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Enhanced memory colour in peripheral vision: A possible compensation for chromatic loss

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ABSTRACT

The memory colour effect—the bias to perceive objects in their typical colours—can modulate colour appearance and has been proposed to operate via Bayesian mechanisms, combining noisy sensory input with prior knowledge. As colour perception is substantially degraded in peripheral vision, Bayesian modelling predicts that the influence of priors should increase when sensory reliability decreases, suggesting that memory colour effects may be enhanced in peripheral vision. Across three experiments, we tested this prediction. In Experiment 1, participants adjusted the colour of familiar objects to appear grey or natural, either foveally or at 10° eccentricity. Grey settings for peripheral stimuli were systematically biased away from the object's typical colour more than for central stimuli, indicating a stronger memory colour effect. Experiment 2 replicated these findings and confirmed that the effect magnitude scales with sensory uncertainty, as predicted by Bayesian modelling. In Experiment 3, using a forced-choice task, participants compared central and peripheral versions of the same object, presumably both affected by memory colour. The peripheral stimulus was more likely to be judged as grey then the central stimulus when shifted away from its typical colour, further confirming an enhanced memory colour effect in the periphery. These results demonstrate that memory colour biases are amplified in peripheral vision, supporting a Bayesian framework and highlighting a functional role for object knowledge in compensating for peripheral chromatic loss. Memory colour may help maintain the vividness of colour perception across the visual field.

1. Introduction

When we view the world around us, we have the impression of a sharp and detailed image across the entire visual field. However, this impression is at least in part illusory. We see with highest acuity only within a very small region, about the size of a thumbnail at arm's length. Visual processing is greatly reduced across the remaining visual field.

This is because the structure of the visual system changes with eccentricity (Strasburger et al., 2011) leading to differences in visual acuity, contrast sensitivity, and colour sensitivity as well as in the perceived appearance of basic visual features such as spatial frequency, luminance, and chromatic saturation (Davis, 1990; Greenstein & Hood, 1981; McKeefry et al., 2007; Rovamo et al., 1992; Weale, 1953).

Chromatic sensitivity declines steeply with eccentricity, with both detection and discrimination thresholds increasing as stimuli move away from the fovea (Hansen et al., 2009; Mullen & Kingdom, 1996; Nagy & Doyal, 1993). Peripheral stimuli are often perceived as less saturated and shifted in hue compared to foveal stimuli (Abramov et al., 1991; Ayama & Sakurai, 2003; McKeefry et al., 2007; Moreland & Cruz, 1959; Nerger et al., 1995). This degradation arises from both anatomical and functional constraints:

cone density decreases dramatically toward the periphery (Curcio et al., 1990), the number of spectrally opponent ganglion cells decreases with eccentricity (Zrenner & Gouras, 1983) and their receptive fields get larger (Dacey, 1993; Goodchild et al., 1996).

As a result, observers may experience a reduction in perceived colour vividness and accuracy in peripheral stimuli.

When sensory input is ambiguous, the visual system often leverages prior knowledge to fill in missing information. The classic "light–from–above" assumption (you expect illumination from above) helps resolve ambiguous shading or depth cues, resulting in a consistent perceptual bias that aligns with the prior (Brewster, 1826; Mamassian & Goutcher, 2001; Sun & Perona, 1998). Also, when contextual information is limited and the reflected light from a surface resembles natural daylight variation, the perceived colour of the surface can change dramatically depending on the different assumptions people make about the illumination (Gegenfurtner et al., 2015; Toscani, Gegenfurtner, & Doerschner, 2017; Witzel et al., 2017a, 2017b). The use of priors to fill-in missing information is computationally similar to colourization algorithms in artificial intelligence, which can infer plausible chromatic values for grayscale images by relying on statistical priors of object–colour associations (e.g., Cheng et al., 2015). In human vision, the

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memory colour effect provides strong evidence for similar mechanisms: Hansen et al. (2006) showed that observers adjusting the colour of a banana to appear neutral tended to shift it toward bluish hues, revealing a perceptual bias toward the object's canonical yellow. This phenomenon has been replicated and extended by Olkkonen et al. (2008), and Witzel et al., (2011) who demonstrated that such biases occur across a range of colour-diagnostic objects (e.g., strawberries, grapes, and watermelons). Such an effect has been shown with artificial objects, suggesting that it is learned over the lifespan (Witzel et al., 2011), and depends on familiarity, for example with brand logos (Kimura et al., 2013). In addition to the classic grey–setting paradigm (Hansen et al., 2006), memory colour effects have been shown across a range of experimental methods, including hue scaling, where participants estimate proportions of unique hues in a stimulus, showing, for example, that photos of bananas or lemons are perceived as more yellow than uniform disks (Hansen & Gegenfurtner, 2006) and a simple forced–choice task (Witzel, 2016). Moreover, the strength of colour afterimages is affected by colour knowledge, providing additional evidence of memory colour effects (Lupyan, 2015). Furthermore, adaptation to images that contain no chromatic information but imply colour through the memory colour of their content can produce perceptual biases similar to those caused by chromatic adaptation to the actual colour (Lee & Mather, 2019). This effect has been interpreted as evidence of adaptation in chromatic signalling mechanisms that receive top-down input from knowledge of object colour. A Neuroimaging study (Bannert & Bartels, 2013) suggests that memory colour influences early visual processing. When colour-diagnostic objects are shown in grayscale, patterns of activity in primary visual cortex (V1) can predict their typical colour. Additional decoding results and similarity analyses implicate mid-level regions such as V4 in carrying these memory-colour signals and projecting them to V1.

Granzier & Gegenfurtner (2012) demonstrated that object colour knowledge improves colour constancy even under unfamiliar illuminants, highlighting the functional role of priors in maintaining perceptual stability. However, this effect is very small and not always replicated (Kanematsu & Brainard, 2014).

Effects of prior knowledge on perception extend beyond vision: in haptic perception, prior knowledge about an object's typical surface properties biases the perceived softness, helping to disambiguate ambiguous tactile cues during exploration (Metzger & Drewing, 2019).

Witzel et al., (2018) proposed a Bayesian framework for the memory colour effect, in which perception is modelled as a combination of noisy sensory input with a prior centred around the canonical colour of an object. This model accounts for the observed bias magnitudes, which are generally small, on the order of $\sim$ 8% of the chromatic distance from grey to the object's typical colour (Olkkonen et al., 2008; Witzel et al., 2011). However, Bayesian theory predicts that the weight of the prior should increase as sensory reliability decreases. Thus, in the periphery—where colour signals are weaker—the memory colour effect may be substantially stronger.

Recent findings further suggest that colour awareness in the periphery is surprisingly limited. Using immersive virtual reality, Cohen et al. (2020) demonstrated that observers often fail to detect when more than 90% of their peripheral visual field is desaturated. This indicates that the brain may be "filling in" peripheral colour based on expectations and prior knowledge, rather than relying exclusively on bottom-up sensory input. Central information can be used to "fill-out" missing details in the periphery (Stewart et al., 2020). Visual properties such as lightness, motion, colour, orientation, and size presented in the periphery are biased by information presented in central vision, effectively creating a uniform display by biasing the appearance of peripheral elements toward the features of those presented at the centre (Otten et al., 2017). However, when realistic 3D objects are investigated, such extrapolation mechanisms seem to work only within object boundaries, when a certain degree of uniformity is likely to occur (Toscani, Gegenfurtner, & Valsecchi, 2017). Thus, filling-in mechanisms cannot be entirely responsible for our impression of vivid colours in peripheral vision, as in most cases, many objects are presented across the visual field. However, prior knowledge can bias the perceived colour of objects toward their typical or expected colours—an effect similarly implemented in image colourization algorithms. The impressive performance of these algorithms (e.g., Cheng et al., 2015; Larsson et al., 2016; Zhang et al., 2016) demonstrates that object colour statistics are stable and consistent enough to enable realistic colour reconstruction.

Building on these findings, we test the hypothesis that memory colour biases are larger in peripheral vision compared to central vision, as predicted by Bayesian models of perception. Demonstrating an enhanced memory colour effect in the periphery would not only corroborate the Bayesian account but also suggest that memory colour plays a key role in perceptual filling-in, extending beyond its established role in colour constancy (Granzier & Gegenfurtner, 2012).

In one experiment we used the same methods as in Hansen et al. (2006) with stimuli presented in central vision and at 10 degrees of visual angle in the periphery. In a second experiment we replicated the results in experiment one, but with less objects and more repetitions of the colour settings, to better estimate perceptual variance to test predictions of the Bayesian Framework. In a third experiment, we directly asked participants to compare central and peripheral stimuli in order to test whether the perceptual bias caused by memory colour is stronger in the periphery. For this we used a forced choice paradigm in an online experiment, similar to Witzel, (2016).

