Pupil size reveals the perceptual quality and effortless nature of synesthesia

Christoph Strauch[1] ✉, **Casper Leenaars**[1], **Romke Rouw**[2]

[1]Experimental Psychology, Helmholtz Institute, Utrecht University, Utrecht, Netherlands • [2]Brain & Cognition, Department of Psychology, University of Amsterdam, Amsterdam, Netherlands

Reviewed Preprint
v1 • March 6, 2026
Not revised

Reviewed Preprint
v2 • May 28, 2026
Revised by authors

✉ **For correspondence:**
c.strauch@uu.nl

Competing interests: No competing interests declared

Funding: See page 15

Reviewing editor: Joshua I Gold, University of Pennsylvania, United States

eLife Assessment

This study used pupillometry to provide an objective assessment of a form of synesthesia in which people see additional color when reading numbers. It provides **convincing** evidence that subjective color ratings are matched by changes in pupil size that recapitulate brightness-mediated changes when exposed to the real color. The work provides a **valuable** contribution to the literature on both synesthetic perception and the use of pupillometry to probe perception and related psychological processes.

https://doi.org/10.7554/eLife.110390.2.sa4

Abstract

Synesthesia describes cross-over processes that can generate ’extra’ conscious percepts, such as seeing additional color when reading numbers. While existing research focuses on the mechanisms and effects of synesthetic associations, it often overlooks its most distinctive feature: unique sensory phenomenology. Here, we introduce pupillometry as an objective physiological measure of synesthetic color phenomenology. Across 16 grapheme-color synesthetes and two matched control groups, pupil responses tracked the brightness of synesthetic colors under constant physical visual input, scaling with selfreported strength. Synesthetic colors elicited pupil dynamics comparable to real colors, dissociating synesthetes from non-synesthetes. These responses emerged too rapidly to reflect imagery and scaled with reported color brightness, revealing cross-over caused genuine perceptual processing. Controls required to generate color associations showed greater effort-linked pupil dilation than synesthetes or controls who did not report colors, providing evidence for the effortless nature of synesthesia. Synesthesia thus provides a tractable human model for studying physiologically measurable phenomenology.

Significance statement

How can we measure what someone actually experiences? Synesthesia, in which stimuli such as numbers can evoke cross-over sensations like seeing colors, provides a rare test case. Here we make this extraordinary sensation objectively measurable and show that it has a distinct sensory signature. We find that pupil size reflects the brightness of synesthetic colors even when physical light remains constant. Pupils constrict for bright colors and dilate for dark ones, revealing the quality and strength of the percept. These responses emerge rapidly and differ from those of non-synesthetes. Together, synesthesia provides a tractable model for studying internally generated sensations, with pupillometry offering a direct, measurable window into conscious perception.

1 Introduction

Two observers presented with the exact same visual stimulus may experience a qualitatively very different percept [e.g., "the dress" 1]. While intuitively this may seem puzzling, theories on consciousness and vision explain such phenomena by noting that human perception, rather than a direct reftection of the external (shared) world, emerges in a constructive process of adjusting incoming sensory signals against our idiosyncratic expectations, knowledge and experiences [2–6]. This constructed understanding becomes especially apparent in color perception; even though color space is clearly defined in its physical and perceptual dimensions [7], it still fails to capture the "*what-it-is-like*" aspect of an individual's color experience [1, 7].

Not surprisingly, being able to measure, understand, and eventually describe the emergence of these subjective qualia is therefore one of most hotly debated questions in the neurosciences, philosophy and beyond [5, 8–10]. Here, we present a natural experiment of subjective color phenomenology; a condition called graphemecolor synesthesia [11–14]. For grapheme-color synesthetes, certain linguistic inducers (e.g., grapheme '4') automatically and consistently trigger additional and idiosyncratic conscious color percepts (e.g., a bright-blue color) alongside the veridical sensory input.

The different synesthesia types all share the defining characteristics of an additional conscious and consistent experience. Synesthetes can verbally report their additional experience, and synesthetic sensations can be measured in behavioral paradigms such as the 'synesthetic Stroop' effect, or brain activation patterns in sensory cortex [15]. Furthermore, test-retest paradigms show how synesthetic, but not non-synesthetic associations are highly specific and consistent [16–18]. Thus, over the past decades, research has established synesthesia as a 'real' condition that can reliably be identified using behavior, neurophysiology, and neuroimaging [11, 13, 15–19]. The most remarkable aspect of synesthesia is the subjective perceptual phenomenology of the induced additional sensation, i.e., color in grapheme-color synesthesia. This sets synesthetic sensations apart from (color) memory, thought, or amodal association. Synesthesia can thus offer an interesting doorway into examining qualia, the subjective perceptual phenomenology or first person (what's-it-like) perspective. Furthermore, much like ordinary perception, the synesthetic experience is described as 'automatic' in the sense that it comes effortlessly [13, 20, 21] [albeit not pre-attentive, see 22, 23]; the concurrent synesthetic color is 'just there', even if incongruent with the task at hand [15, 20, 21]. Because each synesthete has a stable set of grapheme–color pairings, the color phenomenology can be examined independently of the physical properties of the inducing stimuli. Therefore, synesthesia might provide a unique window into how the brain's constructive processes can generate additional, conscious content, cross-over experiences, often across modalities, going all the way down to the level of sensory phenomenology.

The measurement of such sensory phenomenology primarily relies on subjective reports and introspection, methods often criticized for potential unreliability and susceptibility to biases or expectancy effects [e.g., 24–26]. These concerns extend to synesthesia research, where objective measurements are called for to corroborate subjective reports [27–29]. Instead, current paradigms capturing synesthesia employ objective measures, but fail to capture its phenomenology [16, 21, 22, 30]. Behavioral and neurophysiological findings suggesting synesthetic colors behave like printed colors in turn have been questioned regarding replicability and interpretability [23, 31–33]. In short, the lack of agreed-upon objective methodology is a critical roadblock obstructing scientific examination of the extraordinary synesthetic phenomenology. By extension, this locks the condition's potential to inform our understanding of the constructive top-down cross-over processes that can generate additional conscious percepts.

We propose that pupillometry is the tool to break this gridlock. Pupil size constricts in response to externally increased brightness and dilates when brightness decreases. Remarkably, akin to our color phenomenology not directly following from physical color input, the pupillary light response does not strictly follow the physical light entering the eye, but reftects the percept as interpreted by the viewer [34–42]. Research has revealed such sensitivity to perceptual phenomenology in unimodal contexts [e.g., phenomenological vividness of an (imagined) visual image 40, 43, 44]. Building on this evidence, we hypothesized that the cross-over color phenomenology in synesthesia, if truly sensory in nature, could likewise be inferred from changes in pupil size. Hereby, the direction and magnitude of these changes should provide a scaled response reftecting the brightness of the experienced synesthetic colors; pupillometry may thus provide both qualitative and quantitative characterizations of the synesthetic color phenomenology (see Figure

1a and b for an illustration of the rationale and proposed mechanism). If synesthetic cross-activations indeed reach all the way down to low-level (sensory) processes, pupillometry can track their precise temporal onset, as well as provide scaled measurements of their phenomenological properties (i.e., the relative change in pupil size corresponding to the brightness of the synesthetic color).

To investigate this, we tested 16 grapheme-color synesthetes and two control groups of 16 participants each. Participants viewed graphemes (digits) on a computer screen during eyetracking, and indicated, after each trial, which color most closely matched with the respective grapheme (see Figure 1c for paradigm).

2 Results

2.1 More consistent and strongly coupled colors in synesthetes

Selected colors are visualized per participant in Figure 2a. Synesthetes reported colors more consistently ($t(30) = 9.910$, $p < 0.001$, $d = 3.504$, 95% CI = [2.370, 4.614] (in line with previous work, see [see e.g. 16, 45, 46]) and more strongly coupled to graphemes ($t(30) = 12.690$, $p < 0.001$, $d = 4.487$, 95% CI = [3.150, 5.801]) than controls (see Figure 2b). There was considerable variation in reported color lightness for all participants (see Figure 2c, d), setting the basis for a possible inference of color phenomenology via the pupil light responses in both synesthetes and controls. Importantly, reported lightness of colors almost exactly matched between controls ($M = 0.478$, $SD = 0.065$, lightness scaled between 0 = black and 1 = white) and synesthetes ($M = 0.479$, $SD = 0.070$; $t(30) = 0.031$, $p = 0.975$, $d = 0.011$, 95% CI = [-0.704, 0.682]; $BF_{01} = 2.973$). Together, our synesthete participants were grapheme-color synesthetes as per the gold standard of the field [16], reporting specific, strong and consistent colors in response to graphemes.

2.2 Pupil responses reveal the quality of synesthetic color perception

Having established similar reported-color lightness levels between active controls and synesthetes, we next investigated whether the pupil light response betrays synesthetic color. Perceived, (covertly) attended, or even imagined brightness modulates pupil size in the same direction as changes in physical luminance - i.e., in both directions, constriction *and* dilation [see 47, 48, for reviews]. We therefore expected bright perceived synesthetic colors to be betrayed by relative pupil constriction and dark synesthetic colors to be betrayed by relative pupil dilation. We did not expect non-synesthetes to show pupil size alterations in accordance with the brightness of their associated colors. Pupil responses to reported color lightness were analyzed separately for synesthetes and active controls. A visual inspection of per-timepoint demeaned pupil traces for participants having at least 25 trials in above and below median lightness bins respectively (Figure 3) demonstrates larger pupil sizes for dark graphemes and smaller pupil sizes for light graphemes in synesthetes (mid row, Block 1). In controls, this was very weak, if present at all (top row, Block 1). As expected, when splitting pupil size for colored discs similarly along lightness, synesthete pupil size demonstrated descriptively even larger and earlier changes than for synesthetic color. Dependent-samples t-tests for averaged pupil size in response to graphemes (stimulus interval) between 800 ms and 4000 ms, split by (reported) color lightness, showed different pupil responses for synesthetes both for synesthetic colors (Figure 3d, $t(11) = 4.669$, $p = 0.001$) and externally triggered light responses in synesthetes (Block 2, see Figure 1c; Figure 3f, $t(10) = 4.550$, $p = 0.001$), but not in controls (Figure 3b, $t(12) = 0.850$, $p = 0.412$).

