ORIGINAL PAPER

Automatic, Early Color-Specific Neural Responses to Object Color Knowledge

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Abstract

Some familiar objects are associated with specific colors, e.g., rubber ducks with yellow. Whether and at what stage neural responses occur to these color associations remain open questions. We recorded frequency-tagged electroencephalogram (EEG) responses to periodic presentations of yellow-associated objects, shown among sequences of non-periodic blue-, red-, and green-associated objects. Both color and grayscale versions of the objects elicited yellow-specific responses, indicating an automatic activation of color knowledge from object shape. Follow-up experiments replicated these effects with green-specific responses, and demonstrated modulated responses for incongruent color/object associations. Importantly, the onset of color-specific responses was as early to grayscale as actually colored stimuli (before 100 ms), the latter additionally eliciting a conventional later response (approximately 140–230 ms) to actual stimulus color. This suggests that the neural representation of familiar objects includes both diagnostic shape and color properties, such that shape can elicit associated color-specific responses before actual color-specific responses occur.

Introduction

Objects typically are defined specifically by their shape, and thus shape information is often sufficient for basic-level visual object recognition (Grossberg and Mingolla 1985; Biedermann 1987; Biederman and Ju 1988). While surface attributes, such as texture and color, are often not

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object-specific, they nevertheless contribute substantially to object recognition (Marr and Nishihara 1978; Tanaka et al. 2001). In part, color may assist in object recognition by providing cues to image segmentation and thus shape: for example, color can be more reliable than luminance for defining object boundaries, since luminance variations often also arise from shading (Kingdom et al. 2004), and color is among the most powerful cues for perceptually grouping and spatially organizing the visual stimulus (Wolfe and Horowitz 2004). Yet color also provides object-diagnostic information, for even clearly segmented objects shown in color are typically recognized faster and more accurately than when shown in grayscale (Price and Humphreys 1987; Wurm et al. 1993; Humphrey et al. 1994; Tanaka and Presnell 1999; Nagai and Yokosawa 2003; Therriault et al. 2009; Rossion and Pourtois 2004; Bramao et al. 2011; Hagen et al. 2014).

The contribution of color to object recognition is not equal for all objects. For example, color contributes more towards the recognition of structurally similar objects (e.g., some fruits and vegetables) or when an object exemplar has an atypical or degraded shape (Markoff 1972; Price and Humphreys, 1989; Wurm et al. 1993; Joseph and Proffitt 1996; Tanaka and Presnell 1999; Liebe et al. 2009). Yet, the objects benefiting the most from the presence of color are those for

which familiar objects have a learned association with a specific color, so-called "color-diagnostic" objects (e.g., Helmholtz 1867; Joseph and Proffitt 1996; Tanaka and Presnell 1999; Naor-Raz et al. 2003; Rossion and Pourtois 2004; for a meta-analysis: Bramao et al. 2011). Such color-associated objects are present across a variety of object types, including natural, artificial, living, non-living, and animated: e.g., blueberries (blue), lobsters (red), US dollar bills (green), and Pikachus (yellow; for further examples of color-associated objects, see Appendix B of Joseph and Proffitt 1996; Table 1 of Tanaka and Presnell 1999; Appendix 1 of Naor-Raz et al. 2003; Appendix A of Nagai and Yokosawa 2003; Appendix 5 of Rossion and Pourtois 2004; Fig. 3 of Witzel et al. 2011). When such color-associated objects are presented in incongruent colors, i.e., any color other than their typical color, object recognition performance is lower in terms of accuracy and/or response time relative to objects presented in congruent color and, to a lesser extent, in grayscale (Price and Humphreys 1987; Joseph and Proffitt 1996; Tanaka and Presnell 1999; Therriault et al. 2009; Hagen et al. 2014). For these objects, the specific color/object association allows color to provide a diagnostic cue for object recognition. Moreover, it is possible that this association allows object shape to provide a cue for object color: color naming is less accurate and/or delayed for incongruent relative to congruent color-associated objects (Bruner and Postman 1949; Ratner and McCarthy 1990; Naor-Raz et al. 2003).

These observations suggest that the recognition of color-specific objects by shape alone automatically evokes their color associations. Indeed, the perception of color-specific objects may be drawn towards the associated color of the object, i.e., the "memory color", particularly when the presented color is categorically ambiguous, e.g., yellow-orange, or presented in the context of challenging viewing conditions (e.g., Duncker 1939; Bruner and Postman 1949; Mitterer and de Ruiter 2008; Vandenbroucke et al. 2016). Such color association effects have been further demonstrated in work suggesting that grayscale object images can appear subtly tinged with their characteristic hue (Hansen et al. 2006; Olkkonen et al. 2008; Witzel et al. 2011), and that chromatic afterimages of objects appear more vivid when corresponding to their typically associated colors (Lupyan 2015).

Functional neuroimaging studies have reported that color-associated grayscale objects activate visual regions of the human brain associated with color perception, including in the fusiform gyrus (Martin et al. 1995; Simmons et al. 2007; Slotnick, 2009). More recently, these findings have inspired the successful decoding of the associated color of grayscale color-specific images from actual color responses with functional neuroimaging in visual regions or whole-brain analyses, even when subjects performed orthogonal, i.e., non-color-related, tasks (fMRI: Bannert and Bartels 2013;

Vandenbroucke et al. 2016; MEG: Teichmann et al. 2019a, b, 2020). However, some of these studies have used only a few objects per color category (e.g., two in Bannert and Bartels 2013), and have reported divergent results in terms of the cortical areas responding to memory color (V1: Bannert and Bartels 2013; V3, V4, VOI, LOC, and prefrontal areas: Vandenbroucke et al. 2016). Nevertheless, in light of these findings, it appears possible that color-specific brain responses are automatically activated by the visual shape of the color-associated objects. However, whether shape information automatically elicits an associated color response as measured with EEG, and how that response differs from the response to an actual color stimulus, remain to our knowledge unknown.

These issues directly refer to the question of the temporal stage(s) of visual object processing/representation at which color and shape components are related. On one hand, a late role of color (after about 100 ms; e.g., Marr and Nishihara 1978; Biedermann 1987; Proverbio et al. 2004; Therriault et al. 2009; Teichmann et al. 2020), is proposed in a hierarchical view of visual perception. In this view, color processing is only influenced by shape-based expectations at later stages of visual processing, following feedback from high-level visual areas. This implies that chromatic and spatial representations are relatively independent in early visual processing, which has been supported by some lines of evidence. For example, color or shape differences (e.g., in orientation or size) are salient cues supporting rapid visual search, yet an arbitrary color-shape conjunction requires attention to be detected (e.g., Triesman 1982; Wolfe et al.). Similarly, some aspects of spatial vision (e.g., acuity and disparity processing) and motion perception can become degraded for images defined only by chromatic contrast (Cavanagh et al. 1984; Mullen 1985; Shevell and Kingdom 2008), and color tends to be more labile and fill-in between boundaries defined by spatial variations in luminance (Pinna et al. 2001; van Lier et al. 2009), results which have added to the ongoing interest and debate about the modularity of visual processing, particularly for color and form (e.g. Livingstone and Hubel 1984; Zeki and Shipp 1988; Merigan and Maunsell 1993; Lennie 1998; Sincich and Horton 2005; Shapley and Hawken 2011). On the other hand, an early role for associated color (before about 100 ms; e.g., Price and Humphreys 1989; Naor-Raz et al. 2003; Rossion and Pourtois 2004; Lu et al. 2010; Hagen et al. 2014; Teichmann et al. 2019a, b) is present in a framework in which object color knowledge, through past experience, constrains, and perhaps even generates, color perception (e.g., Helmholtz 1867; Gregory 1966; Thompson 1995; Lotto and Purves 2002). This view necessitates that object color and shape are rapidly, automatically integrated in object recognition. There is evidence for such an interaction in early visual

processing: for example, cells in the primary visual cortex are often tuned to both spatial and chromatic information (Thorell et al. 1984; Johnson et al. 2001) and can be selective to conjunctions of color and form (Seymour et al. 2010). Psychophysically, adaptation and masking are selective for both the shape and color of the stimuli (McCollough 1965; Bradley et al. 1988; Clifford et al. 2003), and chromatic contrast can support many spatial discriminations (Webster et al. 1990; Krauskopf and Farell 1991). Evidence for both early and late roles of color, and how it relates to shape in visual object processing, do not limit an influence of color to any stage of visual processing (Johnson and Mullen 2016).