In all experiments we found stronger memory colour effect in the periphery. In experiment two, based on the estimated perceptual variance in central and peripheral vision, we could predict a stronger memory colour in the periphery. Experiment confirmed the result with a different task in which central and peripheral stimuli were directly compared.

2. Participants

Twelve participants participated in experiment 1 (8 females), five in experiment 2 (3 females) and 20 in experiment 3 (19 females) – after excluding 25 for low performance on catch trials (please see the procedure section). Participants were recruited on a voluntary basis and received either credits or Amazon vouchers as compensation for their time. All participants provided informed consent prior to taking part. They reported no known neurological impairments or colour blindness. Vision was normal or corrected to normal. The study was approved by the Bournemouth University Research Ethics Committee and conducted in accordance with the principles of the Declaration of Helsinki.

3. Experiment 1

3.1. Stimuli

We used photographs of 6 fruits and vegetables (Fig. 1)., roughly spanning second quadrant of the *iso*-luminant plane of DKL colour space (Derrington et al., 1984), which represents the majority of fruit and vegetable reflectances (Ennis et al., 2018). Photographs were taken with a Nikon D70 camera, under daylight illumination. The stimuli were shown with the largest dimension rescaled to measure approximately 5 degrees of visual angle (dva).

3.2. Procedure

Participants completed two tasks: first, they adjusted each object to its original colour, then they adjusted the objects to appear grey. The order of the objects was randomized. Participants performed both tasks first with objects presented in central vision, and then with objects presented at 10 degrees of visual angle. The experiment was blocked, with one repetition for each condition within each block. After completing one block, a second block began, and this continued until the

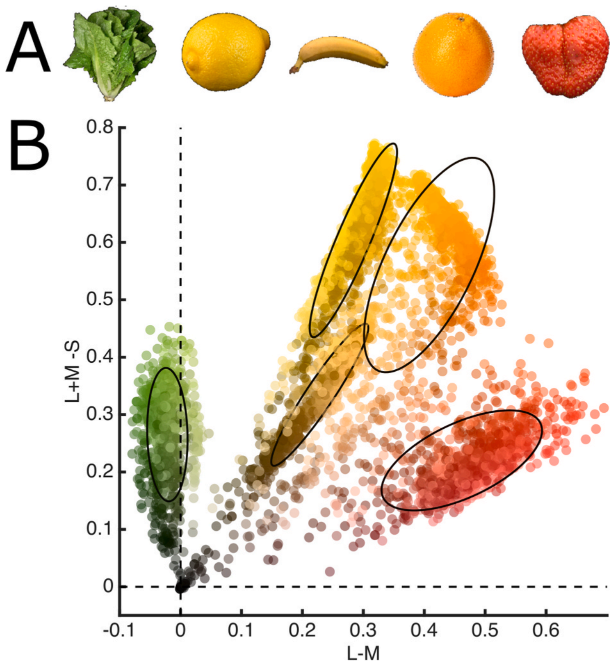

Fig. 1. ***Stimuli used in Experiment 1.*** A) Photographs of fruits and vegetables, arranged from left to right according to hue angle, progressing from vertical to horizontal as in B). B) Colour distributions of the fruits and vegetables shown in A), plotted in the DKL isoluminant plane. A random subsample of 1,000 pixels is displayed. The colour of each data point corresponds to the original rgb colour of the respective pixel. Black lines represent PCA ellipses for each fruit or vegetable, summarizing the variability of each stimulus and helping to distinguish their distributions.

experiment was terminated after one hour, to prevent participant fatigue and ensure accurate colour settings. This yields a variable number of settings for each object and condition. We monitored eye movements in real time to ensure that peripheral stimuli were centred at 10 dva. In the peripheral conditions, participants fixated on a central red fixation dot while the peripheral stimulus was shown for adjustment. If they moved their gaze away from the fixation dot by more than 1 dva, the peripheral stimulus was no longer displayed.

Similar to Hansen et al., (2006) participants could adjust the colour distribution of the stimuli in DKL space. They adjusted the position of the mean along the L–M axis using the left (to decrease) and right (to increase) arrow keys, and along the L + M−S axis using the up (to decrease) and down (to increase) arrow keys. After each key press, the difference in angle and radius were calculated between the mean before the adjustment and the new mean obtained with the latest adjustment. Then, the colour of every pixel of the object was rotated according to the difference angle and scaled according to the ratio of the radii (see figure Fig. 2 for example adjustments).

Formally, let a be the mean angle of the color distribution and r the mean radius. Let $R_i = (a_i, r_i)$ the reference point colour in polar coordinates at adjustment i, and $R_{i+1} = (a_{i+1}, r_{i+1})$ the colour of the reference at adjustment $i + 1$. For each pixel P_j at adjustment $i + 1$ we shifted its polar coordinates as follows:

$$P_{j(i+1)} = \left(a_i - a_{i+1}, r_{ji}\frac{r_{i+1}}{r_i}\right)(\text{with j} = [1, \text{npixels}])$$

3.3. Eye-tracking

Using a desktop-mounted eye-tracker (EyeLink 1000; SR Research Ltd, Osgoode, Ontario, Canada), gaze position signals were recorded and sampled at 1000 Hz. The display was viewed binocularly, but only the right eye was tracked. We performed a standard calibration procedure at the beginning of each experiment (Toscani et al., 2013).

3.4. Colour Calibration and definition of DKL Colour Space

We used a standard calibration procedure (Gil Rodríguez et al., 2022; Toscani et al., 2019) to linearise the screen and make sure that we displayed the desired colour. We measured the gamma curves of each channel and their chromaticity with the Spyder 4 colourimeter (Datacolor, Lawrenceville, NJ). This colourimeter’s measurement accuracy is equivalent to professional, high-cost photometers (MKII and PR-670) (Lin et al., 2023). Our screen had the following chromaticity: red primary CIE xyY coordinate (x: 0.6413, y: 0.3274, Y: 57.61 cd/m2), green (x: 0.3104, y: 0.6256, Y: 256.98 cd/m2), and blue (x: 0.1514, y: 0.0568, Y: 26.2 cd/m2). The gamma exponents were 1.913, 1.567 and 2.096, for the red, green and blue channels, respectively. After linearising the screen, we could use the chromaticities to convert between the rgb and XYZ colour spaces. The CIE xyY coordinates of the mid-grey background were (0.3046, 0.3689, 108.18 cd/m^2). The root mean square error (RMSE) between desired and measured XYZ values, computed at mid-level bit values for each of the three channels and averaged across channels, was 1.7626 (X), 1.1678 (Y), and 5.9904 (Z).

The axes of Derrington–Krauskopf–Lennie (DKL) colour space were defined following Hansen and Gegenfurtner, (2006). The isoluminant plane was specified relative to the monitor’s mid-grey background, and all stimuli were generated within this plane. Based on the measured primaries, we derived the DKL-to-RGB transformation matrix in Table 1, calculated using Smith and Pokorny (1975) 2° cone fundamental.

3.5. Results

Fig. 2 shows the results for Experiment 1. When the stimuli are presented in the centre, the grey settings for the fruits and vegetables are similar to the grey settings for the circles (Fig. 2A, panels in the top row); when presented in the periphery, the grey settings for the fruits and vegetables tend to be more clearly shifted away from the grey settings for the circles, in the direction opposite to their typical colour, as expected for the memory colour effect.

Fig. 2B & 2C show the objects rendered with their average settings, when participants were asked to set them as their typical colour (Fig. 2B) or grey (Fig. 2C).

As evident also from the diagrams in Fig. 2A, that the typical settings are very similar whether the stimuli are presented in the centre or in the periphery.

The grey settings for the stimuli presented in the centre (top row) appear more achromatic than those for the stimuli presented in the periphery (bottom row), which tend to be shifted away from their typical colour (Fig. 2C). This is particularly evident for the banana and the lemon, which are set to a bluish tint; the lettuce, set to a reddish tint; and the orange, which is set to a greenish tint.

We computed the memory colour index (Fig. 2D) as in previous research (Hansen et al., 2006; Olkkonen et al., 2008; Witzel et al., 2011). For each observer and each object, we projected the average grey setting onto the line connecting the average typical setting and the average grey setting for the circle. We then divided this projection by the distance between the average grey setting for the circle and the average typical setting. A positive value was assigned when the projected point lay beyond the typical colour setting (i.e., away from it), and a negative value when it fell between the typical colour setting and the grey setting for the circle. For the central condition we computed the memory colour index based on the typical colour and grey settings obtained in central vision, for the peripheral vision we used the ones obtained in peripheral vision, to avoid to create spurious results due to peripheral vison biases such as desaturation or hue shifts (e.g., McKeefry et al., 2007).

