7814, t(663) = 2.634, p = 0.0413.

<u>For saturation x deviancy</u>: Higher saturation standards elicited higher amplitudes (all other ps > 0.635):

Higher saturation standard vs. higher saturation deviant: 0.6363, 95%CI 0.393-0.879, t(663) = 5.116, p <.0001

Higher saturation standard vs. desaturated standard: 0.4580, 95%CI 0.162 – 0.754, t(663) = 3.043, p = 0.0128

Higher saturation standard vs. desaturated deviant: 0.5258, 95%CI 0.228-0.824, t(663) = 3.464, p = 0.0030

<u>For lightness x deviancy</u>: Lower lightness deviants elicited lower amplitudes (all other ps > 0.781):

standard higher lightness - deviant lower lightness: 0.58541, 95%CI 0.287-0.883, t(663) = 3.856, p< 0.001

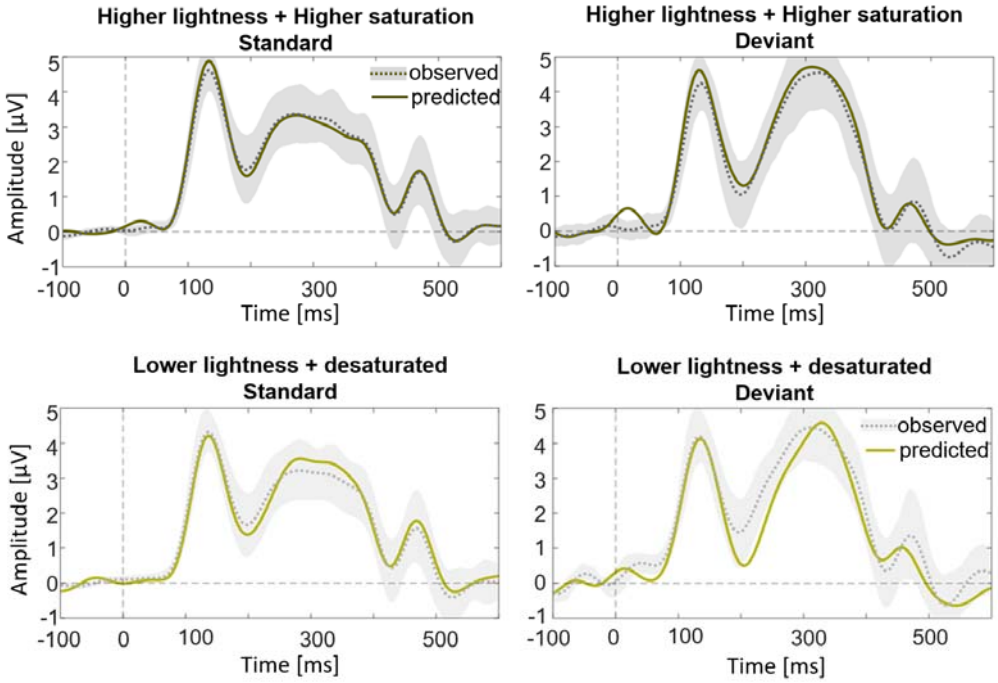
deviant higher lightness - deviant lower lightness: 0.46846, 95% CI 0.173-0.764, t(663) = 3.095, p = 0.0107

standard lower lightness - deviant lower lightness: 0.58713, 95% CI 0.254-0.920, t(663) = 3.451, p = 0.0034

For hue: Green elicits lower amplitude than red:

green vs. red: -0.283, 95%CI -0.105- -0.461, t(663) = -3.115, p = 0.0019

Finally, we tested how stimuli with lower lightness or saturation sum up to evaluate the degree to which lightness and saturation are processed by separable neural resources – if this would be the case, the predicted waveform for feature conjunctions (higher lightness and saturation, higher lightness but desaturated, lower lightness but saturated, or lower lightness and desaturated) should correspond to predictions made by averaging waveforms for single feature changes. Figure S.4 below depicts predicted (full line) and observed (dotted line with grey 95%Cis).



S4. Supplementary Figure 4. Visual evoked potentials observed in conditions that combined lightness and saturation changes, as well as waveforms predicted by averaging responses from VEPs elicited by changes in only one of the two features (lightness or saturation). Shaded grey area corresponds to a 95% between-subject CI for observed data.

As can be seen, the departure from the predicted waveform can be seen during the N1-P300 transition in the desaturated, lower lightness deviants – these stimuli were recorded in blocks with

higher and more saturated standards, while single features from which the predictions are derived from blocks in which the standards to which the participants were adapted possessed only one of these two features. Higher responses in the N1-P300 window are indicative of a stronger response to a weaker stimulus, which warrants further investigation to glean how normalisation pools may constrain VEP responses.