The few electro/magnetoencephalography (EEG and MEG, respectively) findings on the timing of color in object recognition are inconsistent. Teichmann et al. (2019a, b) reported earlier color-specific responses to colored shapes than grayscale objects (65 vs. 190 ms, respectively), based on the success of a multivariate pattern-analysis classifier trained on colored shapes with full-brain MEG. However, the use of different stimuli for actually colored and grayscale stimuli (abstract shapes and natural objects, respectively), may have contributed to these latency differences. When natural objects were used in both color and grayscale color-decoding in a later study (Teichmann et al. 2019b), "accessing colour via real colour perception and implied colour activation occurred at the same time, around 150 ms" (p. 28). Other studies have not reported significant latency differences between event-related potentials (ERPs) evoked by color, grayscale, or incongruently colored objects (Proverbio et al. 2004; Lu et al. 2010; Bramao et al. 2012b; Lloyd-Jones et al. 2012).

However, in these ERP studies, some differences in latency of color-associated effects have been inferred from the onset of amplitude differences across color *vs.* grayscale or congruent *vs.* incongruent color objects. Such differences were reported at the earliest components for congruent color vs. grayscale object stimuli (Lu et al. 2010: N1 and later components decreased for congruent color *vs.* grayscale/incongruent color; Bramao et al. 2012b: P1 and N1 increased for color *vs.* grayscale, but not yet for incongruent color vs. grayscale (Lu et al. 2010). In other studies, differences were reported for congruent color only at later components (Proverbio et al. 2004: N2 increased when attending to color for congruent *vs.* incongruent shapes; Lloyd-Jones et al. 2012: P2 and P3 decreased for congruent *vs.* incongruent color; Bramao et al. 2012b: N400 increased for diagnostic vs. non-diagnostic color). A common limitation of these studies is that responses to different object color categories were averaged together, despite evidence that the spatial and temporal dynamics of EEG responses to different colors can differ substantially (e.g., Regan 1966; Riggs and Sternheim 1968; Allison et al. 1993; Anllo-Vento et al. 1998; Retter et al. 2020; Sutterer et al. 2021; Chauhan et al. 2023).

In the present study, we address: (1) whether object-associated, color-specific neural responses can be recorded for objects with strong color-associations; and (2) the unresolved issue of the timecourse at which color impacts visual object processing. For both these questions, we apply a sensitive "oddball" frequency-tagging EEG approach, that enables separating color-specific oddball responses (here, at 1 Hz; e.g., to yellow) from more general visual responses (at 4 Hz, to shape, non-specific color, etc.; e.g., Rossion et al. 2015; for reviews: Norcia et al. 2015; Rossion et al. 2020). This isolation of these color-specific responses at 1 Hz is applicable in both the frequency-domain and the time-domain: in both cases, more general visual responses at 4 Hz are selectively excluded from the analyses (see Rossion et al. 2020).

First, we objectively quantify the 1-Hz, color-specific neural responses in the frequency domain to familiar, color-associated objects, displayed in actual color; next, using grayscale versions of these objects, we quantify the contribution of any object-associated color signal to the 1-Hz, color-specific response, again in the frequency domain. Our findings indicate that while there is an effect of color on visual object stimulation responses, color-associated object shape alone can evoke substantial color-specific neural responses. Interestingly, similar color-specific response onset latencies recorded for actual color and grayscale object images suggest that object-color associations onset as rapidly for implied as actual color. A divergence of the neural responses for the two types of stimuli occurs only later, with the emergence of the more sluggish chromatic responses to actual stimulus color.

Materials and Methods

Participants

Sixteen participants took part in Experiment 1 (targeting yellow-associated object responses), who aged from 18 to 35 years old (M = 24.5 years; SD = 5.27 years); eleven identified as female, and five as male; thirteen as right-, and three as left-handed. Sixteen participants also took part in Experiments 2 and 3, in a single testing session. These latter participants were aged 20–30 years old (M = 24.6 years; SD = 3.67 years); eleven identified as female, and five as male; fourteen as right- and one as left-handed, and one as ambidextrous. All reported normal or corrected-to-normal visual acuity, as well as normal color vision. Sample size per experiment was determined relative to previous within-samples, frequency-tagging EEG studies concerning color perception, for which the sensitivity and reliability, even at the individual level, is high (e.g., 14 participants, medium effect sizes for color differences, over 80% of individuals

with significant responses: Retter et al. 2020; Or et al. 2019; see also the review of Norcia et al. 2015). Each experiment was performed only once, and no participants were excluded from the analyses.

Stimuli

Objects with a strongly associated color were chosen with considerations for color category and object type. Ultimately, 24 object images were selected, balanced for color category (red, green, blue, and yellow) and object type (fruit/vegetable, cartoon character, manmade, and animal), and controlled for low-level attributes (Fig. 1a).

With regard to color association strength ("color diagnosticity"), we first selected images of 40 candidate objects, with reference to previous studies (Tanaka and Presnell 1999; Naor-Raz et al. 2003; Witzel et al. 2011). In an informal survey, we presented these images in grayscale to a room of 110 undergraduate students. Participants were asked "what color do you think the item is?", and instructed to fill in a sheet to indicate their response from the following list: red, orange, yellow, green, blue, purple, gray, and don't know. Color association was assessed by the percent agreement across participants for the most frequent color selected. Objects with the highest color association ratings were selected while maintaining balance in color category and object type, resulting in a minimum of 93% color naming agreement on average within each color category (range 93–96%).

The resulting stimuli of each color category consisted of two fruits/vegetables, two cartoon characters, one manmade object, and one animal. These objects were as follows, for red: strawberry, cherries, Elmo, Devil, fire extinguisher, and lobster; yellow: corn, banana, Pikachu, SpongeBob, star sticker, and rubber duck; green: broccoli, celery, Grinch, Shrek, dollar bill, and frog; blue: blueberries, eggplant, Cookie Monster, Smurf, mailbox, and whale. Note that the eggplant was actually named as purple, but was nevertheless included in the (untargeted) blue set to match for object type. The object images were coarsely selected for similarity in visual appearance: for example, the cartoon characters were restricted to two-dimensional renderings with similar postures, and the animal was consistently a toy version.

To control for low-level attributes, the images of these objects were first isolated from their background, cropped to their external edges, and resized to a common rectangular area. A grayscale set of these images was created with custom software, and both the colored and grayscale set were equalized in terms of mean luminance and root mean-squared luminance contrast. The colors for the different objects were adjusted to coincide with different hue angles relative to neutral gray (CIE 1931 x,y = 0.310, 0.316) within a version of the MacLeod-Boynton chromaticity diagram scaled to roughly equate threshold sensitivity along the cardinal axes (see Fig. S1 of Winkler et al. 2015). For the different color categories, the mean hue angle in the space was set to: 355° (red), 315° (yellow), 205° (green), and 135° (blue), with all images' mean hues restricted to a 10° range
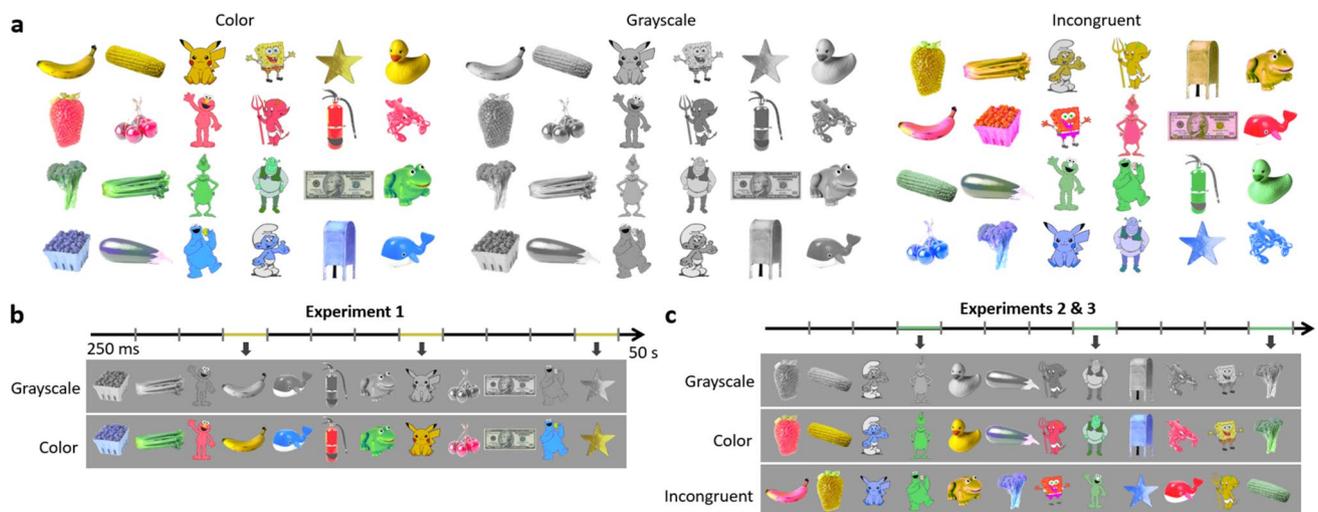

Fig. 1 **a**) The 24 color-associated stimuli used in the experiments, shown as appearing in diagnostic color (left), grayscale (middle), and incongruent color (right) conditions. **b**) The trial design of Experiment 1, targeting yellow-associated objects, is depicted for each the grayscale and color conditions. Stimuli were presented every 250 ms (at 4 Hz) in 50 s sequences, throughout which a yellow-associated object appeared every 1 s (1 Hz), i.e., as every fourth image. The order of the green-, red-, and blue-associated images was fully randomized within every sequence for each participant. **c**) The trial design of Experiments 2 and 3, targeting green-associated object responses. Experiment 3 consisted of an incongruent condition, in which targeted non-green-associated objects appeared in green.

within each category, in order of the mean hue rankings of the original images. A set of incongruent color stimuli was made for Experiment 3, by assigning a non-associated color category to each image, while maintaining balance across object type.