The memory colour effect was around zero or negative when the stimuli were presented in central vision and positive when presented in the periphery. A two-way repeated-measures ANOVA revealed a sig-

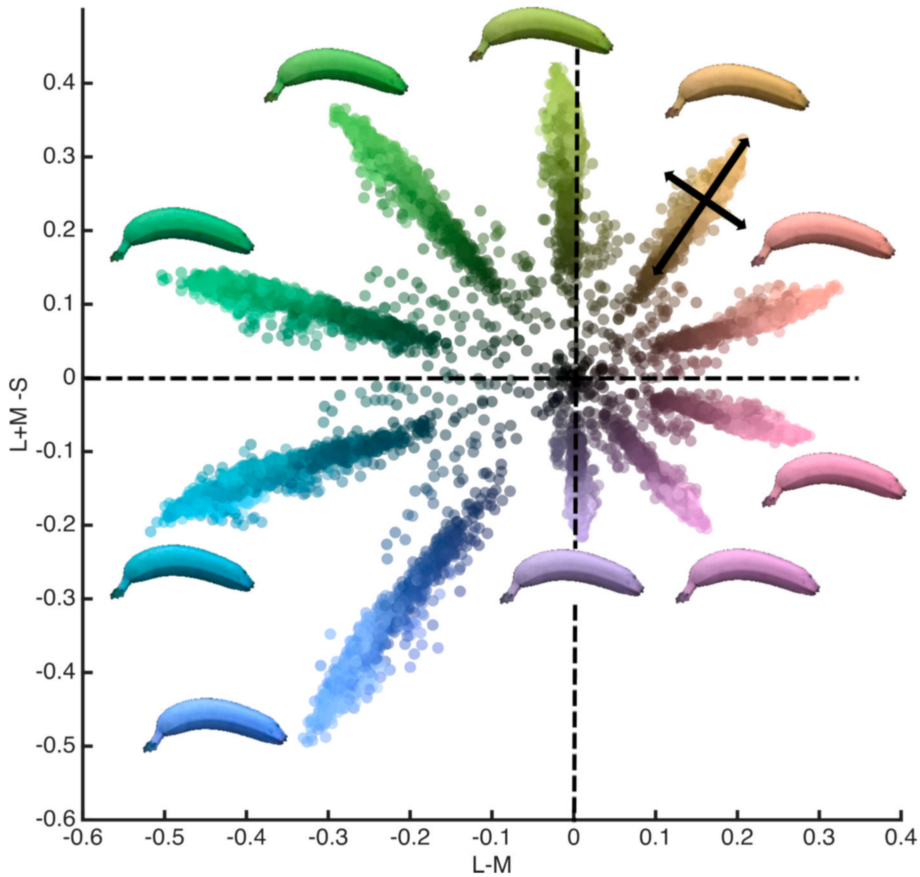

Fig. 2. Adjustments. Example of shifted distributions for one of our stimuli in the DKL isoluminant plane. By shifting the mean they could rotate the distribution effectively changing the stimulus' hue and scale the radius of each pixel, effectively changing chroma.

Table 1
DKL-to-RGB transformation matrix.

	L + M	L-M	S-(L + M)
R	1	1	−0.2366
G	1	−0.2243	−0.2366
B	1	0.0011	−1

nificant main effect of eccentricity, confirming a stronger memory colour effect in peripheral vision ($F(1,11) = 6.66$, $p = 0.03$, η_p^2=.377). The main effect of stimulus and the interaction were not significant.

4. Experiment 2

The stimuli were the same as in Experiment 1, but only three objects: banana, lettuce and strawberry. The procedure was also the same as in Experiment 1, but all participants performed 10 adjustments per condition.

4.1. Results

Fig. 4 shows the settings and the memory colour index for experiment 2. Results replicate the findings in Experiment 1.

Again, a two-way repeated-measures ANOVA revealed a significant main effect of eccentricity, confirming a stronger memory colour effect in peripheral vision ($F(1,4) = 8.6$, $p = 0.043$, η_p^2=.682). The main effect of stimulus and the interaction were not significant.

We used the Bayesian optimal integration framework to predict the memory colour effect in the centre and in the periphery. In this framework, the final estimate of an object's colour appearance results from the weighted integration of two sources of information: the prior and the sensory input. The prior represents prior knowledge about the typical colour of an object—such as the canonical yellow of a banana—and is characterised by a mean μ_p and a variance σ_p^2 along the memory colour direction (as described in Witzel et al., 2018). The sensory input corresponds the grey adjustment for the circle which does not have a typical colour; it is described by mean μ_s and a variance σ_s^2.

Bayesian integration combines these two sources by weighting them inversely proportional to their variances. The resulting estimate μ_{est} is given by:

$$\mu_{est} = \mu_p w_p + \mu_s w_s$$

with the weights defined as:

$$w_p = \frac{\frac{1}{\sigma_p^2}}{\frac{1}{\sigma_p^2} + \frac{1}{\sigma_s^2}} \quad w_s = \frac{\frac{1}{\sigma_s^2}}{\frac{1}{\sigma_p^2} + \frac{1}{\sigma_s^2}}$$

This means that the more reliable (i.e., less variable) a source is, the more it contributes to the final estimate. Since object colour knowledge is typically acquired through foveal (central) viewing, we assume that the prior is always central—that is, the same across conditions, independent of whether the current sensory input is central or peripheral. Thus we estimated σ_p^2 from the variance of the central typical color settings.

The sensory input, however, differs between centre and periphery, with peripheral vision generally associated with increased variance (σ_s^2) due to reduced sensitivity.

Importantly, we do not account for motor noise or other sources of variability in the adjustment process. These noise sources are likely shared across conditions and would contribute similarly to both the