2.2.1 Pupil size betrays the lightness of synesthetic color

To optimally account for the data structure, we next ran a linear-mixed effects model (LME) predicting pupil size. The LME effectively considers all trials and was fitted for the average pupil size between 800 ms and 4000 ms (reported in brackets) as well as separately for every timepoint in the stimulus interval (visualized in Figure 4). Starting from a full model containing all interactions between the following factors, the final LME for synesthetes (for both discretized and

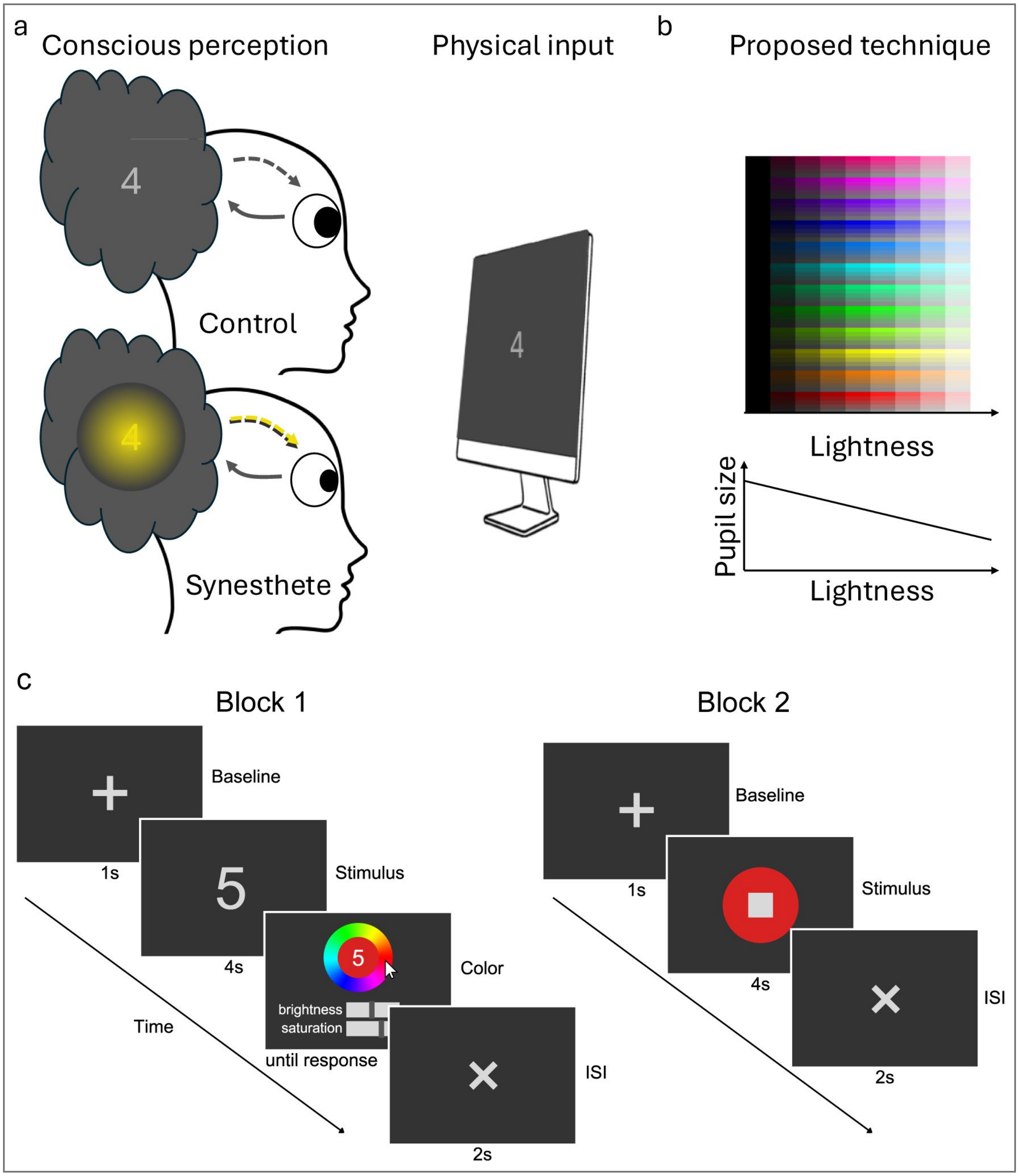


Figure 1. Mechanism and paradigm.

a phenomenology results from external (solid arrow) and internal contributions (dashed arrow). The integrated brightness should affect pupil size: Light (dark) synesthetic colors should cause constrictions (dilations) at equal physical luminance in synesthetes, but not in controls where externally and internally generated brightnesses align. **b** We expected synesthetes' pupils to be larger for reported lower brightness and smaller for reported higher brightness. **c** Paradigm. Block 1: a digit was presented. Participants (except passive controls) subsequently indicated the color that most closely corresponded to the digit in their opinion. This was followed by an interstimulus interval (ISI). Block 2 (synesthetes only): a disk was presented, colored according to the synesthete's average indicated color for that digit. At its center sat a gray patch matching the luminance and pixel area of the original digit from Block 1, together allowing assessment of externally triggered light responses.

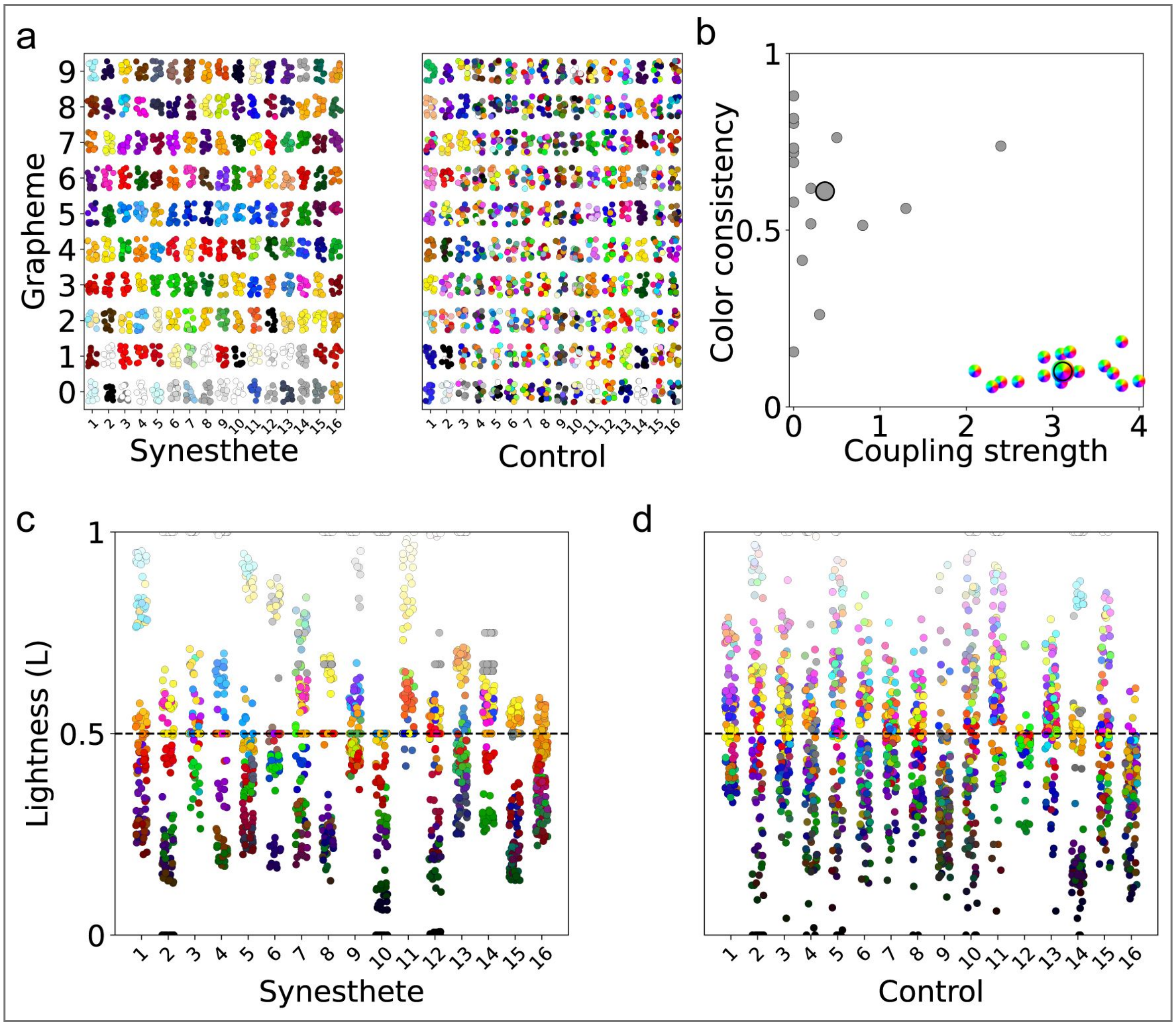


Figure 2.

a Reported colors per grapheme on all trials for synesthetes (left) and controls (right). **b** Synesthetes showed (near) perfect grapheme-color consistency and moderate to very strong grapheme-color couplings (rainbow circles), while controls reported none to moderate coupling and varied in consistency (grey circles). Note that higher consistency is reftected in lower color distance, hence lower values [17]. Larger dots indicate group means. **c,d** (HS)Lightness of color reports per synesthete (c) and control (d). Blacked dashed line represents lightness being 0.5. See Supplementary Figure 1 for color reports on the hue and saturation axes.