To test whether additional image attributes might vary across object color categories, the grayscale objects were also examined in terms of additional (higher-order) image statistics, namely in terms of spatial frequency content (using scripts from Torralba and Oliva 2003; Bainbridge and Oliva 2015), global contrast factor (Matkovic et al. 2005) and gist (spatial envelope; Oliva and Torralba 2001). No significant differences were found (see Supplemental Material), although it remains a possibility that the stimuli have some mean differences by color category (e.g., in curvature, local contrast, etc.). Note that the neural responses to grayscale objects may be expected to be particularly uniform across object exemplars within participants, since color memories have been shown to be biased to prototypical color category membership (for objects: Van Gulick and Tarr 2010; for color patches: Boynton et al. 1989; Uchikawa and Shinoda 1996; Bae et al. 2015; see also Bartleson 1960).

Experimental Design

The experimental design employs the periodic presentation of one stimulus category (here, at 1 Hz) embedded at a fixed repetition rate within a faster stimulus presentation rate (4 Hz), sometimes referred to as an "oddball" paradigm (e.g., Rossion et al. 2015; for reviews: Norcia et al. 2015; Rossion, Retter and Liu-Shuang, 2020). There were two conditions in Experiment 1, targeting yellow-specific responses at 1 Hz: *grayscale* and *color* images. In the former, all images were presented in grayscale, and in the latter, the same images were presented in color. In Experiment 2, these two conditions were replicated while targeting green-specific responses at 1 Hz. In Experiment 3, a novel condition targeting 1-Hz green-specific responses was tested: *incongruent* images, in which the color of each of the object images was replaced with a non-associated color (Fig. 1a right). Participants were presented with four 50-s sequence repetitions for each condition, leading to a total of 3.3 min of recording per condition (6.7 min of recording in Experiment 1; 10 min in Experiment 2). The conditions were presented in blocked order, counter-balanced across participants. In Experiments 2 and 3, the grayscale condition was always presented first, to prevent an influence on the object's associated color from having first seen the incongruently colored images.

Throughout each sequence, stimuli were presented at a rate of 4 Hz, i.e., every 250 ms. With a 50% square-wave duty cycle, each image was displayed at full contrast for 125 ms, followed by 125 ms of the gray background between successive images. In accordance with the "oddball" design, in Experiment 1, yellow-associated images appeared every 1 s, at a rate of 1 Hz, within the sequence; in Experiment 2, green-associated images appeared at 1 Hz; in Experiment 3, incongruently green-colored objects appeared at 1 Hz. The order of presentation of the other, non-target color-associated objects was fully randomized within every sequence for every participant (Fig. 1b). Thus, responses to a consistent object-color association (i.e., yellow-selective responses in Experiment 1; green-selective responses in Experiment 2) were expected at 1 Hz and its specific harmonics (2, 3, 5 Hz, etc.), while responses to object presentation in general were expected at 4 Hz and its harmonics (see Retter et al. 2021). Alternatively, if the responses to stimuli at 1-Hz were not generalizable across exemplars, or were not discriminable from those at 4 Hz, no 1-Hz response would be predicted (Norcia et al. 2015; Rossion et al. 2020).

Participants could initiate trials at their own pace. Upon commencement of each trial, the testing sequence was preceded by 1–2 s of a fixation cross, in order to orient attention and decrease exact prediction of image onset, followed by 1 s of gradual stimulus contrast increase (fade-in), to avoid abrupt eye movements. Each sequence was followed by 1 s of fade-out and 1–2 s of the fixation cross, with similar logic and to delay movements upon trial completion. Only the 50-s testing sequence was retained for analysis.

The stimuli were presented on a gray background with a mean luminance of 61.5 cd/m^2, equal to the mean luminance of the test images. The monitor was a Display + +LCD with a 120 Hz screen refresh rate, gamma-corrected based on calibrations obtained with a PhotoResearch PR655 spectroradiometer, and controlled by a standard PC. The monitor was viewed at a distance of 80 cm, such that the images subtended a mean width/ length of 5.26 degrees of visual angle. To reduce size-specific responses, the size varied randomly over a range from 92 to 108% of the size of the original image in 4% steps at each image presentation (Dzhelyova and Rossion 2014). Stimuli were presented over Java SE Version 8. Viewing was binocular and in a room illuminated only by the experimental and acquisition computer displays.

Task

Participants were instructed to attend to the images presented while fixating on a centrally presented fixation cross, which was present throughout the entire testing sequence, superimposed on the images. To encourage fixation and sustained central attention, the participants' task was to press on the space bar each time they detected a brief shape change (250 ms) of the cross to an open circle. This occurred 8

times in each trial, at random intervals above a minimum of 500 ms. Participants were naïve to the experimental manipulation.

EEG Acquisition

EEG was acquired with a 128-channel BioSemi ActiveTwo EEG system. This systems uses Ag–AgCl Active-electrodes, with default electrode locations centered around nine standard 10/20 locations on the primary axes, including a reference feedback loop consisting of two additional channels (a common mode sense and driven right leg; BioSemi B.V., Amsterdam, Netherlands; for exact coordinates, see http://www.biosemi.com/headcap.htm). The BioSemi electrodes were relabeled to closely match those of the more conventional 10/5 system (Oostenveld and Praamstra 2001; for exact relabeling, see Rossion et al. 2015, Figure S2). Additional electrooculogram (EOG) signals were recorded from four flat-type Active-electrodes, positioned above and below the right eye and lateral to the external canthi. Following setup of the EEG system (including insertion of a conductive gel), the offset of each electrode was held below 50 mV. The recordings were saved at a sampling rate of 512 Hz.

EEG Analysis: Preprocessing

Data were (pre)processed with Letswave 6, an open source toolbox (http://nocions.webnode.com/letswave), running over MATLAB R2019b (MathWorks, USA). Data were filtered with a fourth-order, zero-phase Butterworth band-pass filter, with cutoff values below 0.1 Hz and above 100 Hz; to remove contamination from electrical noise, a fast-Fourier transform notch filter was also applied at 60 and 120 Hz, with a width and slope of 0.5 Hz. To correct for muscular artifacts related to eye-blinks, independent-component analysis was applied to remove a single component accounting for blink activity in participants blinking more than 0.2 times/s (6 participants in Experiment 1; overall, $M = 0.16$ blinks/s; $SD = 0.15$ blinks/s; 5 participants in Experiment 2; overall, $M = 0.11$ blinks/s; $SD = 0.10$ blinks/s). To correct for artifact-contaminated channels (containing deflections beyond ± 100 μV in two or more testing sequences), these channels (six or fewer per participant; Experiment 1: $M = 3.4$ channels; Experiment 2: $M = 2.7$ channels) were linearly interpolated with 3–5 symmetrically-surrounding neighboring channels. After filtering and artifact correction, data were re-referenced to the common average of the 128 EEG channels.

EEG Analysis: Frequency-Domain Transform

Preprocessed, individual sequences were isolated in separate 50-s epochs, and averaged in time by condition, to

selectively reduce activity not phase-locked to stimulus presentation. These data were transformed into the frequency domain by means of a Fast Fourier Transform (FFT) for amplitude. This spectrum was normalized by the number of samples output; it had a range of 0–256 Hz and a resolution of 0.02 Hz.