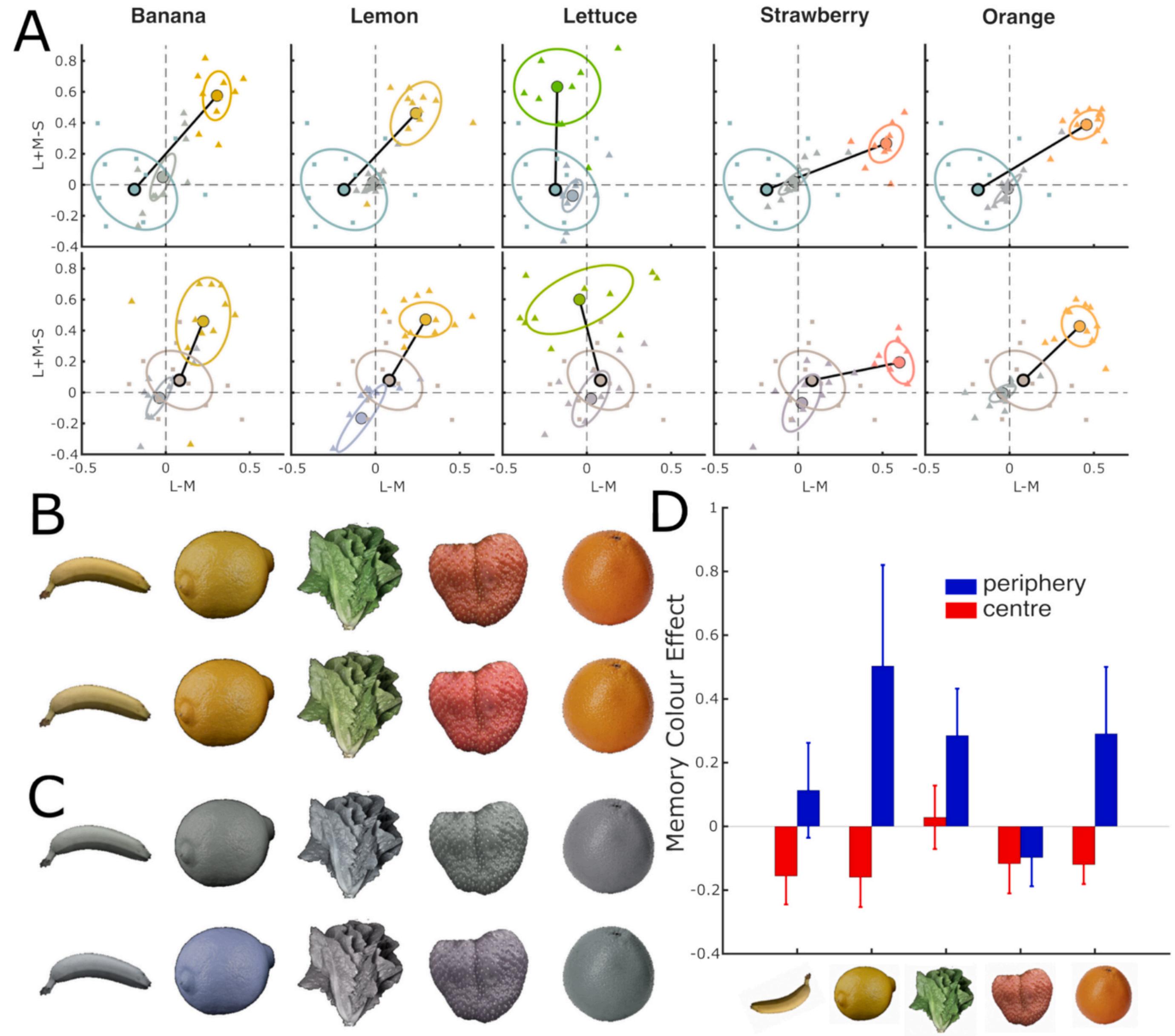

Fig. 3. Results from Experiment 1. A) Colour Adjustments in the isoluminant plane in DKL colourspace. Different diagrams for different stimuli and conditions. Fruits and vegetables in columns, settings for stimuli presented in the centre in the top line, in the periphery in the bottom line. The black line connects the average typical colour setting with the grey setting for the circle stimulus. The other data points represent the average grey settings for the fruit and vegetable stimuli. The small triangles represent the average settings for each participant, for the typical colour and for the grey disk; the squares represent each participant's average grey settings of the objects. The ellipses represent variability across participants and are computed using PCA; their axes are scaled to 0.5 times the variability indicated by the eigenvalues of the covariance matrix. All settings are depicted with their set average colour transformed from DKL to standard rgb. B) Stimuli set to the average natural colour settings when presented in the centre (top row) or in the periphery (bottom row). C) Stimuli set to the average grey settings when presented in the centre (top row) or in the periphery (bottom row). D) Memory colour index (y-axis) for the different stimuli (x-axis) presented in the centre (red bars) and in the periphery (blue bars). Error bars represent the standard error of the mean.

prior and the sensory input variances. As a result, the estimated σ_s^2 and σ_p^2 will be more similar to each other than their actual values, therefore the weighs as well. This will effectively bias the estimated memory colour effect reduce the differences between peripheral and central measures.

Fig. 5A shows that the sensory variance σ_s^2 (averaged across objects) is higher in the periphery than in the centre for all participants. Similarly, Fig. 5B shows that the predicted Memory Colour Effect (averaged across objects) is higher in the periphery than in the centre for all participants.

A paired *t*-test reveals that the Memory Colour Effect is significantly higher in the periphery than in the centre ($t(4) = 2.79$, $p = 0.049$).

5. Experiment 3

Here we directly asked participants to compare the central and peripheral stimuli. This way we directly compare the memory colour effect in central and in peripheral vision. For colour diagnostic object, we assume that memory colour is affecting both the central and the peripheral stimulus. We hypothesize that if memory colour is stronger in the periphery, the peripheral stimulus must be shifted away from the achromatic point toward the opposite colour to appear as grey as the central stimulus.

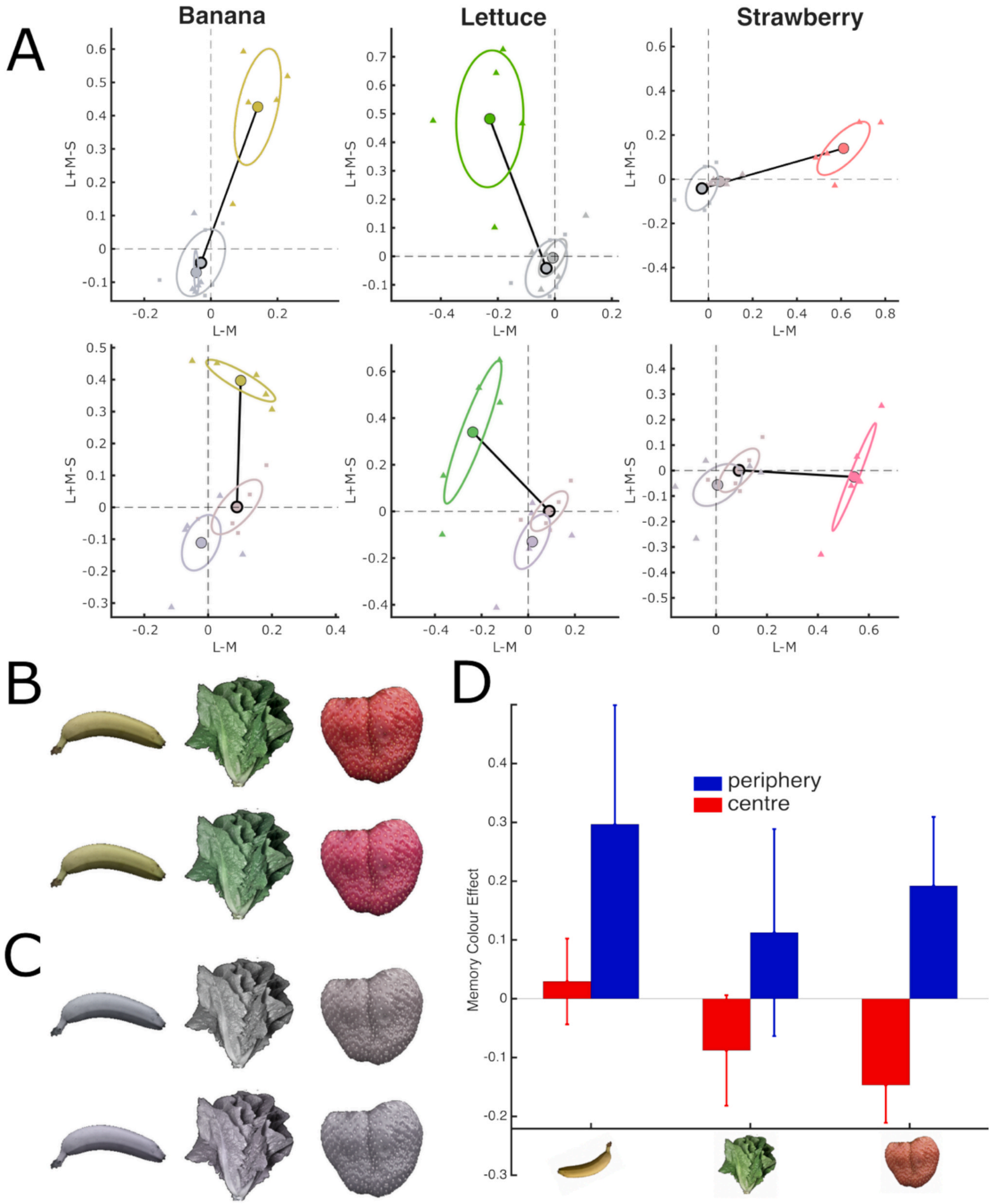

Fig. 4. Results from Experiment 2. A) Colour Adjustments in the isoluminant plane in DKL colourspace. Different diagrams for different stimuli and conditions. Fruits and vegetables in columns, settings for stimuli presented in the centre in the top line, in the periphery in the bottom line. The black line connects the average typical colour setting with the grey setting for the circle stimulus. The other data points represent the average grey settings for the fruit and vegetable stimuli. The small triangles represent the average settings for each participant, for the typical colour and for the grey disk; the squares represent each participant's average grey settings of the objects. The ellipses represent variability across participants and are computed using PCA; their axes are scaled to 0.5 times the variability indicated by the eigenvalues of the covariance matrix. All settings are depicted with their set average colour transformed from DKL to standard rgb. B) Stimuli set to the average natural colour settings when presented in the centre (top row) or in the periphery (bottom row). C) Stimuli set to the average grey settings when presented in the centre (top row) or in the periphery (bottom row). D) Memory colour index (y-axis) for the different stimuli (x-axis) presented in the centre (red bars) and in the periphery (blue bars). Error bars represent the standard error of the mean.

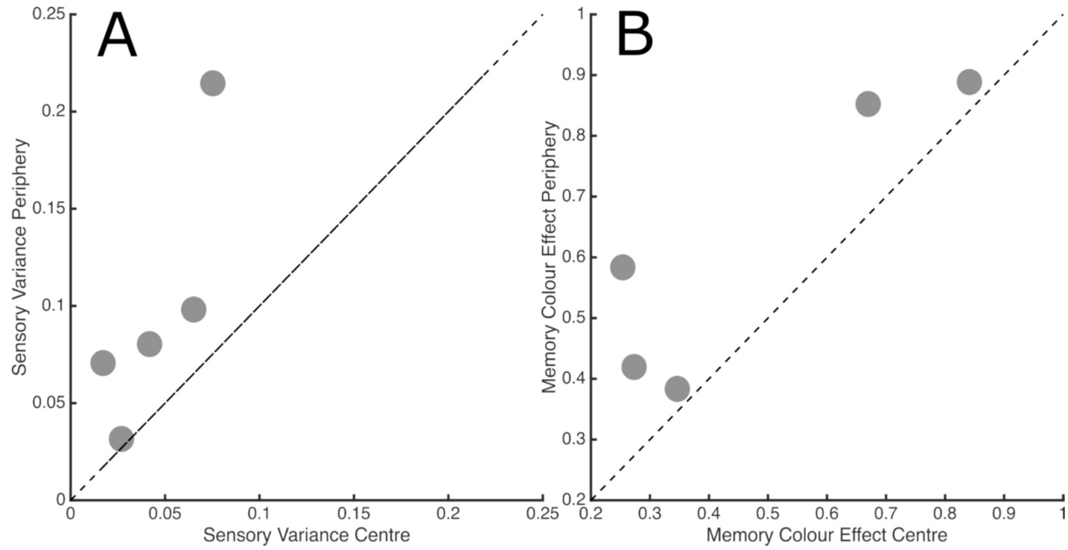

Fig. 5. A) Sensory variance from grey settings of the circle presented in the centre (x-axis) and in the periphery (y-axis). B) Predicted Memory colour effect in the centre (x-axis) and in the periphery (y-axis). Each data point represents data for one participant averaged across objects. The dashed line is the unity line.