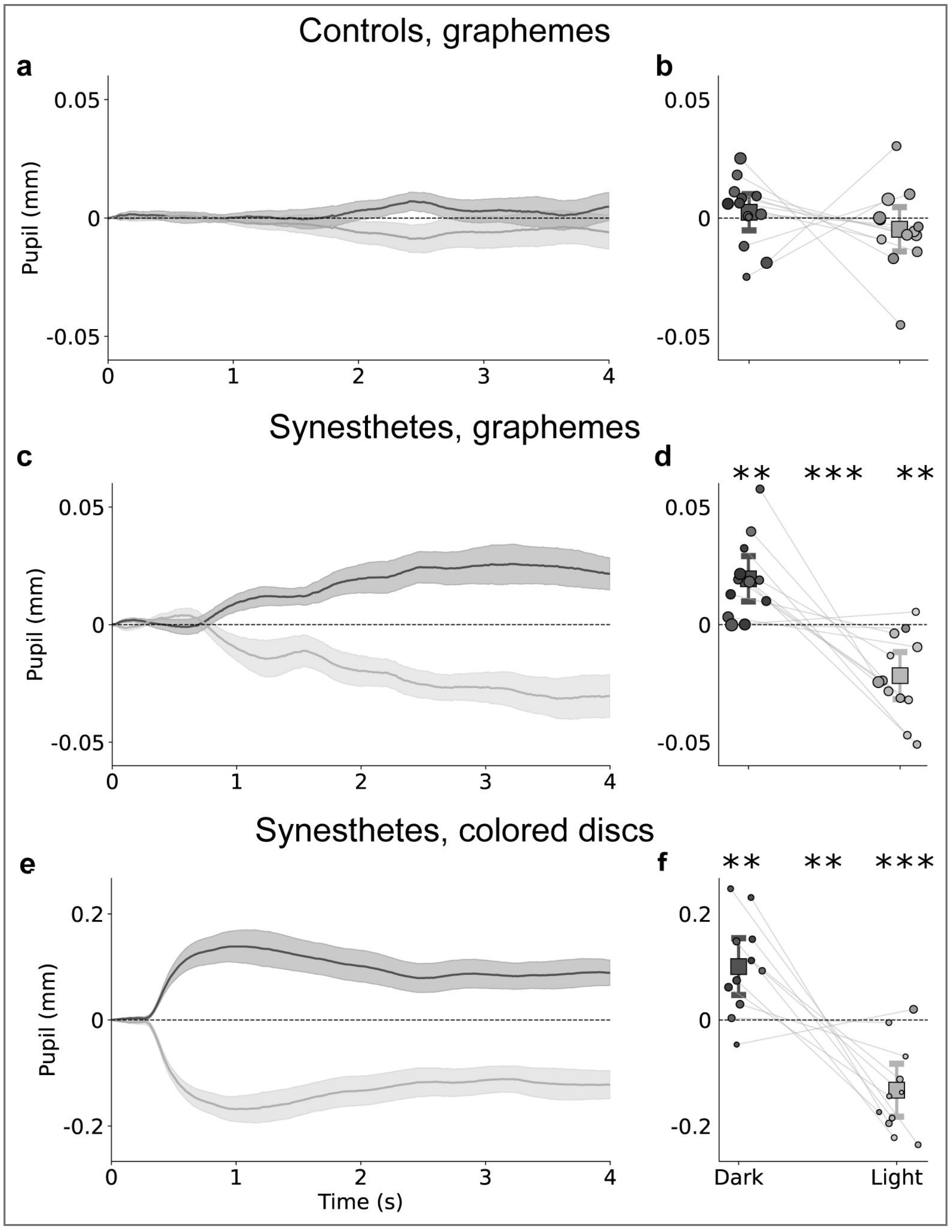


Figure 3. **Pupil size change to graphemes, median-split by reported color lightness (dark gray = low lightness; light gray = high lightness).**

Top row: pupil responses to graphemes in controls. Mid row: pupil responses to graphemes in synesthetes. Bottom row: pupil responses to colored discs in synesthetes (Block 2). **a, c, e** Depict average, baseline-corrected and within-participant demeaned pupil responses. Shaded error bands: ±1 SE across participant means. **b, d, f** depict mean pupil size (800–4000 ms) for dark vs. bright colors. Dots show individual participants; squares denote grand means with 95% CIs as whiskers. Dot luminance corresponds to the participant's average synesthetic color lightness per bin, dot size to the number of trials. **: $p < .01$, ***: $p < 0.001$ based on within samples and one sample t-tests. Significance relative to zero for lightness bins (left, right) and between bins (center). Participants with less than 25 trials per bin excluded for visualization (controls: $n = 3$, synesthetes: $n = 4$, see Supplementary Figures 3 and 4 for visualizations without data exclusion and demeaning, respectively).

9

per-timepoint analyses) was determined using AIC-based backward selection while retaining coupling strength (self-reported strength of color-grapheme coupling) and PA score (projector-associator score, Rouw & Scholte [49]) as predictors for synesthetes, predicting average pupil size between 800 ms and 4000 ms (Wilkinson notation: *Pupil size ~ grapheme + lightness + coupling strength + PA score + lightness * coupling strength + lightness * PA score + lightness * coupling strength * PA score + (1 | participant)*). The effects of all predictors over time on pupil size are depicted in Figure 4a (Supplementary Figure 6 for controls). We found significant modulations of pupil size by the lightness of the grapheme's synesthetic color - sustained and in the to-be-expected time window. Specifically, the pupil constricted more for brighter reported colors, and dilated more for darker reported colors, as predicted (Average pupil size 800-4000 ms, $t = -3.601$, $p < 0.001$). In an LME ran for synesthetes and controls and using only graphemes and lightness as predictors, we found lightness to predict pupil size in synesthetes ($t = -2.844$, $p = 0.004$), but not controls ($t = -0.606$, $p = 0.544$). However, when taking group as interacting factor in a joint LME, there was no interaction of lightness and group ($t = -0.949$, $p = 0.342$). Together, this demonstrates that 1) the pupil reveals the hidden qualia of synesthetic color (along the brightness axis) and 2) that such perception recruits the very same networks as are active during the perception of 'real' differently luminant stimuli itself, down to such a level that even the sensory organ is affected.

2.2.2 Lightness of stronger color-grapheme couplings affects pupil size stronger in synesthetes

The pupil response to synesthetic color lightness was amplified for stronger reported coupling strengths between graphemes and colors (interaction coupling strength * lightness: per-timepoint from ±1700 ms, see Figure 4b); average pupil size 800-4000 ms: $t = -3.093$, $p = 0.002$). In other words, synesthetes have metacognitive insight into the 3) *strength* of their synesthetic color perception as revealed by the pupil response. While a trend for stronger effects of lightness for more projecting synesthetes was observed (average pupil size 800-4000 ms: $t = -1.421$, $p = 0.155$, see Figure 4c), that might mean that the nature of color percepts affects the pupil response to synesthetic color lightness, our data cannot answer this question conclusively. Finally, effects of reported color lightness on pupil size were stronger with higher indicated grapheme-color couplings for individuals with higher PA scores, i.e., less associating, more projecting synesthetes (three-way interaction, ±1900 ms-3300 ms; but not for the average pupil size 800-4000 ms: $t = -1.779$, $p = 0.075$, see Figure 4d). Together, the pupil therefore revealed both *quality and quantity* of selfreported synesthetic colors.

For controls a separate model was run, now without the PA score as predictor (not assessed for controls). Neither lightness ($t = -0.815$, $p = 0.415$), coupling strength ($t = 0.438$, $p = 0.661$), nor their interaction gained significance ($t = -1.058$, $p = 0.290$; all for average pupil size between 800 ms and 4000 ms). Critically, we also ran a LME with the three-way interaction of coupling strength, group, and lightness (Wilkinson notation: *pupil = grapheme + group + lightness * group + coupling strength * lightness * group + (1 | participant)*). This analysis revealed a significant three-way interaction between lightness, coupling strength, and group ($F = 3.86$, $p = .021$), indicating that the lightness × coupling strength effect on pupil size was not equivalent across groups. Decomposing this interaction by group, the lightness × coupling strength slope was significant in synesthetes ($t = -2.59$, $p = .010$) but not in controls ($t = -1.01$, $p = .311$), suggesting that reported lightness and its coupling strength were more consistently related to pupil size in synesthetes than in controls. Note however, that this decomposition does not directly test whether the two slopes significantly differ from each other. We found pupil size to be marginally larger in controls than in synesthetes ($t = 1.94$, $p = .062$; see later sections for more in-depth analyses).

Lastly, we tested whether higher color consistency, the gold-standard assessment of synesthesia [16], predicted stronger pupil responses according to color lightness. It did neither in synesthetes (significant predictors: lightness and interaction of coupling strength and lightness; very limited variance of consistency) nor in controls (no other significant predictors; see Supplementary Material for full analyses). Together, this demonstrates that the consistency of colors was, in this study, not found related to the pupil responses to color brightness.

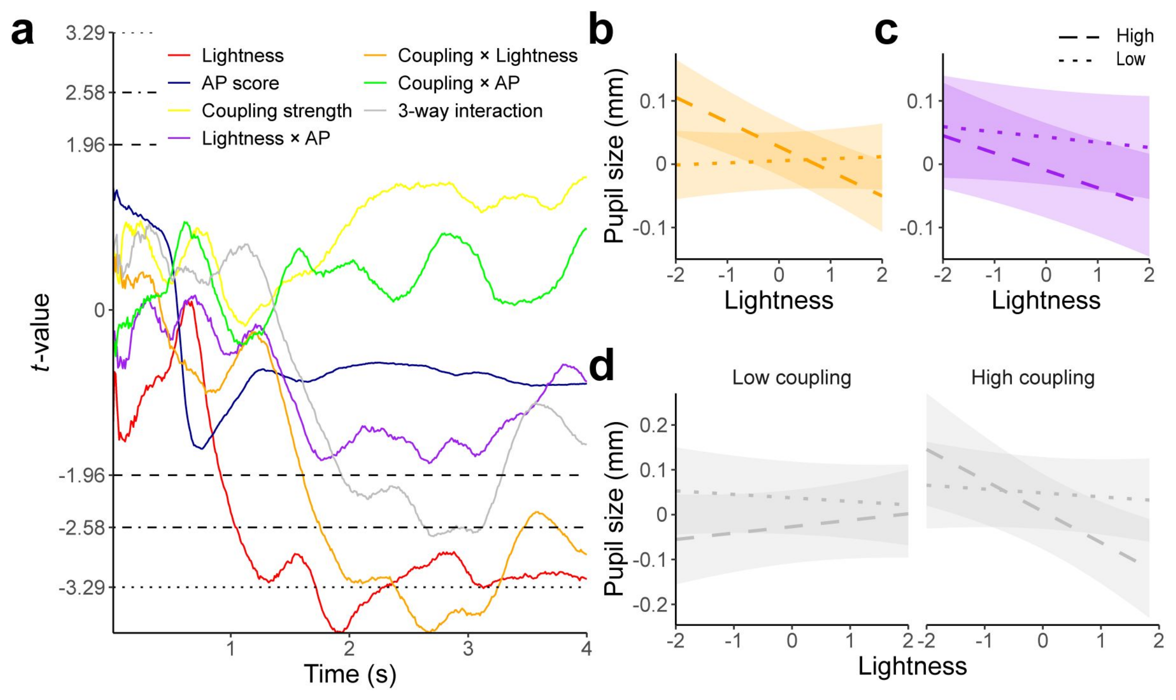


Figure 4. **Results of per-time-point linear mixed effects model (LME) predicting pupil size in synesthetes while presented with graphemes.**