EEG Analysis: Harmonic Frequencies-of-Interest

As mentioned previously, responses to objects (i.e., yellow-selective responses in Experiment 1; and green-selective responses in Experiments 2 and 3) are predicted at 1 Hz and its specific harmonics, while general responses to visual object presentation are predicted at 4 Hz and its harmonics. While responses may occur at harmonics beyond the fundamental frequency, they are expected within a limited range, specific to the type of response occurring (e.g., Retter and Rossion 2016; Jacques et al. 2016; Retter et al. 2021).

In order to determine the frequency ranges of interest here, the signals were pooled across all EEG channels and grand-averaged across participants. These data were then assessed for significance at all harmonics of the fundamental 1 Hz (color-specific) and 4 Hz (stimulus-presentation) responses for each condition, by means of Z-scores ($Z > 1.64$; $p < 0.05$; calculated at each frequency bin, x, with a local baseline defined by the 20 surrounding frequency bins: $Z = (x - \text{baseline mean})/\text{baseline standard deviation}$; e.g., Srinivasan et al., 1999; Retter and Rossion 2016). The maximal harmonic frequency range with contiguous significance, exempting one harmonic, in either condition of Experiment 1 was identified and used in subsequent analyses: for the color-specific responses, this range spanned 1–25 Hz. Note that harmonics coinciding with the stimulus-presentation responses within this range were excluded. For the stimulus-presentation responses, this range spanned 4–56 Hz. These criteria were relatively insensitive to threshold: only one fewer color-specific harmonic would have been selected had a threshold of $p < 0.01$ been used. The same frequencies-of-interest were used in Experiments 2 and 3, after verification that they were reasonably appropriate: green-selective responses were significant until 23 Hz, and until 68 Hz for stimulus-presentation responses.

EEG Analysis: Region-of-Interest (ROI) and Subregions

An occipito-parietal ROI was defined to target visual responses predicted over the posterior cortical surface, without bias across conditions. To this extent, we selected a region of 24 channels (18.8% of all channels), centered medially from Iz to POOz, and extending symmetrically over the left and right parietal cortices. We verified *post-hoc* that the ROI closely encompassed the channels with

the maximal activation across both conditions, for both 1-Hz and 4-Hz responses, of Experiment 1. For the 1-Hz color-specific responses, it encompassed 21 of the maximal 24 channels for both the grayscale and color conditions, averaged across participants; for the 4-Hz stimulus-presentation responses, it again encompassed 21 of the maximal 24 channels for the grayscale condition, and 22 for the color condition. This ROI was later verified for Experiments 2 and 3: it captured 21–22 of the maximal 24 green-selective channels, and 20–21 of the maximal stimulus-presentation channels, in each condition. The same ROI was used across all conditions of all experiments. For more specific response characterization, this ROI was further broken into three subregions, distinguishing medial channels expected to sensitive to low-level visual responses from lateralized channels expected to be more sensitive to higher-level object properties: the left (10 channels), middle (4 midline channels), and right (10 channels) (see Figs. 4 and 5).

EEG Analysis: Quantification and Statistics

Responses were examined across all the EEG channels and harmonic frequencies of interest; however, to summarize the results in quantification and statistical analyses, the primary analyses focused on data collapsed across the ROI (and subregions), through channel-averaging, and frequencies-of-interest, through amplitude summation (Retter and Rossion 2016; Retter et al. 2021). Data were grand-averaged across participants for description and display, as well as for a group-level tests of response significance on the summed harmonic responses (Z-scores: Z > 2.32; p < 0.01). Note that after harmonic responses were combined, a local baseline-correction was applied (given the variable noise level across the frequency spectrum), in the form of a baseline-subtraction, with a baseline defined by the 20 surrounding frequency bins, after excluding the local minimum and maximum (e.g., Rossion et al. 2012; Retter and Rossion 2016).

To statistically compare the responses across conditions at the occipito-parietal ROI, in Experiment 1, one-tailed, paired-sample t-tests were performed, with the prediction that larger amplitude responses would be produced in the color than grayscale condition. A one-way ANOVA was performed to compare the three conditions of Experiments 2 and 3, followed up by one-tailed paired-sample t-tests comparing the color and grayscale condition of Experiment 2 (as in Experiment 1), as well as the color and incongruent conditions. To compare the spatial distribution of responses across the scalp, a repeated-measures analysis of variance (ANOVA) was performed, with factors of *Condition* (two levels in Experiment 1: grayscale and color; three levels in

Experiments 2 and 3: grayscale, color, and incongruent) and *Subregion* (three levels: left, middle, and right). In the case that Mauchly's test of sphericity was violated, a Greenhouse–Geisser correction was applied.

EEG Analysis: Time Domain

Data were analyzed in parallel in the time domain, following preprocessing. To this extent, the data were first low-pass filtered with a fourth-order Butterworth filter at 30 Hz. To isolate the color-specific object responses, the stimulus-presentation responses were selectively removed through a frequency-domain notch filter, applied at all the harmonics of 4 Hz below 30 Hz, with a width and slope of 0.02 Hz. Indeed, one important advantage of the "oddball" paradigm is that the 4-Hz responses common to all stimuli (generic visual responses) can be removed, such that the specific 1-Hz responses are isolated, in the time- as well as frequency-domain (e.g., as in Dzhelyova and Rossion 2014; Retter and Rossion 2016; Jacques et al. 2016; review: Rossion et al. 2020).

The data were cropped in separate segments for each object presentation, from 250 ms prior- and 750 ms post-stimulus onset. The cropped data segments were baseline-corrected by subtracting the average amplitude in the 250 ms preceding stimulus onset, a time window corresponding to one stimulus-presentation cycle. To avoid contamination from eye movements, data segments containing deflections of ± 125 µV in any EOG channel were rejected. Data segments were then averaged by condition. To determine when color-specific response deflections significantly differed from baseline (0 µV), independent t-tests against zero were performed at every time bin from stimulus onset to 750 ms post-stimulus onset; to reduce the chance of false-positive due to the high number of comparisons: this was applied only at the three subregions of interest, rather than at every channel; a threshold of p < 0.01 was selected; and a consecutively criteria of 15 ms of significance (9 consecutive sampling bins) was applied for significance to be considered (e.g., see Retter and Rossion 2016; Quek and Rossion 2017; Or et al. 2019). Similarly, paired-sampled t-tests were applied to determine when the responses from the color and grayscale conditions differed from each other, as well as the color and incongruent conditions in Experiment 2. For description and display, data were grand averaged across participants.

Results

Frequency Domain: Amplitude Spectra

Responses to visual stimulus presentation were evident as high-amplitude peaks in the frequency domain at 4 Hz and
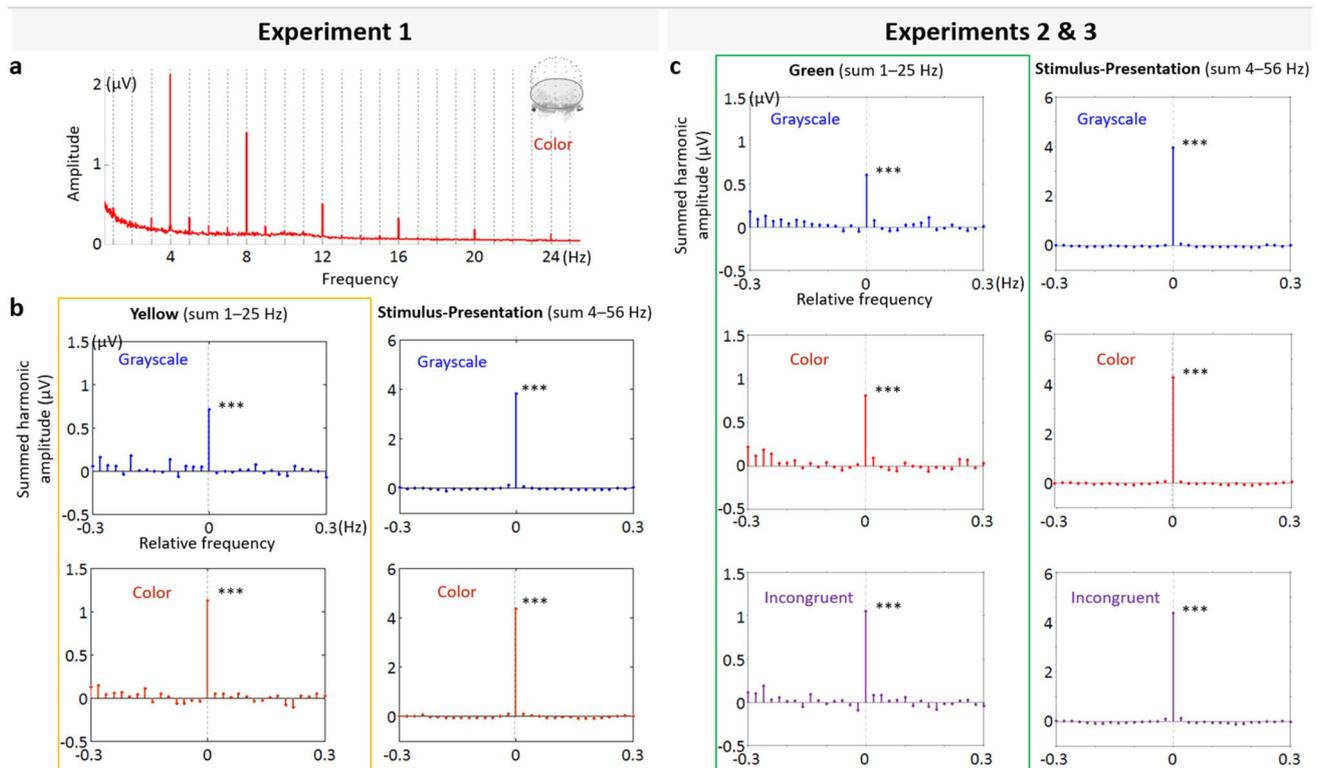
Fig. 2 **a** The frequency-domain amplitude spectra for the color condition of Experiment 1, plotted over the occipito-parietal ROI. Dotted vertical lines indicate the frequencies of 1 Hz and its harmonics. (For corresponding spectra of all conditions, see Fig. S1.) The visual stimulation responses at 4 Hz and its harmonics are indicated with x-axis labels. **b** and **c** Summed baseline-subtracted harmonic responses:

a frequency range of 0.6 Hz is plotted relative to the summed frequency-of-interest and its specific harmonics (f*) set at 0 Hz (the x-axis represents frequency—f*). The surrounding frequency range from 0.3 Hz below to above f* is included to display the local noise amplitude and variability; average noise level is expected at 0 µV. Key: *** = Z > 3.1, p < 0.001

its harmonics. More importantly, color-specific responses were also evident as peaks at 1 Hz and its specific harmonics, for every condition (Fig. 2a for an example: see Fig. S1 for all conditions). To describe these complete responses, the harmonics were summed and baseline-subtracted, from 1 to 25 Hz for color-specific responses (excluding 4 Hz and its harmonics), and from 4 to 56 Hz for stimulus-presentation responses (Experiment 1: Fig. 2b; Experiments 2 and 3: Fig. 2c; see Methods).

Frequency Domain: Amplitude Quantification

Critically, the color-specific responses to objects at 1 Hz and its harmonics were robust even when the color-associated objects were shown in grayscale. The amplitude of the color-specific summed-harmonic response to objects in grayscale was about 70% of that for objects in color (Experiment 1: 63%; Experiment 2: 75%) over the occipito-parietal ROI (Fig. 3a; Table S1a). In comparison, for stimulus-presentation, the grayscale response was about 90% that of color (Experiment 1: 81%; Experiment 2: 93%; Fig. 3b; Table S1b).

This amplitude difference between the yellow-selective responses in the color and grayscale conditions was statistically significant in both experiments: Experiment 1, $t_{15} = 4.22$, $d = 1.29$, $r = 0.54$, $p = 0.0004$; Experiment 2, $t_{15} = 2.94$, $d = 0.70$, $r = 0.33$, $p = 0.0051$ (following a significant one-way ANOVA, $F_{2,45} = 6.94$, $\eta_p^2 = 0.24$, $p = 0.0024$). At the individual level, significant color-specific responses at the occipito-parietal ROI were found in all but one participant in both conditions in Experiment 1, and in all but three participants in the grayscale condition in Experiment 2, underlying the reliability of the main finding that both grayscale and color images are sufficient to elicit color-specific responses to color-associated objects (Table S2). With regard to the corresponding stimulus-presentation responses, these were significantly different in Experiment 1, $t_{15} = 1.75$, $d = 1 = 0.32$, $r = 0.16$, $p = 0.012$ (Fig. 3b), but a one-way ANOVA in Experiments 2 and 3 indicated no significant differences across conditions, $F_{2,45} = 0.41$, $\eta_p^2 = 0.018$, $p = 0.66$.

In the other direction, the color-specific response to incongruently colored objects in Experiment 3 was 131% of that to correctly-colored objects, $t_{15} = -3.10$, $d = -0.70$,
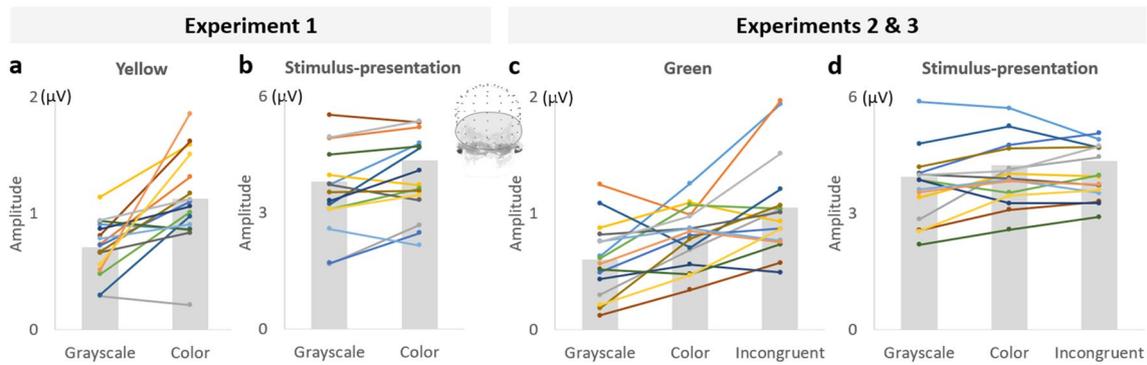
Fig. 3 Summed-harmonic, baseline-subtracted response amplitude (μV) over the occipito-parietal ROI, at the group- (gray bars) and individual- (colored lines) levels. **a** Yellow-selective responses (1–25 Hz) from Experiment 1. **b** Stimulus-presentation responses (4–56 Hz) from Experiment 1. **c** Green-selective responses (1–25 Hz) from Experiments 2 and 3. **b)** Stimulus-presentation responses (4–56 Hz) from Experiments 2 and 3

$r = $ -0.33, $p = 0.0037$. However, there was no appreciable difference in the corresponding (color vs. incongruent) stimulus-presentation responses (Fig. 3c and Table S1).

Frequency Domain: Topography

For a more detailed spatial investigation of these responses, the scalp topographies were plotted (Fig. 4a and c) and the single occipito-parietal ROI was decomposed into its left, right, and middle subregions (Fig. 4b and d). Across the first two experiments, the scalp topographies showed more lateralized color-specific responses for grayscale than color conditions (Fig. 4a and c). Although

the grayscale responses appeared right lateralized for yellow-associated object responses, and left lateralized for green-associated object responses, there was great interindividual variability: indeed, in Experiment 2, there were not more left- than right-lateralized participants (Fig. S2).

In the subregions of interest, in the middle the response in the grayscale condition was about 54% of that of the color condition across the first two experiments, while over the combined left and right subregions, it was about 74% (middle: 53%-54% across experiments; left and right: 82–65% across experiments). In comparison, the stimulus-presentation responses were more similar in the grayscale relative to color conditions, and less specifically over the middle
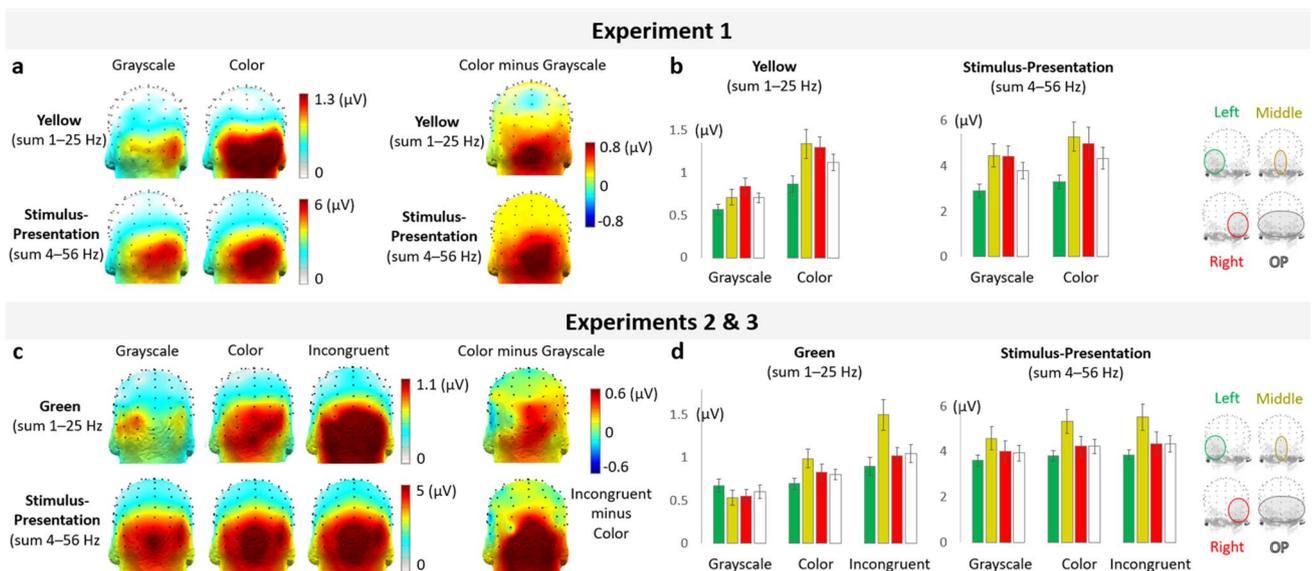