This experiment was done online. We used custom software written in JavaScript and hosted on Pavlovia.

5.1. Procedure

At the beginning of the study, participants performed a procedure to estimate the position of their blind spot. This was done to establish the conversion between screen coordinates and dva, assuming the blind spot is located at approximately 15 degrees of visual angle (Armaly, 1969; Azzi et al., 2015; Meermeier et al., 2023). Participants fixated at a cross in the centre of the screen and adjusted the horizontal position of a circle placed in the vertical centre of the screen using the mouse until it was no longer visible, i.e. it fell in the blind spot. Once the blind spot was located, we could present the peripheral stimuli at 8/15 pixels of the pixel location of the blind spot. This allowed us to present the peripheral stimuli at a random position along the circle defined by 8 dva. This eccentricity was chosen after a pilot, to ensure peripheral stimuli were clearly visible despite the short presentation time of 200 ms. In each trial, two images of the same object were presented for 200 ms, on in the centre and one in the periphery. This, together with the short presentation time, prevented participants to foveate the peripheral stimulus (Hansen et al., 2009).

After that, the participants indicated with the keyboard which of the two objects was more gray, and the new trial begin until the end of the experiment (Fig. 6).

After they responded, a new trial begun with the next stimuli.

The experiment included one colour diagnostic object—a banana, plus one control object, uniform disk approximately of the same number of pixels.

The peripheral stimulus varied in colour, while the central stimulus was grey across all repetitions. Each stimulus was shown in 10 coloured versions and one achromatic version (please see the Stimuli section) for

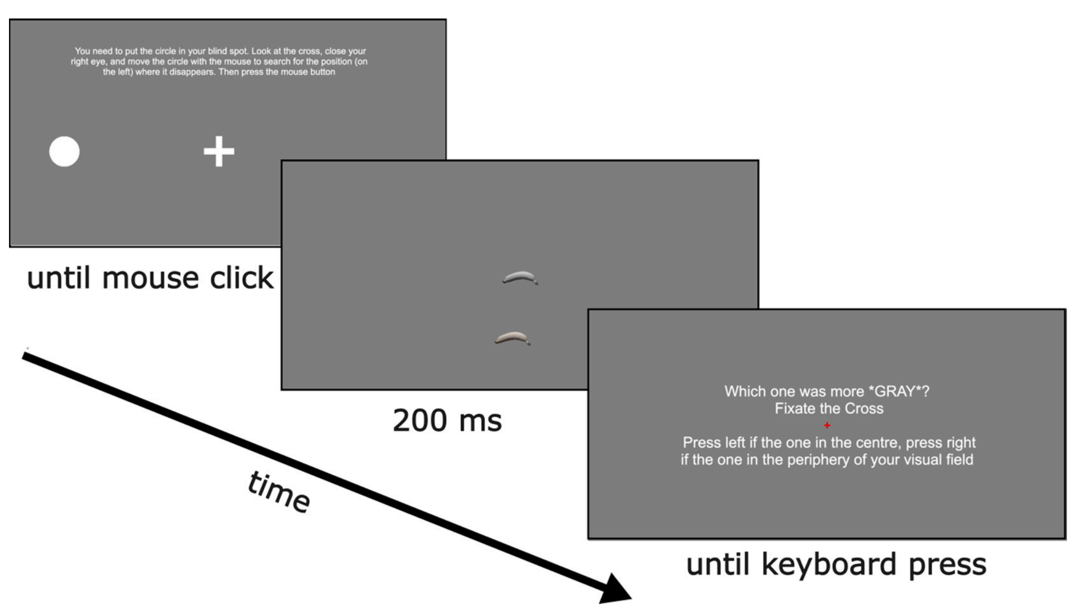

Fig. 6. Procedure of Experiment 3. At the beginning of the experiment the white fixation cross and the circle were presented on a grey screen together with the instruction how to locate the blind spot. After mouse click, the experiment begun and the stimuli were presented for 200 ms, then instructions were shown to fixate on the red cross in the centre and report with the keyboard which stimulus was more grey.

30 repetitions per stimulus, for a total of 30*2*10 = 600 trials. Additionally, there were 24 trials in which the central stimulus was coloured and the peripheral stimulus was grey. These trials were not analysed but were included to give participants the impression that the greyest stimulus could appear either in the centre or in the periphery. Among these 24 trials, 12 presented the central banana at the maximum colour shift—6 towards blue and 6 towards yellow. These trials should be extremely easy to discriminate from the grey peripheral stimulus and were used as catch trials. In our analysis, we included only participants who performed above 70% on the catch trials, assuming that those who performed below this threshold did not sufficiently engage with the experiment. Recruitment was stopped when a sequential Bayesian analysis showed strong evidence in favour of our analysis (Fig. 7E). However, the choice to exclude participants with low catch-trial performance is not critical, as the results remain significant even when all participants are included (please see the results section).

5.2. Stimuli

Our stimuli varied in colour around grey and along the line connecting the mean colour of the original image and the neutral point in the CIE LAB colour space (Fig. 7A & 7B). This was realised by shifting their mean colour five steps towards the mean of the original colour, or the opposite colour. Each step was 4% of the distance between the original colour and the neutral point. There is no particular reason for choosing the CIE LAB colour space but the ease to rely on standard conversion routines between sRGB and CIE LAB making LAB standard space for standard devices.

5.3. Results

As the colour of the peripheral stimulus varies around the neutral point, there will be a version that appears most greyish. At this point, the likelihood of it being judged as grey will be highest—ideally around 50% in the absence of response biases. If there is no Memory colour effect, such point will be around colour shift = 0, i.e. would correspond to the achromatic version of the stimulus. Conversely, the memory colour effect predicts a negative colour shift, as the effect implies that for a stimulus to appear grey, it needs to be colour-shifted away from its typical colour toward the opposite colour. To estimate such colour shift we fitted a gaussian function to participant responses and read out the value corresponding to its peak.

Fig. 7C shows the results for a representative participant. When the circle presented in the periphery is shifted toward yellow or blue, it is seldom chosen as more grey than its central version, the shift at which it is more likely choose as more grey is close to zero. This likelihood in the representative subjects, but also in as a general trend, does not reach 50%, probably because in most trials the central stimulus is grey, which may create a response bias that, nevertheless, does not affect our results. Crucially, the peak probability for the banana corresponds to a negative colour shift (towards blue), indicating a stronger memory colour effect in the periphery. For most participants, the colour shift is more negative for the fruits and vegetables than for the control, which is on average close to zero (0.15 steps, i.e. 0.6% of the distance between the original colour and the neutral point, while it is −2.36 for the banana, i.e. ∼ 9% of the distance between the original colour and the neutral point, towards blue; Fig. 7D). This is confirmed by a significant paired t-test ($t(19) = 3.37$; $p = 0.003$; Cohen's $d = 0.754$). We stopped collecting participants when a sequential Bayesian t-test analysis provided strong evidence ($BF_{01} > 10$) in favour of the alternative hypothesis. This resulted in a sample of 20 participants (Fig. 7E). For the sequential analysis, we only included participants who performed above the catch trial threshold of 70%. At this stage, 25 participants were excluded for low performance. However, this exclusion does not appear to be critical, as the difference between the banana and control conditions remains significant when all 45 participants are included ($t(44) = 2.44$, $p = 0.02$).

6. Discussion

Across three experiments, we consistently observed that memory colour effects are enhanced in peripheral vision compared to central vision. In Experiment 1, using an adjustment task similar to Hansen et al. (2006), participants showed minimal or no bias when stimuli were presented centrally, but reliably biased grey settings in the periphery toward the opponent hue—consistent with an increased influence of memory colour. Experiment 2 replicated this pattern with greater measurement precision and confirmed that sensory variability was higher in the periphery, as expected. Bayesian modelling successfully predicted the observed increase in peripheral memory colour effects. Finally, Experiment 3 provided converging evidence using a direct perceptual comparison between central and peripheral stimuli in a forced-choice paradigm. The colour settings that maximized the perceived neutrality of peripheral stimuli were consistently shifted away from their typical colour, and significantly more so than for a non-diagnostic control object.