Covariates for the individual graphemes and intercept are not visualized here. **a** depicts t-values of the LME over time. Horizontal lines denote significance threshold (p = 0.05 dashed, p = 0.01 dot-dashed, p = 0.001 dotted). Higher lightness was associated with smaller pupil size (red), this effect was stronger for stronger reported grapheme-color couplings (orange), with a trend for higher PA scores (purple). Furthermore, higher lightness constricted the pupil more for stronger grapheme-color couplings in synesthetes with higher PA scores (gray, three-way interaction). **b-d** visualize interactions for the LME run on the average pupil size between 800 ms and 4000 ms. Dotted denotes low, dashed high of median splits. **b** Interaction of grapheme-color coupling strength with lightness: lightness affected the pupil more when grapheme color couplings were reported higher. **c** Interaction of PA scores with lightness: lightness affected the pupil more for synesthetes with higher PA scores, but note that this effect only reached borderline significance for a short interval. **d** three-way interaction of lightness, coupling strength, and PA score. See Supplementary Figure 6 for the same model in controls.

2.3 Pupil responses demonstrate the automaticity of synesthetic colors

Having established the qualia and quantity of synesthetic colors through pupillary responses, we next turned to the other core defining feature of synesthesia: its presumed *effortless* nature. Synesthetes report the colors to emerge automatically - rather than via active and effortful cognitive (e.g., memory) processes.

2.3.1 Synesthetic colors affect pupil size delayed relative to physically presented colors

In Block 1, synesthetes viewed individual digits, and as the pupil revealed, an evoked characteristic (synesthetic) color. In Block 2, we then physically presented, for each digit, its previously determined average synesthetic color as a colored disc on the screen. At the center of each disc sat a gray rectangle whose luminance and pixel area matched the original digit's lightness and size from Block 1 (see Figure 1c). As expected, physically presented color discs let the pupil constrict strongly in response to bright and dilate in response to dark colors, respectively. Equally expected, this effect was numerically and statistically more pronounced than the response to synesthetic colors [akin to stronger effects for direct fixation compared with covert attention only, see 37]. Interestingly, the time course of the pupil response to physical vs synesthetic color differed markedly. Specifically, pupil size first responded significantly to physical luminance after 330 ms (see Supplementary Figure 7 for per-timepoint LME; in line with response latencies of similar control populations, see Koevoet *et al.* [39], Bergamin & Kardon [50], and Strauch *et al.* [51]), but only responded significantly to synesthetic lightness at about 870 ms (see also Figure 3c vs e and Figure 4 for per-timepoint LME). Assuming that internally generated lightness does elicit a pupil light response with similar latency as the physically triggered lightness reflex arc (330 ms here), this implies that synesthetic perception has to emerge within 540 ms, including the recognition of the digit itself. This fast emergence makes it highly unlikely that synesthetes imagined a color after processing a grapheme, as this must take up more time [52].

2.3.2 Reporting colors to graphemes is more effortful for controls than for synesthetes

Lastly, we reasoned that synesthetic color perception should be relatively low in effort. We therefore exploited another, distinct feature of pupillary responses: In absence of any luminance changes, pupils *dilate* more from baseline the more effort is exerted [e.g. 48, 53–57]. Figure 5a visualizes pupil size change to baseline. Figure 5b depicts average pupil size change to baseline between 800 ms and 4000 ms per participant. Mental effort presents in task-evoked pupil dilations, yet other factors simultaneously affect the pupil, such as luminance and contrast changes at trial onset, as well as slower trends across the session (e.g., fatigue). To reduce the influence of these slower, non-trial-locked fluctuations while retaining the trialevoked dynamics, we calculated the first derivative of the pupil time course to assess the velocity of pupillary changes (Butterworth filter, 18 Hz, order 3, 2.5 Hz lowpass, following our previous works [58, 59]). Figure 5c depicts this derivative, Figure 5d the average derivative per participant between 700 ms and 2000 ms (where we observed the effect). We found a stronger pupil dilation rate for active (reporting colors) compared with passive controls (not reporting colors; t = -4.254, p < 0.001) and for active controls compared with synesthetes (t = -2.828, p = 0.007), but no difference between synesthetes and passive controls (t = 1.424, p = 0.161, all on the interval 700 ms-2000 ms, LME formula in Wilkinson notation: $pupil = group + (1 \mid participant)$). Together, this demonstrates that having to report a color after seeing the grapheme is associated with pupil dilation in controls. This pupil dilation is absent in synesthetes and in controls not having to indicate any color. We interpret this effect to reflect differences in effort, not least because reported lightness was similar for synesthetes and active controls overall (see Figure 2c,d). This higher degree of effort in active controls as compared with passive controls and synesthetes may not be so surprising, given that the task to report a color when not seeing a color is not trivial. We argue that the obtained difference between active controls and synesthetes performing the exact same task is an additional consequence of the reported 'automatic' (effortless) nature with which synesthetes can indicate colors for graphemes. Together, the time course of effects and the reduced degree of effort needed for synesthetes during the task provides converging (and perhaps conclusive) evidence that synesthetic percepts are indeed fast and effortless, in line with synesthetes' subjective reports [46].

3 Discussion

We demonstrate that pupil size changes reveal the qualia of synesthetic (graphemecolor) percepts. Specifically, pupils constricted when viewing digits that evoked brighter synesthetic colors and dilated to digits that evoked darker synesthetic colors. In contrast, non-synesthetes presented with the exact same physical input did not show modulation of pupil size to the brightness of their associated colors. Synesthetes (but not controls) showed high color consistency, in line with the diagnostic 'gold standard' maintained in the field [16, 17]. While such standardized objective diagnostics [e.g., 15–17, 60] reliably separate synesthetes from non-synesthetes, our findings directly corroborate the most discerning and -arguablymost fascinating characteristic of grapheme-color synesthesia; the reported phenomenology of the synesthetic color.

This offers practical and theoretical progress in clarifying the boundary between synesthetes and non-synesthetes [61–63]. Conceptual cross-over correspondences, which are consistent at the group level, can also be observed in the general population [14, 64, 65]. Moreover, synesthesia-like Stroop effects can be induced in non-synesthetes through training [66, 67]. However, as illustrated by the traditional Stroop effect [68], neither consistent color associations nor Stroop-like conflicts depend on sensory color phenomenology. Our technique, linking synesthetic brightness and pupil size for the first time, maps out phenomenological features of cross-over (grapheme-to-color) experiences. In synesthetes, pupillometry tracked the qualia of associated colors along the brightness axis indicating that similar networks are engaged as during perception of 'real' (printed) differently luminant stimuli.

The effect of color lightness on pupil size scaled with the indicated *strength* of individual grapheme–color couplings, physiologically validating synesthetes' metacognitive insight into their own associations [69]. In future work, per-trial ratings could take this a step further by assessing moment-to-moment fluctuations and their neural correlates.

Along with the conscious perception of color, a main feature of synesthetic color experiences is that they happen automatically [e.g., 70]. Note that 'automaticity' in this study means the reported effortless nature of the additional sensations, as synesthetic sensations are unlikely evoked pre-attentively (see [71]). As increases in mental effort are tightly coupled with pupillary dilations [e.g. 48, 53, 54, 56, 72], we could put this to a direct test. Indeed, we found faster pupil dilation in active controls than in passive controls at constant physical stimulation. This stronger effort-linked increase in pupil dilation in active controls (preparing to report a color after viewing the digit) as compared with passive controls (observing the same digits but without color task) most likely reflected the non-trivial nature of the color task for non-synesthetes. Furthermore, active controls exhibited greater pupil dilation and thus effort than synesthetes, even though both groups received the same color-reporting task. Pupil size change rates showed no significant difference between synesthetes (asked to pick a color after viewing digits) and passive controls (no subsequent task). Unlike non-synesthetes, synesthetes thus measurably experience their synesthetic colors effortlessly, as their conscious color phenomenology allowed them to see and pick the right color, much like non-synesthetes view an actual (typeface) color.