Fig. 4 **a** and **c** Summed-harmonic response scalp topographies in the grayscale and color conditions (Experiments 1 and 2), and incongruent condition (Experiment 3), as well as their differences. **b** and **d** Mean summed-harmonic responses at the occipito-parietal (OP) ROI and its three subregions: left, middle, and right (illustrated on the head plots on the right of panel (**b**)
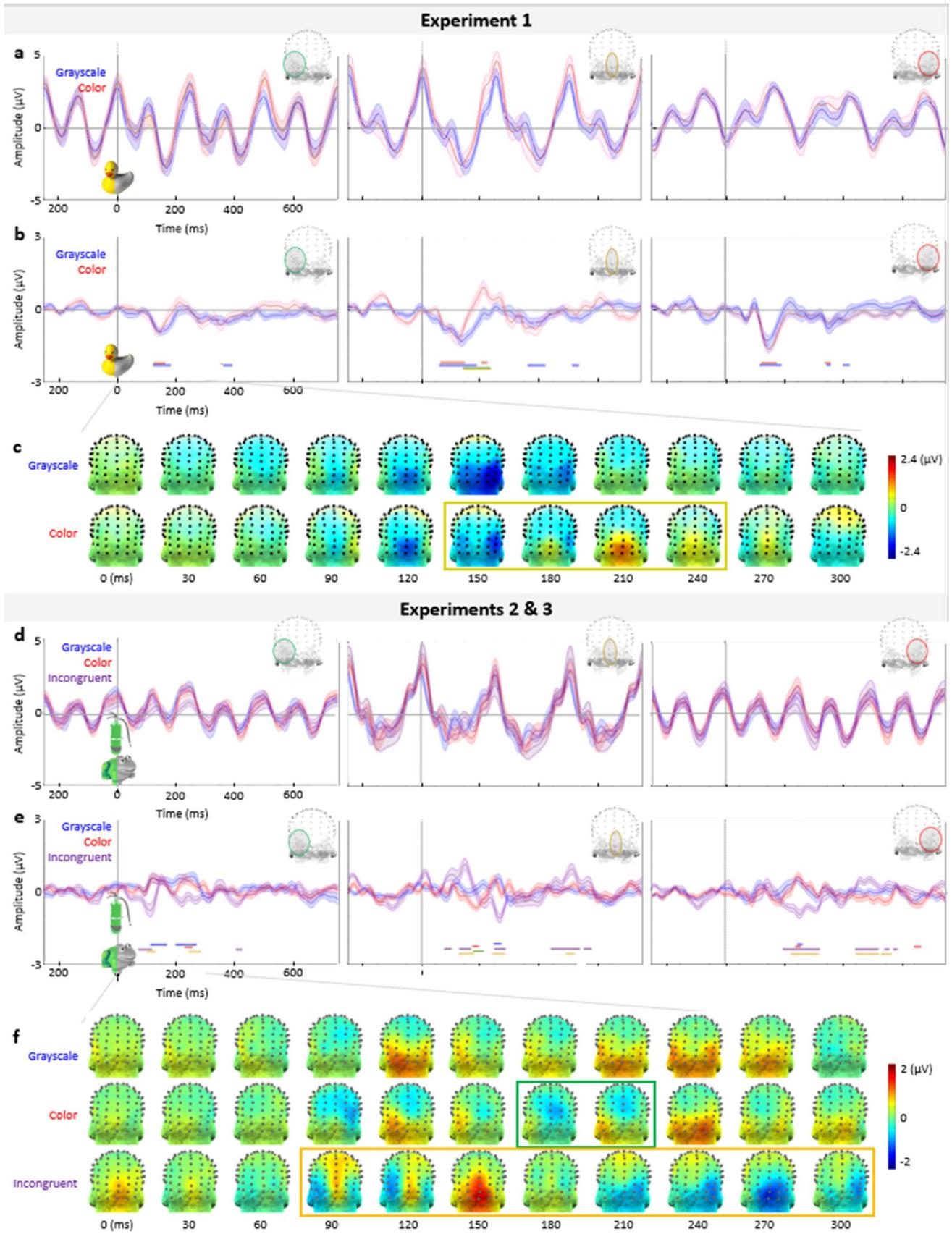
◀**Fig. 5** Temporal dynamics. **a** Time-domain responses in the grayscale (blue waveform) and color (red waveform) conditions, related to yellow-associated object stimulus onset (0 ms; exemplified with a yellow/gray rubber duck; in Experiment 1), at the three scalp subregions (left, middle, and right panels, respectively). These responses reflect the responses to all objects (presented at 4 Hz, i.e., every 250 ms) as well as the responses specific to yellow-associated objects. The dark waveforms are the average across subjects, with the shaded areas indicating ± 1 SE. **b** After filtering out the general visual EEG responses at 4 Hz and its harmonics, the time-course of the yellow-associated object responses may be isolated. This panel is plotted as in (**a**), except with a different amplitude scale. Additionally, the time windows of significant deflections for each condition are indicated by solid lines below the waveforms in the corresponding color by condition; significant differences across conditions, occurring only at the middle subregion, are indicated in yellow-green. **c** Response scalp topographies across time: sampled every 30 ms from stimulus onset. The approximate time window of significant differences between conditions, i.e., a positive deflection over the middle subregion in the color condition, is highlighted with a yellow outline over that condition. **d** Responses including those to stimulus-presentation as well as those specific to green-associated (Experiment 2) or incongruently-green (Experiment 3; purple waveform) objects; **e** Stimulus-presentation filtered. **f** Response scalp topographies for Experiments 2 and 3, plotted as in (**c**), with a green outline over the color condition; differences between the color and incongruent conditions are outlined in orange over the incongruent condition.

subregion: about 85% middle, and 92% over the left and right subregions (middle: 84–56% across experiments; left and right: 95–88% across experiments).

In Experiment 1, these spatial differences for color-specific responses across conditions were confirmed in a repeated-measures ANOVA, with factors of *condition* and *subregion,* which yielded a moderate interaction between these factors, $F_{2,30} = 4.03$, $p = 0.042$, $\eta_p^2 = 0.37$. Note that the main effect of this ANOVA replicated the large difference of *condition,* $F_{1,15} = 18.7$, $p = 0.001$, $\eta_p^2 = 0.56$; the main effect of *subregion* was not robust, $F_{1,30} = 2.96$, $p = 0.084$, $\eta_p^2 = 0.30$. Similarly, in Experiments 2 and 3, there was an interaction between *condition* and *subregion*, $F_{4,15} = 6.33$, $p = 0.0003$, $\eta_p^2 = 0.30$, and a substantial main effect of *condition,* $F_{2,15} = 18.6$, $p < 0.0001$, $\eta_p^2 = 0.55$. There was also a main effect of *subregion*, $F_{2,15} = 6.63$, $p = 0.0041$, $\eta_p^2 = 0.31$.

Temporal Dynamics

To investigate the temporal dynamics of the color-specific responses, the data were analyzed in the time domain, in terms of event-averaged responses time-locked to the onset of yellow-associated (Experiment 1), green-associated (Experiment 2), or incongruent green (Experiment 3) object stimulus presentation, over the occipito-parietal subregions (see Methods).