Taken together, these results provide strong empirical support for the hypothesis that the visual system increasingly relies on prior knowledge—specifically, object-associated colour priors—as the reliability of sensory input decreases. Since this is a typical prediction of Bayesian models, our results suggest that memory colour effects follow a Bayesian process (as proposed by Witzel et al., 2018) and that prior knowledge is especially important in peripheral vision, where sensory input is weaker.

In fact, these results suggest a functional role for memory colour in maintaining the subjective appearance of a colourful peripheral visual world, compensating for the chromatic degradation that occurs with increasing eccentricity (Abramov et al., 1991; McKeefry et al., 2007b). While such degradation is shown with colour detection experiments (e.g. Hansen et al., 2009) and increase variability in peripheral colour judgements (e.g. Abramov et al., 1991), it may vary between stimuli. Similarly to Witzel (2016), we used variability in grey settings as a proxy for sensory noise; we found higher variability in peripheral vision for every participant (Fig. 5A), suggesting reduced reliability of the chromatic signals also with our stimuli.

Memory colour effects are generally rather small (Witzel et al., 2011) and have traditionally been interpreted as an aid for colour constancy (Granzier & Gegenfurtner, 2012; Hansen et al., 2006; Witzel & Gegenfurtner, 2018 – but see Kanematsu & Brainard, 2014), one of the many mechanisms involved in maintaining stable colour perception across different illuminations (Kraft & Brainard, 1999; Rodríguez et al., 2024; Toscani et al., 2025). Our study suggests another potentially more prominent function of memory colour: helping to fill in missing peripheral information. Other evidence of the role of prior knowledge in peripheral vision comes from studies of peripheral size perception (Bosco et al., 2015; Valsecchi et al., 2020; Valsecchi & Gegenfurtner, 2016) showing that our brain learns the contingency between how a stimulus appears in peripheral vision and how it looks when foveated. Through repeated exposure to predictable changes during eye movements observers come to anticipate the foveal appearance of peripheral stimuli. Prior knowledge is crucial for filling in missing details in peripheral vision and creating the impression of uniform vision across the visual field in natural scenes where more objects are present. In fact, while extrapolating from information from foveal vision to peripheral vision has been shown a mechanism to 'fill out' the missing information (Otten et al., 2017), research on lightness perception suggests that this happens only within objects boundaries, when it is reasonable to assume a certain degree of continuity between information presented in central and in peripheral vision (Toscani, Gegenfurtner, & Valsecchi, 2017).

While we could clearly show that the memory colour effect is stronger in peripheral vision, we failed to demonstrate its occurrence in central vision, replicating the original findings. One reason for this could be that our data are much more noisy than the ones reported in previous

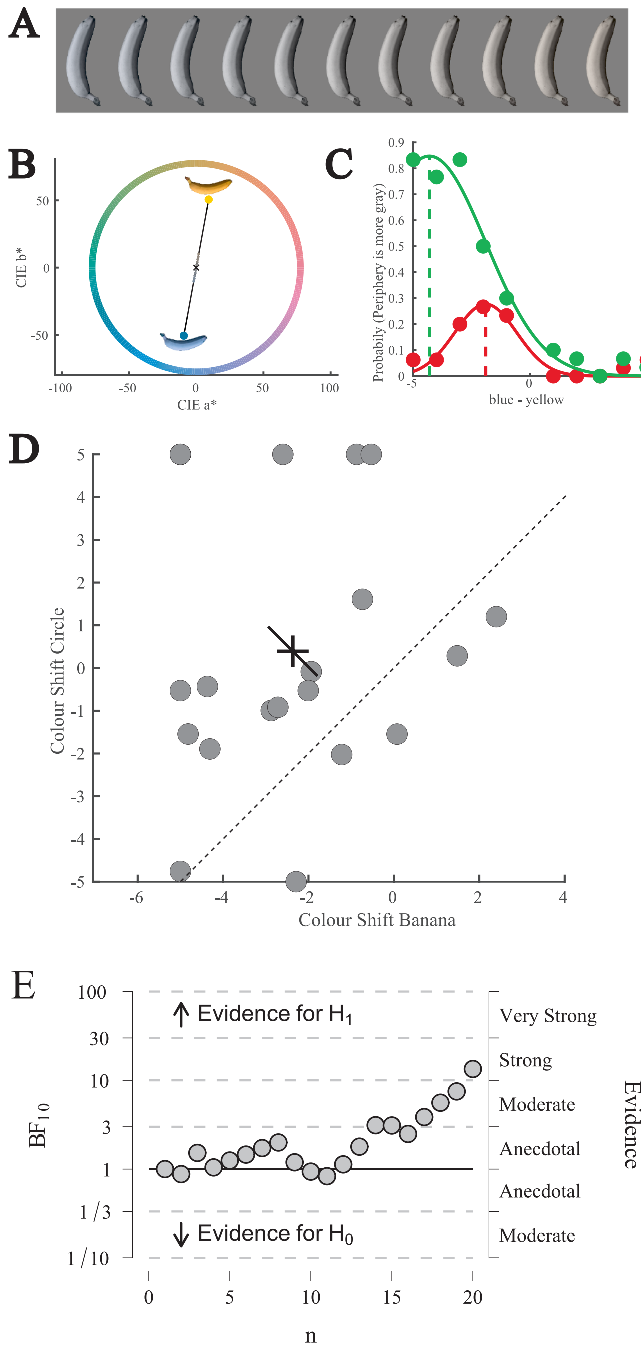

Fig. 7. Stimuli and Results for Experiment 3. A) example colour variation for the banana stimulus, varying from the opposite colour to the typical colour; greenish sock in its original version on the right B) Chromatic steps of the mean colour of the banana stimulus in colour space. The banana is shown in its original yellow colour and in the opposite colour. The means of the typical and opposite colours are connected by a black line that crosses the neutral point (indicated by a cross). The ten dots along this line around the cross represent five steps toward the typical colour and five steps toward the opposite colour of the banana. These dots correspond to the mean colours of the ten versions of the coloured banana. Their displayed colour reflects the RGB values corresponding to their respective CIE LAB coordinates. C) Example results for one participant. Colour shift ([-5 5]) on the x-axis, probability of choosing the peripheral stimulus on the y-axis. Green data points represent the aggregated responses for the three fruits and vegetables, red for the sock (control). The continuous lines represent gaussian curves fitted to the data. The vertical dashed lines represent the point at which the peripheral stimulus is more likely to be selected as more grey. D) Colour shift yielding the highest likelihood of the peripheral stimulus being judged as grey, for the fruits and vegetables (x-axis) and for the sock (y-axis). The dashed line represents the unity line, the cross the 2D mean and the error bar the standard error of the mean difference between the values along the x-axis and the y-axis. Each data point represents one participant. E) Sequential Bayesian analysis for the paired *t*-test, which we used to assess the significance of the difference between the points of maximum grey likelihood for the banana and the circle. Number of participants on the x-axis, Bayes Factor in favour of the alternative hypothesis BF_{10} on the y-axis.

research (Witzel et al., 2018). If we take the variance in the grey settings for the circle as a measure of sensory, motor noise and the other sources of variability in the adjustment process, we can assume that this noise is present in all measurements and compare across studies. While in previous research such noise is < 0.01 dkl units (Witzel et al., 2018), in our study we found ~ 0.05 dkl units – after converting to the scaling of the dkl colour space used for their device (for their screen's chromaticity, please see Olkkonen et al., 2008). This suggests that our data are noisier, and thus fail to reveal smaller effects than the ones we found in peripheral vision. One reason for this higher noise could be that in the above studies (Olkkonen et al., 2008; Witzel, 2016; Witzel et al., 2011), participants adjusted the colour of a reference point (the highest chroma pixel) in the DKL isoluminant Cartesian plane. Then, the entire distribution was rotated and stretched in polar coordinates to apply the same transformation (in polar coordinates) to the reference point after each adjustment, affecting all pixels. While we used the same adjustment procedures and transformations, our reference point was the mean chromaticity rather than the most saturated pixel. Adjusting the mean chromaticity of an object can introduce more noise because the mean depends on the contribution of all pixels, including shadows, highlights, texture variations, and regions that are not strongly diagnostic of the object's typical colour, while to judge the colour of objects we mostly rely on high-saturation regions (Giesel & Gegenfurtner, 2010; E. Kimura, 2018; Sunaga & Yamashita, 2007; Toscani et al., 2013). Trying to adjust the appearance by changing the mean, when appearance depends mostly on other parts of the distribution, may have made the task harder and observers less precise in achieving the settings they wanted, potentially hiding a small effect. Remarkably, larger effects like the ones we detected in peripheral vision are more robust with respect to methodological choices and the fact that we found memory colour with a slightly different method and when is more expected, i.e. with the less reliable peripheral sensory input, provides additional evidence of the memory colour effect itself.