Effort-evoked pupil dilation also speaks to an important theoretical question, as synesthetes often report richer mental imagery [73, 74]; could our findings reflect an active color-imagery strategy [akin to 40, 43, 44] rather than automatic color emergence? We deem this highly unlikely. First, generating and maintaining mental images is effortful and produces according pupil dilations [43, 44, 53, 75, 76]. Second, the response timeline supports automatic generation. Synesthetic color affected pupil size after 870 ms. Assuming a constant pupil light response latency to external colors (here 330 ms, see [50]) and internally generated colors, plus at least 150 ms for digit

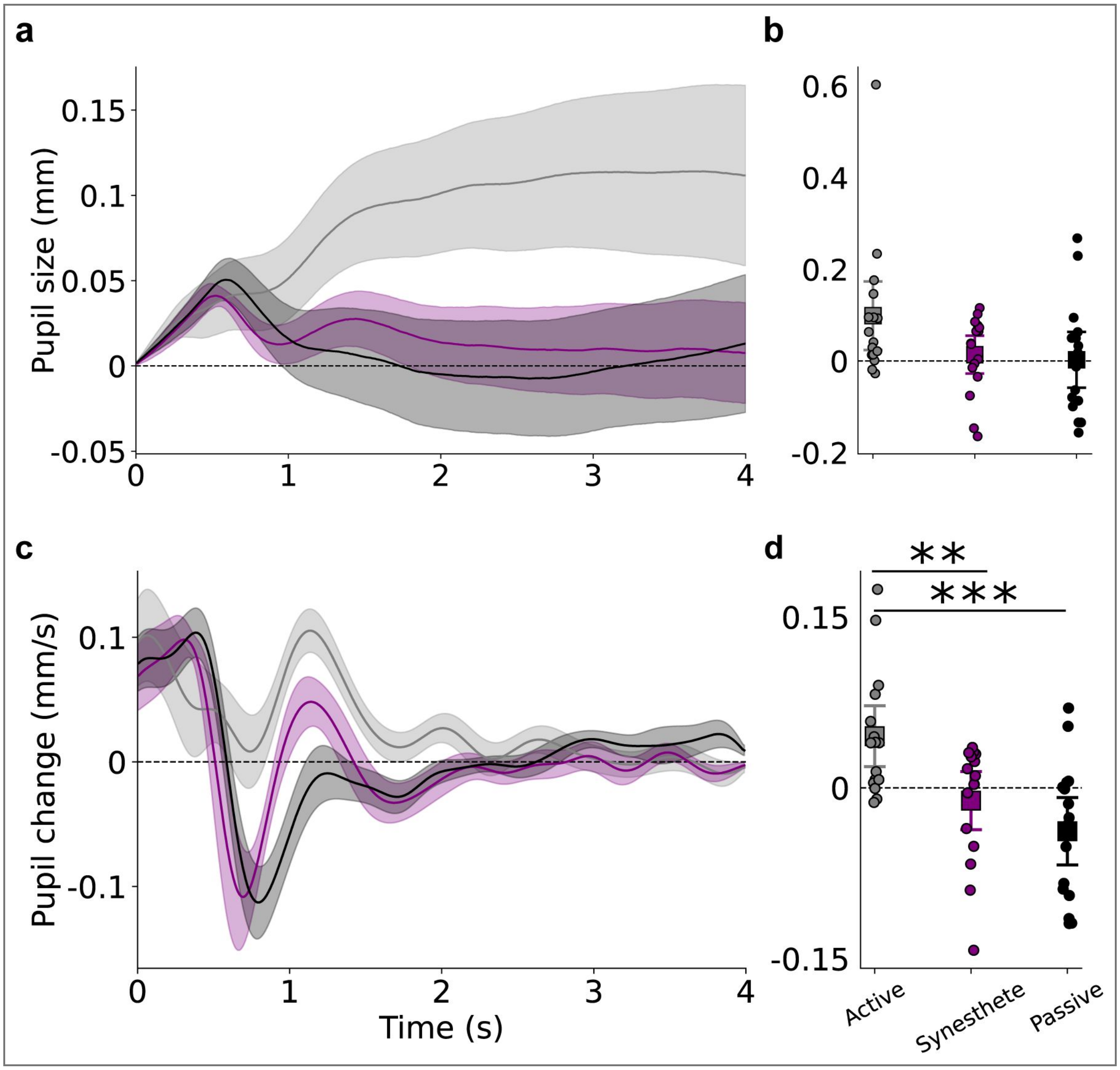


Figure 5. **Average pupil responses to graphemes from baseline, split by group: controls picking a color forced-choice ('active', gray), controls passively viewing the graphemes ('passive', black), and synesthetes (purple).**

a Pupils dilated more for active controls than both synesthetes and passive controls. Shaded error bands represent 95% confidence intervals across participant means. Horizontal black line represents average pupil size during baseline. **b** Mean pupil size (0.8 s–4 s interval) per group and participant. Dots show individual participants; squares denote grand means with 95% CIs. **c** as a, but for the velocity of pupil size changes (first derivative, filtered). **d** as b, but for the velocity of pupil size changes and the 0.7 s-2 s interval. *p* < .01: **, *p* < .001: ***, based on two-sided independent sample t-tests.

recognition [77, 78], this leaves only 390 ms for imagery - which in turn has been shown to be slower [500 ms+, based on MEG, 52]. Our fast pupil responses support previous physiological studies showing early emergence of the synesthetic response [19], and a proposed synesthetic physiological mechanism of a recurrent loop from grapheme recognition to color perception during the forward sweep of visually presented information [79]. Future work could further specify this mechanism using pupillometry.

Pupillometry thus allows to measure several key aspects of synesthesia, most prominently the unique phenomenology, the precise temporal onset, time course and strength of these effects, but also the degree of effort evoked by color reports. The measure is further unobtrusive, relatively inexpensive, and has a high signal- to-noise ratio for a physiological marker. Perhaps most importantly, pupillometry physiologically tracks synesthetic brightness in the sensory organ itself. Compared to neuroimaging studies [12, 15, 49], pupillometry may offer a more direct window into synesthetic phenomenology, as the directionality between pupil light reflex and perceived brightness is straightforward. Finally, improved understanding of the underlying processes can be obtained by contrasting responses to perceived versus actual (physical) brightness, given that the pupil light reflex is a well-characterised reflex arc involving few inferential steps. Furthermore, this method adds a metric allowing between-trial or between-participant quantitative comparisons that is not present in subjective reports: if two individuals indicate seeing a ’bright-blue’ experience on a questionnaire, does this mean that their experiences are the same? Can their intensities ever be compared? Pupillometry thus extends the synesthesia research toolbox by providing an objective metric with shared measurement unit for the quality and strength of inducer-to-concurrent links, suited both across and within individuals. Future studies could examine to what degree training a nonsynesthete to associate specific colors to particular inducers (e.g., digits), can provide similar patterns of results as genuine synesthesia [67, 80, 81]. Could learning produce similar brightness-related pupil effects in non-synesthetes? Similarly, would effort-linked responses diminish with increased training duration? The perhaps most interesting question relates to response latencies: Would a trained participant ever be able to produce brightness-related pupil effects as fast as a synesthete?

Taking a broader perspective, this work further informs about cross-over processes: associations stored in a synesthete’s brain can guide the constructive mechanisms that generate additional conscious sensations. Consistent with this view, recent work has identified cross-modal predictive-coding mechanisms, in which unimodal predictions are integrated across distributed networks to form cross-modal representations [82]. We suggest that synesthesia may exemplify such a (often) cross-modal constructive process, extending to the level of additional sensory color phenomenology. Indeed, synesthesia is an important phenomenon in context of interdisciplinary consciousness research. Fascinatingly, a synesthete may see a presented number 4 as bright-blue, while knowing and seeing it as dark gray *at the same time* [83, 84]. Such idiosyncratic “extra” challenge the leading frameworks of consciousness. Integrated Information Theory [10] posits that each unified conscious moment corresponds to a single maximally integrated causal complex, yet (stronger projecting) synesthetes experience an additional color dimension bound to the same grapheme. Similarly, Global Workspace Theory holds that only one content is broadcast at a time [e.g. 9, 85, 86], yet shape and synesthetic color co-occupy the global workspace without interference. By varying the luminance of inducers while measuring the pupil light response in synesthetes, future work may disambiguate the (relative) strength of these two contributors to perception. Similarly, the here demonstrated perceptual nature of synesthetic perception may inform research into internally generated percepts and their properties. With the findings and technique proposed here, it remains inaccessible what it ’feels like to be a bat’ [87], yet we may come closer to objectively measure the seamless ’controlled hallucinations’ [5] that we experience as reality.

4 Methods

4.1 Participants, inclusion, and ethics

Sixteen synesthetes (M_{age} = 23.94, SD_{age} = 3.40, 13 women, 3 men), n = 16 age-matched control participants watching graphemes passively (M_{age} = 23.50, SD_{age} = 2.11, 9 women, 7 men), as well as n = 16 age-matched 'active' control participants watching graphemes and indicating colors forced-choice (M_{age} = 24.75, SD_{age} = 4.20, 14 women, 2 men), all with otherwise normal or corrected-to-normal vision took part in the tasks. No participants were excluded. All participants had normal or corrected-to-normal vision without eye diseases. Synesthetes and controls were recruited through a snowball sample using a survey that was sent to thousands of people in the Netherlands and neighboring countries, using messenger apps and forums (Whatsapp, Signal, Reddit). Furthermore, the survey was distributed to a worldwide synesthesia network [88, 89] and participants with synesthesia of a concurrently running study at the University of Amsterdam were approached. Respondents indicated their form of synesthesia if present. Controls indicated not having synesthesia. The experimental procedure was approved by Utrecht University's Faculty of Social Sciences ethical review board (24-0521). We herein predicted our main finding - the pupil light response to reflect the quality of synesthetic color. All participants gave written informed consent prior to participation.

4.2 Apparatus

Gaze position and pupil size were recorded at 1000 Hz using an Eyelink 1000 desktop mount (SR Research, Ontario, Canada) in a brightness- and sound-attenuated, mostly dark laboratory. A chin- and forehead-rest limited head movements. Stimuli were presented using PsychoPy [v.2024.2.3; 90] on an ASUS ROG PG278Q monitor (2560 x 1440, 100 Hz) positioned 67.5 cm away from eye position. The monitor was not linearized. The eye-tracker was calibrated and validated (7 points) at the beginning of the session and recalibrated whenever necessary throughout the experiment.

4.3 Procedure, task, and stimuli

Before the experiment, grapheme-color synesthetes indicated where they see their synesthetic colors, (in the mind versus in the outside world) on the 'projector-associator' (PA) questionnaire, answering twelve questions on a five-point Likert scale [49]. Furthermore, participants (active controls and synesthetes) assessed for each grapheme separately the subjective strength of color-grapheme couplings on a 5-point scale from 0 ('None', no color coupling) to 4 ('Very strong', very strong color coupling). This rating is referred to as coupling strength in this manuscript. See Supplementary Materials for the questionnaire used.