Initially, the responses to yellow- or green-associated/incongruent objects were obscured by the responses to other objects (appearing every 250 ms, i.e., at − 250 ms, 250 ms, and 500 ms here; Experiment 1: Fig. 5a**;** Experiments 2 and 3: Fig. 5d). To isolate color-specific object responses, the waveforms were notch-filtered at the stimulus-presentation rate, 4 Hz, and its harmonics. Note that the response aspects common to the stimulus presentation are removed by the notch filter, such that if no differential response to the target stimuli at 1 Hz is recorded, no substantial deflections from the baseline would be present.

There were significant deflections in both the grayscale and color conditions, in a range of about 60 to 670 ms post-stimulus onset across the first two experiments (Fig. 5b and e). In Experiment 1, these responses first onset in a negative deflection over the middle subregion (grayscale: 61 ms; color: 65 ms). A negative deflection was also seen later over the left and right subregions, first reaching significance at 119 and 125 ms over the right subregion in the grayscale and color conditions, respectively, and at 123 and 127 ms over the left subregion. In total, there were no differences in the onset latency of the yellow-associated response across the grayscale and color conditions. In Experiment 2, color-specific responses first onset in a negative deflection over the middle subregion in the color condition (172 ms), but in a positive deflection over the left subregion in the grayscale condition (109 ms). Note that the differences in the temporal dynamics of the responses specific to yellow and green objects (in Experiments 1 and 2, respectively) supports the presence of color-specific responses in the frequency domain.

Importantly, the significant differences between the color and grayscale conditions occurred in a later time window, from 140–230 ms post-stimulus onset, over the middle subregion (Experiment 1: 141–234 ms; Experiment 2: 174–211 ms; paired sample t-tests; p < 0.01; Fig. 5b and e). In both experiments, this was present as a deflection present in the color but not grayscale condition: Experiment 1, a positive deflection peaking at 211 ms; Experiment 2: a negative deflection peaking at 188 ms (Fig. 5c and d). There were no other appreciable differences across conditions in either the subregion waveforms, or the scalp topographies, in either experiment.

In Experiment 3, there were also significant, early, specific deflections to incongruently-colored green objects. However, these presented first over the left subregion, at 68 ms, shortly followed by the middle subregion, at 76 ms (Fig. 5e). The responses to incongruently-colored green stimuli also showed relatively early, significant differences from those to congruently-colored green stimuli, first emerging at 98 ms over the left subregion, followed by 125 ms over the middle subregion (Fig. 5e and f).

Discussion

Summary

We designed an experiment to isolate selective responses to objects of one color category (yellow in Experiment 1; green in Experiments 2 and 3), presented at a rate of 1 Hz within a 4 Hz stream of otherwise non-periodic object colors. We found color-specific responses reflecting the differing spatial and temporal dynamics of EEG responses to different colors (e.g., Regan 1966; Riggs and Sternheim 1968; Allison et al. 1993; Anllo-Vento et al. 1998; Retter et al. 2020; Sutterer et al. 2021; Chauhan et al. 2023), for stimuli with strongly associated colors shown in actual color. Critically, these automatic, color-specific responses were also generated from grayscale stimulation, possibly through object knowledge (Experiments 1 and 2), and were modulated for incongruently-colored objects (Experiment 3). The early onset (before 100 ms) of these color-specific responses to object-color associations in all stimulus conditions contrasted with a later response to the actual color in the stimuli (after 140 ms post-stimulus onset). These results suggest that shape and diagnostic color information are bound in object representations, such that shape cues alone are sufficient to generate a rapid response to the associated color, even though the responses to actual color in the stimulus propagate more slowly.

Color-Specific EEG Responses to Actually Colored Stimuli

Selective neural responses were recorded at 1 Hz and its harmonics to yellow (Experiment 1) or green (Experiment 2) objects shown in their associated color. This demonstrates a neural response at the consistent presentation frequency of the target color that is distinct from the responses to non-periodic presentations of three other object color categories, also shown in their associated color (color condition; Fig. 2). Different responses to different colors have been reported in a few previous EEG studies (e.g., Regan 1966; Riggs and Sternheim 1968; Anllo-Vento et al. 1998; Retter et al. 2020; Sutterer et al. 2021; Chauhan et al. 2023). This is unsurprising given differences in amplitude and latency as a function of cone-opponent cortical inputs (e.g., Robson and Kulikowski 1998; Rabin et al. 1994; Lee et al. 2009). However, these results have been previously reported only at the group level, typically with a small number of electrodes, and were largely descriptive: here, we objectively quantify color-specific responses to actual color stimuli in the frequency domain which are significant at the individual participant level (in 15/16 participants in Experiment

1; and 16/16 participants in Experiment 2; Table S2; see Fig. 3a and c). In our results, the high sensitivity to the target color is likely enabled by the extensive spatial coverage of high-density EEG (given the variability in the response scalp topography across individual participants), as well as the high signal-to-noise ratio afforded by frequency tagging (Regan 1966; Norcia et al. 2015).

There are several reasons to conclude that this color-specific (e.g., to yellow at 1 Hz, vs. intra-sequential non-periodic red, blue, and green) response does not emerge as an artifact of our paradigm. First, there was no confound of frequency of occurrence across object color categories: all object images appeared equally as often in each sequence on average. While all object colors thus on average were occurring at a rate of 1 Hz, we empirically demonstrated that no response would occur at 1 Hz and its harmonics without a specific periodically-presented color: in a control condition added with the last five participants of Experiment 1, we presented all the colored objects non-periodically, and found no 1-Hz response (Fig. S3). Secondly, the "oddball" paradigm used here has been demonstrated to be immune to temporal predictability of the target stimuli (Quek and Rossion 2017). Although oddball periodicity is typically not reported by any participants (e.g., Retter et al. 2020; 2021), even in the context of expectation manipulation responses to surprising oddball responses have been shown not to differ from those to more predictable ones (Feuerriegel et al. 2018). Additionally, discriminable responses to different object image types are unlikely to be attributed to general expectation (or random stimulus combinations; Jacques et al. 2016).

Third, the yellow-selective response we record in this paradigm is similar in terms of scalp topography to a yellow/gray asymmetry response reported in a previous study (Retter et al. 2020). Similarly, the differences in the temporal dynamics of yellow-selective and green-selective responses, with the actual-color specific peaks at 211 vs. 188 ms, respectively, are not incompatible with studies showing variable timecourses for yellow and green stimuli (Adrian 1945; Shipley, Jones and Fry 1965; Paulus 1984; Chauhan et al. 2023). A specific response was present consistently for both yellow and green objects, and was modulated by incongruent color in Experiment 3. Finally, we performed an item-based analysis on the time-domain responses to individual objects in Experiment 1, and verified that the responses to actual color were present consistently across individual object stimuli (Fig. S4), again suggesting that the responses at 1 Hz and its harmonics do appear to capture color-specific neural responses.

That the amplitude of the color-specific response to colored objects was larger than that to grayscale objects in the frequency domain may represent the contribution of an additional response to the actual stimulus color, in line with typical neural responses to non-object color stimuli.

It should be remembered that the color-specific responses recorded here are *differential* responses to objects presented at 1 Hz, *vs.* object presentation in general, at 4 Hz. The color-specific responses are thus more reduced for grayscale vs. color stimuli than would be expected from a general effect of color, as indexed by the responses at the stimulus-presentation rate (again, the grayscale responses were about 70% of the amplitude of actual color responses for the color-specific responses over the occipito-parietal ROI, but about 90% for the stimulus presentation responses; Fig. 3; see also Or et al. 2019, for no general effect of color at 12 Hz). On the other hand, when stimuli were shown in incongruent colors in Experiment 3, the largest response was produced, (Fig. 4d**;** as in Lu et al. 2010; Lloyd-Jones et al. 2012; but not in Proverbio et al. 2004), possibly indicating a conflict of the associated and actual colors.

Color-Associated Objects Elicit Color-Specific EEG Responses to Grayscale Images

We recorded selective responses to yellow- (Experiment 1) and green- (Experiment 2) associated objects at 1 Hz and its harmonics, even when all the objects were shown in grayscale (grayscale condition; Fig. 2). As addressed in the Introduction, previous studies have shown that color memory influences the perceived color of objects, through a convergence of various experimental approaches. Indeed, color-specific responses to grayscale stimuli have been previously reported with functional magnetic resonance imaging (Bannert and Bartels 2013; Vandenbroucke et al. 2016) and MEG (Teichmann et al. 2019a, b, 2020). Here, the report of color-specific responses to grayscale objects with EEG, which to our knowledge is novel, supports and extends these previous studies.