Different from other studies, we did not include a noise texture as a control stimulus, hence in principle the differences in grey settings between our stimuli and the uniform circle could be due to the different texture. However, previous research using noisy texture patches has ruled out this explanation (Hansen et al., 2006; Olkkonen et al., 2008), and we have no reason to expect it would differ in peripheral vision. Furthermore, if the effect were driven by the contrast between objects with non-uniform textures and the uniform disk, it should be present for all objects; however, qualitative inspection of our results does not suggest that this is the case, e.g. no effect with the strawberry.

For some stimulus—particularly orange—several pixels in the original version reach the gamut boundary. This may suggest that the natural saturation of the object is too high to be displayed on a computer screen. If so, the gamut limit may constrain participants' ability to select more saturated colours. This restriction may reduce the variability in their settings: even if participants intended to adjust a more saturated average, the gamut boundary forces their selections to cluster at the edge, along the typical hue angle, limiting exploration in chroma and thus reducing the dimensionality of the task (the variability in natural settings for the orange is indeed relatively small – Fig. 3A). Because we calculate memory colour relative to the average chroma of the natural settings, this constraint could slightly inflate the measured effect as compared to the other stimuli. However, the observed memory colour effect for orange was not unusually large. Moreover, the stimuli used in Experiment 2, which do not reach the gamut boundaries to the same extent, still produced a replication of the effect. Therefore, while gamut limits could influence variability and affect effect size estimates, they cannot account for the overall pattern of results.

To quantify the Memory Colour Effect, we assumed that grey-setting shifts would occur along the line connecting the typical colour and subjective grey. This holds for some stimuli (lemon, orange, and banana) but not for others, consistent with previous reports(Hansen et al., 2006; Olkkonen et al., 2008; Witzel et al., 2011), and neither our data nor earlier studies strictly demonstrate such line-based cancellation. A possible reason is that DKL space is not perceptually uniform; although a uniform space might address this, we retained DKL for comparability with prior work, and commonly used MacAdam-based spaces (e.g., Lab, Luv) are themselves not perfectly uniform (Malacara, 2011). Importantly, the effect appears strongest for yellow/orange stimuli (as well as the centre–periphery difference we report), where grey settings do fall along the expected opposite direction, so we do not consider this a major concern.

Our research shows that, on average, memory colour effects are stronger in peripheral vision. This is consistent with their Bayesian interpretation and may also help explain why peripheral vision appears rich in detail and qualitatively similar across eccentricities despite structural limitations. However, memory colour effects are known to differ across stimuli (Olkkonen et al., 2008; Witzel et al., 2011). For instance, our results from Experiment 1 show no effect for the strawberry, neither in central nor in peripheral vision. This is consistent with previous studies that also found no effect for the strawberry and, more generally, smaller effects for objects whose typical colour lies away from the daylight axis. It has been proposed that we are exposed to greater hue variability along the daylight axis, reflecting how illumination varies; thus, consistent with the Bayesian framework, the influence of prior knowledge is stronger along this axis. However, our data are only partly consistent with this, because while we found a strong peripheral effect for the banana, orange, and lemon, we also found a comparable effect for the lettuce in Experiment 1 and for the strawberry in Experiment 2. Presumably, the peripheral effects we measure are large enough to be evident even away from the daylight axis.

It is worth noting that the explicit reference to the "centre" and "periphery" of the visual field in the task instructions could, in principle, bias participants to report stronger effects in the periphery. Task-dependent influences on colour perception are well documented, and even small differences in wording can affect perceptual judgements (Arend & Reeves, 1986) and associated eye-movement behaviour (Cornelissen & Brenner, 1995). However, such a response bias would be expected to influence reports for both stimulus types similarly. We therefore have no specific reason to assume that any wording-related bias would differentially affect the banana compared with the control circle, and thus it is unlikely to account for the observed difference between conditions.

It has been suggested that many purported top-down effects on perception—including memory colour—are actually judgment or response biases, and would not persist in displays where images are shown side by side, allowing for direct perceptual comparison (Firestone & Scholl, 2016). Similar to Witzel (2016), in Experiment 3 participants directly compared central and peripheral stimuli, ruling out the possibility that our results are due to a response bias in the colour setting procedure. More generally, the fact that we replicated the finding using a different task and without precise colour calibration suggests that the effect is robust and likely to be genuine.

The present study provides compelling evidence that memory colour effects are enhanced in peripheral vision, supporting the idea that the brain increasingly relies on prior knowledge when sensory input is less reliable. This finding confirms a key prediction of Bayesian perceptual models and suggests that memory colour plays a functional role in preserving the appearance of a colourful visual world, even in regions where chromatic sensitivity is low.

CRediT authorship contribution statement

Anna Metzger: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Matteo Valsecchi:** Writing – review & editing, Writing – original draft, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Matteo Toscani:** Writing – review & editing, Writing – original draft, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence

the work reported in this paper.