The experiment started with calibration and validation of the eyetracker. Next, participants began with Block 1 of the task (see Figure 1c). Participants were first presented with a fixation cross for 1 s on a dark gray screen, if gaze was successfully kept central during this baseline screen (within 1.5 °visual angle from the center), this was followed by a random single digit number (0-9, letter height: 1.42° visual angle), presented for 4 s. Digits occupying more physical space on the screen (e.g., '8') were presented less bright than digits occupying less space on the screen (e.g., '1'), scaled between 65% and 75% of the luminance range of the screen. Subsequent to this decisive measurement phase, participants saw the same digit as before as a reference on the screen. Participants were asked to use their mouse to indicate hue, saturation, and lightness (HSL) using sliders. These sliders changed the color of a circle surrounding the reference digit. The herewith obtained per-trial lightness values (L of HSL) form the main predictor in the manuscript. Only synesthetes were allowed to press 'space' to indicate the absence of any synesthetic color in which case the lightness of the screen background was used. Active controls were forced to always indicate a color, passive controls did not indicate a color. Participants were instructed not to blink or look away from the central character during baseline and stimulus phase to prevent pupil foreshortening errors and luminance confounds [48]. Consequently, trials containing blinks or gaze deviating more than 1.5°visual angle from the center were discarded and had to be repeated in random sequence until 120 valid trials (i.e., 12 trials per digit/grapheme) were collected. Trials were followed by a 2 s interstimulus interval, indicated by a centrally presented ’x’ during which participants could blink or look away. In total, pupil responses of 5,760 trials were assessed in Block 1 in total, 1,920 from each of the three groups.

Only in synesthetes, we subsequently assessed pupil light responses to physically presented colors (Block 2, see Figure 1c). Block 2 was similar to Block 1, except that no digits were presented during the stimulus phase, but a centrally presented colored disc of 1.98 °visual angle in diameter, again on a dark gray screen. Ten different colors were presented in random sequence, one per trial. The color of the disc corresponded to the average per digit recreated color by the synesthete. Additionally, a smaller gray square was presented in the center of the disc, corresponding the same grayness value and number of pixels as the corresponding digit during Block 1. I.e., if a participant chose an on-average bright-blue for a ’5’ in Block 1, they were presented with a bright-blue in Block 2 with a central gray box corresponding to the grayness and number of pixels contained in the ’5’. Just as for Block 1, trials were followed by an interstimulus interval. Again, participants had to keep gaze in the center and not blink (trials with blinks were repeated in random sequence). Every ten trials, a pause screen allowed participants to take a break. Per color, 5 trials were assessed, i.e., 50 trials in total. In total, pupil responses of 800 trials were assessed from synesthetes in Block 2. The experiment took about 60 minutes in total for synesthetes and about 15 minutes for passive controls (40 for active controls).

4.4 Data processing

All data were processed using custom Python (v3.10) and R (v4.4.3) scripts.

4.4.1 Pupil data

Pupillometric data were preprocessed following [48, 91]. Data were first filtered for valid trials only and downsampled to 100 Hz. Pupillary data were transformed from arbitrary eyelink units to millimeters using a conversion factor obtained with an artificial eye [see 92]. Data were then subtractively baseline corrected using the mean pupil size during the last 50 ms of the baseline directly preceding the stimulus phase. Baseline pupil sizes did not differ between groups ($F(2, 45) = 0.707$, $p = 0.499$). Statistical tests over time were not corrected for type-1 error, which is why we recommend caution before interpreting short and briefty significant intervals strongly and to rely on analyses performed on averages per timebin in doubt.

4.4.2 Color reports

Per-trial reported colors in RGB space were converted to HLS (hue, lightness, saturation) color space. The lightness domain was used to infer the qualia of synesthetic color. Color consistency was calculated following [17] under slight adjustments. For each participant and grapheme, the mean pairwise Euclidean distance between all twelve RGB color selections was computed and subsequently averaged. Smaller values indicate smaller color distance and thus higher internal color consistency.

4.4.3 Questionnaire data

Questionnaire data (excluding the screening questionnaire) were collected on paper before the start of the eye-tracking task; responses were later digitalized. We calculated the projector-associator (PA) score following Rouw & Scholte [49]. Furthermore, we assessed the subjective strength of the coupling between each grapheme and color (referred to as ’coupling strength’ elsewhere; see Supplementary Materials for the questionnaire).

Data availability

Data availability and code availability: Full materials, data, and analyses are available via the Open Science Framework *https://osf.io/b6d8j/*.

Acknowledgements

We thank Tessie Hamers for assistance with piloting and all participants for their contribution. Christoph Strauch received funding from the Dutch Research Council (NWO), Veni grant (VI.Veni.241G.005, 10.61686/EEGGV23807).

Additional files

Supplementary Materials.

Additional information

Funding

Funder	Grant reference number	Author
Nederlandse Organisatie voor Wetenschappelijk Onderzoek (NWO)	https://doi.org/10.61686/EEGGV23807	Christoph Strauch

Author ORCID iDs

Christoph Strauch: https://orcid.org/0000-0002-6380-8635
Romke Rouw: https://orcid.org/0000-0001-9697-5360

References

1. **Gegenfurtner K. R.,** Bloj M., Toscani M (2015) The many colours of 'the dress'. *Current Biology* **25**:R543-R544 https://doi.org/10.1016/j.cub.2015.04.043 | PubMed
2. **Von Helmholtz H.** (1867) *Handbuch der physiologischen Optik ger* Leopold Voss: Leipzig.
3. **Rao R. P.,** Ballard D. H (1999) Predictive coding in the visual cortex: a functional interpretation of some extra-classical receptive-field effects. *Nature neuroscience* **2**:79-87 https://doi.org/10.1038/4580 | PubMed
4. **Friston K** (2005) A theory of cortical responses. *Philosophical transactions of the Royal Society B: Biological sciences* **360**:815-836 https://doi.org/10.1098/rstb.2005.1622 | PubMed
5. **Seth A. K.** (2019) Our inner universes. *Scientific American* **321**:40-47 https://doi.org/10.1038/scientificamerican0919-40 | PubMed
6. **Dennett D. C.** (1991) *Consciousness explained* Penguin uk.
7. **Hurlbert A.** (2007) Colour constancy. *Current Biology* **17**:R906-R907 https://doi.org/10.1016/j.cub.2007.08.022 | PubMed
8. **Chalmers D. J** (1995) Facing up to the problem of consciousness. *Journal of consciousness studies* **2**:200-219
9. **Baars B. J** (2005) Global workspace theory of consciousness: toward a cognitive neuroscience of human experience. *Progress in brain research* **150**:45-53 https://doi.org/10.1016/s0079-6123(05)50004-9 | PubMed
10. **Tononi G** (2004) An information integration theory of consciousness. *BMC neuroscience* **5**:1-22 https://doi.org/10.1186/1471-2202-5-42 | PubMed
11. **Hubbard E. M.,** Ramachandran V (2005) Neurocognitive Mechanisms of Synesthesia. *Neuron* **48**:509-520 https://doi.org/10.1016/j.neuron.2005.10.012 | PubMed
12. **Van Leeuwen T. M.,** Den Ouden H. E. M., Hagoort P (2011) Effective Connectivity Determines the Nature of Subjective Experience in Grapheme-Color Synesthesia. *Journal of Neuroscience* **31**:9879-9884 https://doi.org/10.1523/jneurosci.0569-11.2011 | PubMed

13. **Ramachandran V. S.,** Hubbard E. M (2001) Psychophysical investigations into the neural basis of synaesthesia. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **268**:979-983 https://doi.org/10.1098/rspb.2000.1576 | PubMed
14. **Simner J.,** et al. (2005) Non-random associations of graphemes to colours in synaesthetic and non-synaesthetic populations. *Cognitive Neuropsychology* **22**:1069-1085 https://doi.org/10.1080/02643290500200122 | PubMed
15. **Laeng B.,** Hugdahl K., Specht K (2011) The neural correlate of colour distances revealed with competing synaesthetic and real colours. *Cortex* **47**:320-331 https://doi.org/10.1016/j.cortex.2009.09.004 | PubMed
16. **Eagleman D. M.,** Kagan A. D., Nelson S. S., Sagaram D., Sarma A. K (2007) A standardized test battery for the study of synesthesia. *Journal of neuroscience methods* **159**:139-145 https://doi.org/10.1016/j.jneumeth.2006.07.012 | PubMed
17. **Rothen N.,** Seth A. K., Witzel C., Ward J (2013) Diagnosing synaesthesia with online colour pickers: maximising sensitivity and specificity. *Journal of neuroscience methods* **215**:156-160 https://doi.org/10.1016/j.jneumeth.2013.02.009 | PubMed
18. **Root N.,** et al. (2025) How “diagnostic” criteria interact to shape synesthetic behavior: The role of self-report and test–retest consistency in synesthesia research. *Consciousness and Cognition* **129**:103819 https://doi.org/10.1016/j.concog.2025.103819 | PubMed
19. **Brang D.,** Kanai S., Ramachandran V. S., Coulson S (2011) Contextual Priming in Grapheme–Color Synesthetes and Yoked Controls: 400 msec in the Life of a Synesthete. *Journal of Cognitive Neuroscience* **23**:1681-1696 https://doi.org/10.1162/jocn.2010.21486 | PubMed
20. **Cytowic R. E** (1989) Synesthesia and mapping of subjective sensory dimensions. *Neurology* **39**:849-850 https://doi.org/10.1212/wnl.39.6.849 | PubMed
21. **Dixon M. J.,** Smilek D., Cudahy C., Merikle P. M (2000) Five plus two equals yellow. *Nature* **406**:365-365 https://doi.org/10.1038/35019148 | PubMed
22. **Ward J.,** Jonas C., Dienes Z., Seth A (2010) Grapheme-colour synaesthesia improves detection of embedded shapes, but without pre-attentive ‘pop-out’of synaesthetic colour. *Proceedings of the Royal Society B: Biological Sciences* **277**:1021-1026 https://doi.org/10.1098/rspb.2009.1765 | PubMed
23. **Rich A. N.,** Karstoft K.-I (2013) Exploring the benefit of synaesthetic colours: Testing for “pop-out” in individuals with grapheme–colour synaesthesia. *Cognitive neuropsychology* **30**:110-125 https://doi.org/10.1080/02643294.2013.805686 | PubMed
24. **Schwitzgebel E** (2008) The unreliability of naive introspection. *Philosophical Review* **117**:245-273 https://doi.org/10.1215/00318108-2007-037
25. **Spener M** (2024) *Introspection: First-person access in science and agency* Oxford University Press.
26. **Nisbett R. E.,** Wilson T. D (1977) Telling more than we can know: Verbal reports on mental processes. *Psychological review* **84**:231 https://doi.org/10.1037/0033-295x.84.3.231
27. **Simner J.,** et al. (2006) Synaesthesia: The prevalence of atypical cross-modal experiences. *Perception* **35**:1024-1033 https://doi.org/10.1068/p5469 | PubMed
28. **Amin M.,** et al. (2011) Understanding grapheme personification: A social synaesthesia?. *Journal of Neuropsychology* **5**:255-282 https://doi.org/10.1111/j.1748-6653.2011.02016.x | PubMed
29. **Piazza M.,** Pinel P., Dehaene S (2006) Objective correlates of an unusual subjective experience: A single-case study of number–form synaesthesia. *Cognitive Neuropsychology* **23**:1162-1173 https://doi.org/10.1080/02643290600780080 | PubMed
30. **Rouw R.,** Root N. B (2019) Distinct colours in the ‘synaesthetic colour palette’. *Philosophical Transactions of the Royal Society B: Biological Sciences* **374**:20190028 https://doi.org/10.1098/rstb.2019.0028 | PubMed
31. **Hupé J.-M.,** Dojat M (2015) A critical review of the neuroimaging literature on synesthesia. *Frontiers in human neuroscience* **9**:103 https://doi.org/10.3389/fnhum.2015.00103 | PubMed