Previous EEG studies have instead measured effects of color memory that are non-specific to a color category, i.e., contrasts of color *vs.* grayscale or color *vs.* incongruent color objects, averaging across color categories (8 different color categories: Proverbio et al. 2004; color category uncontrolled among 96 objects: Lu et al. 2010; color category uncontrolled among 54 high color-diagnostic objects: Bramao et al. 2012b; color category uncontrolled among 150 objects: Lloyd-Jones et al. 2012). Not only did these previous EEG studies report inconsistent differences in the amplitude of color *vs.* grayscale objects responses, but these effects cannot be taken as reflecting color-specific responses associated with objects. In fact, when only color *vs.* grayscale object responses are compared, the response differences could be more related to a general effect of color, as we also observe on the 4 Hz stimulus presentation rate in our study (i.e., a grayscale response of about 90% that of color). Additionally, no previous study quantified the difference in response amplitude between implied *vs.* actual color.

The presence of color-specific responses to grayscale objects here, about 70% of the amplitude of response to actually-colored objects, suggests that color-specific responses may arise from associations between the representational shape and color information of diagnostically colored objects. That is, shape alone may automatically and rapidly trigger full neural representations of objects, including their associated color knowledge. For example, the brain's response to seeing the shape of a yellow rubber duck may automatically activate a network of cortical regions representing this object through its attributes, including its yellow color. In this vein, it has been suggested that color memory responses originate from color-selective regions evoked from object shape associations (e.g., Slotnick 2009, recording learned color-shape associations of abstract visual shapes; see also Simmons et al. 2007). Another possibility is that color knowledge responses originate from regions close to but external from color-selective regions, which may have been influenced by color associations (e.g., Martin et al. 1995, recording shape associations to the presentation of color words; note that similar neural data is interpreted differently by Slotnick 2009). Thus, it remains unknown whether these color memory responses originate from color-selective cortical regions, or whether they are object-selective responses that have been selectively configured by learned color associations.

Importantly, this reduced yet still substantial response amplitude should not be interpreted as the perceptual experience of color in grayscale images. Indeed, under most conditions, grayscale images of color-associated objects actually do appear gray (with the exception of small effects of memory color biases, produced in an unnatural context: e.g., Hansen et al. 2006, reporting 4–13% relative scaling; Lee and Mather 2019, reporting weak chromatic adaptation effects to achromatic implied color stimuli). However, the presence of color-specific association responses does not imply that one is actively perceiving yellow when looking at a grayscale rubber duck. Similarly, large amplitude brain responses to perceiving eyes alone does not imply one is perceiving a whole face (Bentin et al. 1996), and the pattern and rate of "mirror neuron" activity for visually observing motion does not imply one perceives themselves moving (e.g., Kilmer and Lemon 2013). Instead, again, our results suggest that perceiving information about an object's shape may automatically activate representations of other attributes associated with the object, even if they are absent from the current stimulus.

Equal Onset-Latencies are Followed by a Late (~ 140–235 ms) Actual Color Difference

The temporal stage at which color associations may arise from object knowledge remains highly controversial. By

using an "oddball" paradigm, we were able to selectively remove the responses to generic visual stimulation at 4 Hz, and to isolate the color-association specific responses at 1 Hz in the time-domain. While these time-domain responses are elicited by stimuli presented at 1 Hz, unlike those to onset-jittered stimuli as used most commonly in ERP research, there is some evidence that periodicity does not affect the response timecourse (see Fig. 7 of Quek and Rossion 2017; see also Retter and Rossion 2016, showing similar response timecourses to stimuli presented at different periodic rates).

In the time-domain analyses here, we show that when generic visual responses are removed, color-specific, object-associated responses to grayscale objects emerge at the same time as those to actually colored objects (Fig. 5). This suggests that neural responses to objects, derived from shape cues alone, rapidly and automatically trigger associated attributes like color even when this attribute is not part of the current stimulus; and these associated responses occur without a measurable delay between grayscale and colored images. This is in line with some previous EEG studies not reporting amplitude differences for congruent color objects at the earliest ERP components (Proverbio et al. 2004: Lloyd-Jones et al. 2012: Bramao et al. 2012b; see also Lu et al. 2010), and an MEG study of Teichmann et al. (2019b). It is also in line with behavioral studies showing a color advantage in recognizing objects or scenes with associated colors even at the shortest image presentation times (from 10 to 1000 ms per item: Bruner and Postman 1949; from 16–64 ms per image: Gegenfurtner and Rieger 2000; from 13 to 80 ms per image: Hagmann and Potter 2016), providing indirect evidence that color has an early impact on object processing. Further indirect evidence of short-latency color effects has been provided by behavioral studies that show a consistent color advantage in accuracy of object recognition across trials with relatively early or late response times (Rossion and Pourtois 2004; Hagen et al. 2014).

In contrast, the responses to actually colored objects diverged from those to grayscale objects only later, in the form of an additional deflection present only in the actual color condition (Fig. 5). This deflection was present within about 140–235 ms post-stimulus onset; its peak was on average at approximately 200 ms, across experiments. Spatially, this deflection was centered over the middle occipital channels, in agreement with the middle subregion producing the largest amplitude advantage for the color condition in the frequency-domain analysis (e.g., in Experiment 1, compare the scalp topography of the differences across conditions in Fig. 4a with that of this time-domain component in Fig. 5c). The latency of these deflections is in line with the earliest chromatic visually evoked potentials to isoluminant stimuli reported with EEG in the human brain (from about 100–120 ms: e.g., Rabin et al. 1994; Gerth et al. 2003: the C_{II}-C_{III} components; Nunez

et al. 2017; see also Hermann et al. 2022 for color decoding with MEG at 115 ms; and Sutterer et al. 2021; Chauhan et al. 2023). Thus, it is possible that these late deflections are related to typical cortical chromatic processing. A delayed role of actual color is in line with color having a late effect on enhancing image representation in memory (Gegenfurtner and Rieger 2000; for other late effects of color on object categorization: Proverbio et al. 2004; Yao and Einhauser 2008; Bramao et al. 2012b; Lloyd-Jones et al. 2012; Or et al. 2019). It is also in agreement with the separation of color and shape in visual processing (e.g., Triesman 1982; Cavanagh et al. 1984; Zeki and Shipp 1988; Livingstone and Hubel 1984; Pinna et al. 2001), and a view of object recognition as shape-dominant (e.g., Grossberg and Mingolla 1985; Biedermann 1987).

These findings relate to the debate as to which time-course color information is incorporated in object recognition, in combination with object shape. Instead of pointing to a single role of color in object recognition, our electrophysiological data support separate roles of *knowledge* of object color and *actual* stimulus color. This relates to previously made distinctions of color *identification* from color *contrast perception* (Johnson and Mullen 2016), or *stored color knowledge* from *surface color* (Joseph and Proffitt 1996). On one hand, similar color-specific (e.g., yellow-specific) responses to grayscale and actual color stimuli may be a result of color knowledge: the representation of an object may automatically evoke that object's associated color representation, whether or not that color is actually present in the stimulus. On the other hand, differences in color-specific responses to actual color relative to grayscale stimuli may be a result of actual stimulus-color processing.

Interestingly, the present results suggest that access to color knowledge can be triggered by associated shape cues even before responses to the actual color of the objects is processed. In other words, because responses to luminance stimuli are generally faster than to chromatic stimuli, shape cues may invoke color-associations before actual stimulus color is processed. This is perhaps contrary to intuition: while such a model was proposed by Joseph and Proffitt (1996: Model B, Fig. 5), in the context of color knowledge having a larger effect than actual color in a behavioral object recognition task, this was stated conservatively in terms of influence rather than actual processing time.

Indeed, earlier responses to implied than actual color speaks against a common theory of perception in which "top-down" influences of color memory expectations only occur after chromatic processing (e.g., Tanaka et al. 2001; Hansen et al. 2006; Hanslmayr et al. 2008; Bramao et al. 2012a, b). However, an earlier role of color knowledge than actual color is in agreement with a theory of perception in which stimulus recognition marks the onset of perception,

with additional sensory details being incorporated only later in time (see Helmholtz 1867; Gregory 1966; Sergent 1986; Thompson 1995; Lotto and Purves 2002). It is thus possible that, at least in the limited case of familiar objects routinely associated with specific colors (i.e., "color-diagnostic" objects), color knowledge may affect our earliest color perception.

Data availability The EEG datasets acquired for the current study are available from the corresponding author on request.

Declarations

Conflict of interest The authors declare no competing interests.

Ethical approval The study was conducted in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki), and approved by the University of Nevada, Reno's Institutional Review Board.

Consent to participate All participants gave signed, informed consent prior to participation.

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