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References

Abramov, I., Gordon, J., & Chan, H. (1991). Color appearance in the peripheral retina: Effects of stimulus size. *Journal of the Optical Society of America A, 8*(2), 404–414.
Arend, L., & Reeves, A. (1986). Simultaneous color constancy. *Journal of the Optical Society of America A, 3*(10), 1743–1751.
Armaly, M. (1969). The size and location of the normal blind spot. *Archives of Ophthalmology, 81*(2), 192–201.
Ayama, M., & Sakurai, M. (2003). Changes in hue and saturation of chromatic lights presented in the peripheral visual field. *Color Research & Application: Endorsed by Inter-Society Color Council, the Colour Group (Great Britain), Canadian Society for Color, Color Science Association of Japan, Dutch Society for the Study of Color, the Swedish Colour Centre Foundation, Colour Society of Australia. Centre Français de La Couleur, 28*(6), 413–424.
Azzi, J. C., Gattass, R., Lima, B., Soares, J. G., & Fiorani, M. (2015). Precise visuotopic organization of the blind spot representation in primate V1. *Journal of Neurophysiology, 113*(10), 3588–3599.
Bannert, M. M., & Bartels, A. (2013). Decoding the yellow of a gray banana. *Current Biology, 23*(22), 2268–2272.
Bosco, A., Lappe, M., & Fattori, P. (2015). Adaptation of saccades and perceived size after trans-saccadic changes of object size. *Journal of Neuroscience, 35*(43), 14448–14456.
Brewster, D. (1826). On the optical illusion of the conversion of cameos into intaglios, and of intaglios into cameos, with an account of other analogous phenomena. *Edinburgh Journal of Science, 4*(7), 99–108.
Cheng, Z., Yang, Q., & Sheng, B. (2015). *Deep colorization*. 415–423.
Cohen, M. A., Botch, T. L., & Robertson, C. E. (2020). The limits of color awareness during active, real-world vision. *Proceedings of the National Academy of Sciences, 117*(24), 13821–13827.
Cornelissen, F. W., & Brenner, E. (1995). Simultaneous colour constancy revisited: An analysis of viewing strategies. *Vision Research, 35*(17), 2431–2448.
Curcio, C. A., Sloan, K. R., Kalina, R. E., & Hendrickson, A. E. (1990). Human photoreceptor topography. *Journal of Comparative Neurology, 292*(4), 497–523.
Dacey, D. M. (1993). The mosaic of midget ganglion cells in the human retina. *Journal of Neuroscience, 13*(12), 5334–5355.
Davis, E. T. (1990). Modeling shifts in perceived spatial frequency between the fovea and the periphery. *Journal of the Optical Society of America A, 7*(2), 286–296.
Derrington, A. M., Krauskopf, J., & Lennie, P. (1984). Chromatic mechanisms in lateral geniculate nucleus of macaque. *The Journal of Physiology, 357*(1), 241–265.
Ennis, R., Schiller, F., Toscani, M., & Gegenfurtner, K. R. (2018). Hyperspectral database of fruits and vegetables. *JOSA A, 35*(4), B256–B266.
Firestone, C., & Scholl, B. J. (2016). Cognition does not affect perception: Evaluating the evidence for "top-down" effects. *Behavioral and Brain Sciences, 39*, e229.
Gegenfurtner, K. R., Bloj, M., & Toscani, M. (2015). The many colours of 'the dress'. *Current Biology, 25*(13), R543–R544.
Giesel, M., & Gegenfurtner, K. R. (2010). Color appearance of real objects varying in material, hue, and shape. *Journal of Vision, 10*(9), 10–10.
Gil Rodríguez, R., Bayer, F., Toscani, M., Guarnera, D., Guarnera, G. C., & Gegenfurtner, K. R. (2022). Colour calibration of a head mounted display for colour vision research using virtual reality. *SN Computer Science, 3*, 1–10.
Goodchild, A. K., Ghosh, K. K., & Martin, P. R. (1996). Comparison of photoreceptor spatial density and ganglion cell morphology in the retina of human, macaque monkey, cat, and the marmoset *Callithrix jacchus*. *Journal of Comparative Neurology, 366*(1), 55–75.
Granzier, J. J., & Gegenfurtner, K. R. (2012). Effects of memory colour on colour constancy for unknown coloured objects. *I-Perception, 3*(3), 190–215.
Greenstein, V. C., & Hood, D. C. (1981). Variations in brightness at two retinal locations. *Vision Research, 21*(6), 885–891.
Hansen, T., & Gegenfurtner, K. R. (2006). Color scaling of discs and natural objects at different luminance levels. *Visual Neuroscience, 23*(3–4), 603–610.
Hansen, T., Olkkonen, M., Walter, S., & Gegenfurtner, K. R. (2006). Memory modulates color appearance. *Nature Neuroscience, 9*(11), 1367–1368.
Hansen, T., Pracejus, L., & Gegenfurtner, K. R. (2009). Color perception in the intermediate periphery of the visual field. *Journal of Vision, 9*(4), 26–26.
Kanematsu, E., & Brainard, D. H. (2014). No measured effect of a familiar contextual object on color constancy. *Color Research & Application, 39*(4), 347–359.
Kimura, A., Wada, Y., Masuda, T., Goto, S., Tsuzuki, D., Hibino, H., Cai, D., & Dan, I. (2013). Memory color effect induced by familiarity of brand logos. *PLoS One1, 8*(7), Article e68474.
Kimura, E. (2018). Averaging colors of multicolor mosaics. *Journal of the Optical Society of America A, 35*(4), B43–B54.
Kraft, J. M., & Brainard, D. H. (1999). Mechanisms of color constancy under nearly natural viewing. *Proceedings of the National Academy of Sciences, 96*(1), 307–312.
Larsson, G., Maire, M., & Shakhnarovich, G. (2016). *Learning representations for automatic colorization*. 577–593.
Lee, R., & Mather, G. (2019). Chromatic adaptation from achromatic stimuli with implied color. *Attention, Perception, & Psychophysics, 81*(8), 2890–2901.
Lupyan, G. (2015). Object knowledge changes visual appearance: Semantic effects on color afterimages. *Acta Psychologica, 161*, 117–130.
Lin, Z., Ma, Q., & Zhang, Y. (2023). PsyCalibrator: An open-source package for display gamma calibration and luminance and color measurement. *Advances in Methods and Practices in Psychological Science, 6*(2), 25152459221151151.
Malacara, D. (2011). *Color vision and colorimetry: Theory and applications*.
Mamassian, P., & Goutcher, R. (2001). Prior knowledge on the illumination position. *Cognition, 81*(1), B1–B9.
McKeefry, D. J., Murray, I. J., & Parry, N. R. (2007). Perceived shifts in saturation and hue of chromatic stimuli in the near peripheral retina. *Journal of the Optical Society of America A, 24*(10), 3168–3179.
Meermeier, A., Lappe, M., Li, Y. H., Rifai, K., Wahl, S., & Rucci, M. (2023). Fine-scale measurement of the blind spot borders. *Vision Research, 211*, Article 108208.
Metzger, A., & Drewing, K. (2019). Memory influences haptic perception of softness. *Scientific Reports, 9*(1), 14383.
Moreland, J., & Cruz, A. (1959). Colour perception with the peripheral retina. *Optica Acta: International Journal of Optics, 6*(2), 117–151.
Mullen, K. T., & Kingdom, F. A. (1996). Losses in peripheral colour sensitivity predicted from "hit and miss" post-receptoral cone connections. *Vision Research, 36*(13), 1995–2000.
Nagy, A. L., & Doyal, J. A. (1993). Red–green color discrimination as a function of stimulus field size in peripheral vision. *Journal of the Optical Society of America A, 10*(6), 1147–1156.
Nerger, J. L., Volbrecht, V. J., & Ayde, C. J. (1995). Unique hue judgments as a function of test size in the fovea and at 20-deg temporal eccentricity. *Journal of the Optical Society of America A, 12*(6), 1225–1232.
Olkkonen, M., Hansen, T., & Gegenfurtner, K. R. (2008). Color appearance of familiar objects: Effects of object shape, texture, and illumination changes. *Journal of Vision, 8*(5), 13–13.
Otten, M., Pinto, Y., Paffen, C. L., Seth, A. K., & Kanai, R. (2017). The uniformity illusion: Central stimuli can determine peripheral perception. *Psychological Science, 28*(1), 56–68.
Rodríguez, R. G., Hedjar, L., Toscani, M., Guarnera, D., Guarnera, G. C., & Gegenfurtner, K. R. (2024). Color constancy mechanisms in virtual reality environments. *Journal of Vision, 24*(5), 6–6.
Rovamo, J., Franssila, R., & Näsänen, R. (1992). Contrast sensitivity as a function of spatial frequency, viewing distance and eccentricity with and without spatial noise. *Vision Research, 32*(4), 631–637.
Smith, V. C., & Pokorny, J. (1975). Spectral sensitivity of the foveal cone photopigments between 400 and 500 nm. *Vision Research, 15*(2), 161–171.
Stewart, E. E., Valsecchi, M., & Schütz, A. C. (2020). A review of interactions between peripheral and foveal vision. *Journal of Vision, 20*(12), 2–2.
Strasburger, H., Rentschler, I., & Jüttner, M. (2011). Peripheral vision and pattern recognition: A review. *Journal of Vision, 11*(5), 13–13.
Sun, J., & Perona, P. (1998). Where is the sun? *Nature Neuroscience, 1*(3), 183–184.
Sunaga, S., & Yamashita, Y. (2007). Global color impressions of multicolored textured patterns with equal unique hue elements. *Color Research & Application: Endorsed by Inter-Society Color Council, the Colour Group (Great Britain), Canadian Society for Color, Color Science Association of Japan, Dutch Society for the Study of Color, the Swedish Colour Centre Foundation, Colour Society of Australia. Centre Français de La Couleur, 32*(4), 267–277.
Toscani, M., Chen, T., & Guarnera, G. C. (2025). Evaluation of classic colour constancy algorithms on spectrally rendered ground-truth. *Perception*, 03010066251345871.
Toscani, M., Gegenfurtner, K. R., & Doerschner, K. (2017). Differences in illumination estimation in# thedress. *Journal of Vision, 17*(1), 22–22.
Toscani, M., Gegenfurtner, K. R., & Valsecchi, M. (2017). Foveal to peripheral extrapolation of brightness within objects. *Journal of Vision, 17*(9), 14–14.
Toscani, M., Gil, R., Guarnera, D., Guarnera, G., Kalouaz, A., & Gegenfurtner, K. R. (2019). *Assessment of OLED head mounted display for vision research with virtual reality*. 738–745.
Toscani, M., Valsecchi, M., & Gegenfurtner, K. R. (2013). Optimal sampling of visual information for lightness judgments. *Proceedings of the National Academy of Sciences, 110*(27), 11163–11168.
Valsecchi, M., Cassanello, C., Herwig, A., Rolfs, M., & Gegenfurtner, K. R. (2020). A comparison of the temporal and spatial properties of trans-saccadic perceptual recalibration and saccadic adaptation. *Journal of Vision, 20*(4), 2–2.
Valsecchi, M., & Gegenfurtner, K. R. (2016). Dynamic re-calibration of perceived size in fovea and periphery through predictable size changes. *Current Biology, 26*(1), 59–63.
Weale, R. A. (1953). Spectral sensitivity and wave-length discrimination of the peripheral retina. *The Journal of Physiology, 119*(2–3), 170–190.

Witzel, C. (2016). An easy way to show memory color effects. *I-Perception, 7*(5), Article 2041669516663751.
Witzel, C., & Gegenfurtner, K. R. (2018). Color perception: Objects, constancy, and categories. *Annual Review of Vision Science, 4*(1), 475–499.
Witzel, C., Olkkonen, M., & Gegenfurtner, K. R. (2018). A Bayesian model of the memory colour effect. *I-Perception, 9*(3), Article 2041669518771715.
Witzel, C., O'Regan, J. K., & Hansmann-Roth, S. (2017a). The dress and individual differences in the perception of surface properties. *Vision Research, 141*, 76–94.
Witzel, C., Racey, C., & O'Regan, J. K. (2017b). The most reasonable explanation of "the dress": Implicit assumptions about illumination. *Journal of Vision, 17*(2), 1–1.
Witzel, C., Valkova, H., Hansen, T., & Gegenfurtner, K. R. (2011). *Object knowledge modulates colour appearance. I-Perception, 2*(1), 13–49.
Zhang, R., Isola, P., & Efros, A. A. (2016). *Colorful image colorization*. 649–666.
Zrenner, E., & Gouras, P. (1983). Cone opponency in tonic ganglion cells and its variation with eccentricity in rhesus monkey retina. *Colour Vision*, 211–224.