32. **Sagiv N.,** Simner J., Collins J., Butterworth B., Ward J (2006) What is the relationship between synaesthesia and visuo-spatial number forms?. *Cognition* **101**:114-128 https://doi.org/10.1016/j.cognition.2005.09.004 | PubMed
33. **Rothen N.,** Meier B (2009) Do synesthetes have a general advantage in visual search and episodic memory? A case for group studies. *PloS one* **4**:e5037 https://doi.org/10.1371/journal.pone.0005037 | PubMed
34. **Haab O** (1886) Vortrag gesellschaft der ärzte in zürich am 21. November 1885 [Talk Swiss Society of Physicians in Zürich, November 21st 1885]. *Korrespondenzblatt für Schweizer Ärzte* **16**:153
35. **Naber M.,** Frässle S., Einhäuser W (2011) Perceptual Rivalry: Reflexes Reveal the Gradual Nature of Visual Awareness. en. *PLOS One* **6**:e20910 https://doi.org/10.1371/journal.pone.0020910 | PubMed
36. **Naber M.,** Alvarez G. A., Nakayama K (2013) Tracking the allocation of attention using human pupillary oscillations. English. *Frontiers in Psychology* **4** https://doi.org/10.3389/fpsyg.2013.00919 | PubMed
37. **Binda P.,** Pereverzeva M., Murray S. O (2013) Attention to Bright Surfaces Enhances the Pupillary Light Reflex. en. *Journal of Neuroscience* **33**:2199-2204 https://doi.org/10.1523/jneurosci.3440-12.2013 | PubMed
38. **Cai Y.,** Van der Stigchel S., Ganama J., Naber M., Strauch C (2025) Uncovering Distinct Drivers of Covert Attention in Complex Environments With Pupillometry. *Psychophysiology* **62**:e70036 https://doi.org/10.1111/psyp.70036 | PubMed
39. **Koevoet D.,** Naber M., Strauch C., Van der Stigchel S (2025) Presaccadic Attention Shifts Up-and Downwards: Evidence From the Pupil Light Response. *Psychophysiology* **62**:e70047 https://doi.org/10.1111/psyp.70047 | PubMed
40. **Goldflam S** (1922) Zur Frage der sog. willkürlichen Pupillen Bewegung. *Klin. Monatsbl. f. Augenheilk. Bd* **69**:407-428
41. **Binda P.,** Pereverzeva M., Murray S. O (2013) Pupil constrictions to photographs of the sun. *Journal of Vision* **13**:8 https://doi.org/10.1167/13.6.8 | PubMed
42. **Strauch C** (2024) The forgotten wave of early pupillometry research. *Trends in Neurosciences.* https://doi.org/10.1016/j.tins.2024.06.002 | PubMed
43. **Kay L.,** Keogh R., Andrillon T., Pearson J., Serences J. T., Baker C. I., Rolfs M., Breedlove J. (2022) The pupillary light response as a physiological index of aphantasia, sensory and phenomenological imagery strength. *eLife* **11**:e72484 https://doi.org/10.7554/elife.72484 | PubMed
44. **Laeng B.,** Sulutvedt U (2014) The eye pupil adjusts to imaginary light. en. *Psychological Science* **25**:188-197 https://doi.org/10.1177/0956797613503556 | PubMed
45. **Baron-Cohen S.,** Wyke M. A., Binnie C (1987) Hearing words and seeing colours: an experimental investigation of a case of synaesthesia. *Perception* **16**:761-767 https://doi.org/10.1068/p160761 | PubMed
46. **Mattingley J. B.,** Rich A. N., Yelland G., Bradshaw J. L (2001) Unconscious priming eliminates automatic binding of colour and alphanumeric form in synaesthesia. *Nature* **410**:580-582 https://doi.org/10.1038/35069062 | PubMed
47. **Mathôt S.,** Van der Stigchel S (2015) New Light on the Mind's Eye. *Current Directions in Psychological Science* **24**:374-378 https://doi.org/10.1177/0963721415593725 | PubMed
48. **Strauch C.,** Wang C.-A., Einhäuser W., Van der Stigchel S., Naber M (2022) Pupillometry as an integrated readout of distinct attentional networks. *Trends in Neurosciences* **45**:635-647 https://doi.org/10.1016/j.tins.2022.05.003 | PubMed
49. **Rouw R.,** Scholte H. S (2007) Increased structural connectivity in grapheme-color synesthesia. *Nature neuroscience* **10**:792-797 https://doi.org/10.1038/nn1906 | PubMed
50. **Bergamin O.,** Kardon R. H (2003) Latency of the pupil light reflex: sample rate, stimulus intensity, and variation in normal subjects. *Investigative Ophthalmology & Visual Science* **44**:1546-1554 https://doi.org/10.1167/iovs.02-0468 | PubMed

51. **Strauch C.,** Romein C., Naber M., Van der Stigchel S., Ten Brink A. F (2022) The orienting response drives pseudoneglect—Evidence from an objective pupillometric method. *Cortex* **151**:259-271 https://doi.org/10.1016/j.cortex.2022.03.006 | PubMed

52. **Dijkstra N.,** Mostert P., Lange F. P. d., Bosch S., van Gerven M. A. (2018) Differential temporal dynamics during visual imagery and perception. *eLife* **7**:e33904 https://doi.org/10.7554/eLife.33904 | PubMed

53. **Bumke O** (1911) *Die Pupillenstörungen bei Geistes-und Nervenkrankheiten: Physiologie und Pathologie der Irisbewegungen* Verlag von Gustav Fischer.

54. **Mathôt S.** (2018) Pupillometry: Psychology, Physiology, and Function. *Journal of Cognition* **1**:16 https://doi.org/10.5334/joc.18 | PubMed

55. **Koevoet D.,** et al. (2025) Effort Drives Saccade Selection. *eLife* https://doi.org/10.7554/elife.97760 | PubMed

56. **Kahneman D** (1973) *Attention and effort* Citeseer.

57. **Alnæs D.,** et al. (2014) Pupil size signals mental effort deployed during multiple object tracking and predicts brain activity in the dorsal attention network and the locus coeruleus. *Journal of vision* **14**:1-1 https://doi.org/10.1167/14.4.1 | PubMed

58. **Ten Brink A. F.,** Heiner I., Dijkerman H. C., Strauch C (2024) Pupil dilation reveals the intensity of touch. *Psychophysiology* **61**:e14538 https://doi.org/10.1111/psyp.14538 | PubMed

59. **Douze B. T.,** Ten Brink A. F., Dijkerman H. C., Strauch C. (no date) Pupil responses objectively index pharmacologically altered tactile sensitivity (submitted).

60. **Paulsen H.,** Laeng B (2006) Pupillometry of Grapheme-Color Synaesthesia. *Cortex* **42**:290-294 https://doi.org/10.1016/s0010-9452(08)70354-x | PubMed

61. **Martino G.,** Marks L. E. (2001) Synesthesia: Strong and weak. *Current Directions in Psychological Science* **10**:61-65 https://doi.org/10.1111/1467-8721.00116

62. **Deroy O.,** Spence C (2013) Why we are not all synesthetes (not even weakly so). *Psychonomic bulletin & review* **20**:643-664 https://doi.org/10.3758/s13423-013-0387-2 | PubMed

63. **Watson M. R.,** Akins K., Spiker C., Crawford L., Enns J. T (2014) Synesthesia and learning: a critical review and novel theory. *Frontiers in Human Neuroscience* **8** https://doi.org/10.3389/fnhum.2014.00098 | PubMed

64. **Rich A. N.,** Bradshaw J. L., Mattingley J. B (2005) A systematic, large-scale study of synaesthesia: implications for the role of early experience in lexical-colour associations. *Cognition* **98**:53-84 https://doi.org/10.1016/j.cognition.2004.11.003 | PubMed

65. **Rouw R.,** Case L., Gosavi R., Ramachandran V (2014) Color associations for days and letters across different languages. *Frontiers in psychology* **5** https://doi.org/10.3389/fpsyg.2014.00369 | PubMed

66. **Meier B.,** Rothen N (2009) Training grapheme-colour associations produces a synaesthetic Stroop effect, but not a conditioned synaesthetic response. *Neuropsychologia* **47**:1208-1211 https://doi.org/10.1016/j.neuropsychologia.2009.01.009 | PubMed

67. **Colizoli O.,** Murre J. M., Rouw R (2012) Pseudo-synesthesia through reading books with colored letters. *PloS one* **7**:e39799 https://doi.org/10.1371/journal.pone.0039799 | PubMed

68. **Stroop J. R** (1935) Studies of interference in serial verbal reactions. *Journal of experimental psychology* **18**:643 https://doi.org/10.1037/h0054651

69. **Hubbard E. M.,** Manohar S., Ramachandran V. S (2006) Contrast affects the strength of synesthetic colors. *Cortex* **42**:184-194 https://doi.org/10.1016/s0010-9452(08)70343-5 | PubMed

70. **Simner J.,** Bain A. E (2013) A longitudinal study of grapheme-color synesthesia in childhood: 6/7 years to 10/11 years. *Frontiers in human neuroscience* **7**:603 https://doi.org/10.3389/fnhum.2013.00603 | PubMed

71. **Mattingley J. B** (2009) Attention, automaticity, and awareness in synesthesia. *Annals of the New York Academy of Sciences* **1156**:141-167 https://doi.org/10.1111/j.1749-6632.2009.04422.x | PubMed

72. **Koevoet D.,** Strauch C., Van der Stigchel S., Mathôt S., Naber M (2024) Revealing visual working memory operations with pupillometry: Encoding, maintenance, and prioritization. *Wiley Interdisciplinary Reviews: Cognitive Science* **15**:e1668 https://doi.org/10.1002/wcs.1668 | PubMed

73. **Barnett K. J.,** Newell F. N (2008) Synaesthesia is associated with enhanced, selfrated visual imagery. *Consciousness and cognition* **17**:1032-1039 https://doi.org/10.1016/j.concog.2007.05.011 | PubMed

74. **Spiller M. J.,** Jonas C. N., Simner J., Jansari A (2015) Beyond visual imagery: How modality-specific is enhanced mental imagery in synesthesia?. *Consciousness and Cognition* **31**:73-85 https://doi.org/10.1016/j.concog.2014.10.010 | PubMed

75. **Kosslyn S. M.,** Cave C. B., Provost D. A., von Gierke S. M (1988) Sequential processes in image generation. *Cognitive psychology* **20**:319-343 https://doi.org/10.1016/0010-0285(88)90002-3 | PubMed

76. **Henderson R. R.,** Bradley M. M., Lang P. J (2018) Emotional imagery and pupil diameter. *Psychophysiology* **55**:e13050 https://doi.org/10.1111/psyp.13050 | PubMed

77. **Walla P.,** Klimovic P (2025) Time Course of Brain Activity Changes Related to Number (Quantity) Processing Triggered by Digits Versus Number Words: An Event-Related Potential (ERP) Study. *Applied Sciences* **15**:530 https://doi.org/10.3390/app15020530

78. **Park J.,** Chiang C., Brannon E. M., Woldorff M. G (2014) Experience-dependent hemispheric specialization of letters and numbers is revealed in early visual processing. *Journal of cognitive neuroscience* **26**:2239-2249 https://doi.org/10.1162/jocn_a_00621 | PubMed

79. **Laeng B.,** Svartdal F., Oelmann H (2004) Does Color Synesthesia Pose a Paradox for Early-Selection Theories of Attention?. *Psychological Science* **15**:277-281 https://doi.org/10.1111/j.0956-7976.2004.00666.x | PubMed

80. **Bor D.,** Rothen N., Schwartzman D. J., Clayton S., Seth A. K (2014) Adults can be trained to acquire synesthetic experiences. *Scientific reports* **4**:7089 https://doi.org/10.1038/srep07089 | PubMed

81. **Rothen N.,** Meier B (2014) Acquiring synaesthesia: insights from training studies. *Frontiers in human neuroscience* **8** https://doi.org/10.3389/fnhum.2014.00109 | PubMed

82. **Huang Y. T.,** et al. (2024) Crossmodal hierarchical predictive coding for audiovisual sequences in the human brain. *Communications Biology* **7** https://doi.org/10.1038/s42003-024-06677-6 | PubMed

83. **Dixon M. J.,** Smilek D., Merikle P. M (2004) Not all synaesthetes are created equal: Projector versus associator synaesthetes. *Cognitive, Affective. & Behavioral Neuroscience* **4**:335-343 https://doi.org/10.3758/cabn.4.3.335 | PubMed

84. **Mills C. B** (1999) Digit Synaesthesia: A case study using a Stroop-type test. *Cognitive Neuropsychology* **16**:181-191 https://doi.org/10.1080/026432999380951

85. **Baars B. J.** (1988) *A cognitive theory of consciousness* Cambridge University Press.

86. **Dehaene S.,** Lau H., Kouider S. (2017) What is consciousness, and could machines have it?. *Science* **358**:486-492 https://doi.org/10.1126/science.aan8871 | PubMed

87. **Nagel T** (1974) *The language and thought series* Harvard University Press. pp. 159-168

88. **Day S. A.** (no date) Synesthesia-List.

89. **Day S. A.** (2016) *Synesthetes: a handbook* self-published.

90. **Peirce J.,** et al. (2019) PsychoPy2: Experiments in behavior made easy. en. *Behavior Research Methods* **51**:195-203 https://doi.org/10.3758/s13428-018-01193-y | PubMed

91. **Mathôt S.,** Vilotijević A (2023) Methods in cognitive pupillometry: Design, preprocessing, and statistical analysis. en. *Behavior Research Methods* **55**:3055-3077 https://doi.org/10.3758/s13428-022-01957-7 | PubMed

92. **Hayes T. R.,** Petrov A. A (2016) Mapping and correcting the inftuence of gaze position on pupil size measurements. en. *Behavior Research Methods* **48**:510-527 https://doi.org/10.3758/s13428-015-0588-x | PubMed

Peer reviews

Reviewer #1 (Public review):

Summary:

Knowing that small pupil-size variations accompany brightness variations (even when these are illusory), the authors asked whether pupil constrictions would accompany the synesthetic perception of a brighter color (compared with a darker one), induced by the presentation of a black-white character. This grapheme-colour synesthesia is only experienced by few participants, sixteen of whom were enrolled in this study. The results reliably showed that a relative pupil constriction would "betray" the perception of a brighter color in these participants, while no such effect would be observed in control participants who were asked to report a color in association with each grapheme, even though they did not perceive any.

Strengths:

The main strength of the study lays in its combination of psychophysics (brightness ratings) and pupillometry, which allowed for showing clear-cut results.

Weaknesses:

I only see the following relatively minor weaknesses, namely:

- The pupil traces in Figure3 (main results) are heavily pre-processed (per-participant demeaned), loosing any feature besides the effect of interest. As I argued in my first review, I worry that this format gives unrealistic expectations about the effect (the perception of dark/bright colors do not generate a net dilation/constriction of the pupil; perception-related modulations of pupil size are always relative and generally small compared to the numerous other effects registered in pupil size; these include a pupil dilation that is more prominent in the controls and that gets analyzed later on in the manuscript; I do not think that eliminating one of the effects of interests from a main results figure helps the reader understand the results). In the revised manuscript, the authors addressed this concern by adding a Supplementary Figure 4, where a more complete representation of the results is shown (traces from individual trials are baseline corrected and averaged, resulting in more informative timecourses). I would strongly recommend that Supplementary Figure4 is brought to the main text (Figure3 could be presented in Supplementary).

- Responses to physical brightness modulations were only measured in the synesthethes group, not in controls. The authors point out that pupillary light responses have been thoroughly characterized in previous studies, and conclude that synesthethes' responses were in line with the expectations both in terms of amplitude and latency. However, as we are not dealing with standardized measurements, subtle differences in pupil reactivity across the two populations remain a possibility. I recommend that this possibility is mentioned in the discussion.

Impact:

This work is likely to improve our understanding of synesthesia, providing a new tool to quantify the subjective sensations; an interesting potential extension would be using pupillometry for tracking changes over time of the synesthetic experiences, opening up the possibility to evaluate the importance of learning for this peculiar experience.

https://doi.org/10.7554/eLife.110390.2.sa3

Reviewer #2 (Public review):

Synesthesia is a neurological condition where stimulation of one sensory channel leads to involuntary, automatic, and consistent experience of another, unrelated percept. For example, Sir Francis Galton (1880, Nature) famously described the robust tendency of some individual (synesthetes) to associate numerals with a distinct color. Ever since, synesthesia keeps attracting a broad interest in the cognitive neurosciences in light of its implications for the study of domains such as perception, consciousness, and brain connectivity, among others.

Strauch, Leenaars, and Rouw measured pupil size in a group of 16 grapheme-color synesthetes and two matched control groups. The participants were presented with gray digits - that is, visual stimuli having identical physical properties in terms of brightness. Each participant subsequently rated the corresponding evoked color and brightness: unlike controls, synesthetes did so in a very consistent and reliable fashion. Accordingly, this was also shown in their pupils: despite the same objective luminance, digits associated with brighter percepts caused their pupils to constrict and digits associated with darker percepts caused their pupils to dilate more than controls. These results highlight how crossmodal correspondences are deeply rooted in synesthetes, and puts forward pupillometry as a particularly appealing biomarker for some phenomenological experience (at least those grounded in "brightness").

Further strengths of the technique are its temporal resolution and its responsiveness to several constructs. Across several tasks, the authors show for example that responses to synesthetic light are somewhat slower than responses to real light (i.e., they are likely mediated), but at the same time faster than responses to mental imagery. The role of mental imagery can also be reasonably dismissed when considering the second feature of pupil size: its responsiveness to mental effort and cognitive load. The pupils tend to dilate with demanding, challenging tasks, and this was the case when control participants were asked to report the color of a digit for which they did not consistently experience a synesthetic association. The same task was, instead, seemingly effortless for synesthetes, again speaking in favor of the automaticity of number-color correspondences in their case.

Overall, the findings by Strauch, Leenaars, and Rouw are highly significant for the field and likely to be impactful. The strength of their evidence, when accounting for the relatively small sample size and the inherent variability of both phenomenology (color perception and subjective reporting) and physiology (pupil size), is adequate and sufficiently convincing.

Comments on revisions:

I thank the authors for addressing all my comments in a satisfactory way. I think that the paper has improved, especially in terms of transparency of the reporting and clarity of the results.

https://doi.org/10.7554/eLife.110390.2.sa2

Reviewer #3 (Public review):

Summary:

In the present study, the authors examined pupillary responses to uncolored stimuli (number graphemes) among number-color synesthetes and non-synesthetes. After seeing a digit, the synesthetes and active control participants were asked to indicate which color they perceived using three dimensions of hue, saturation, and lightness. The lightness values were the primary independent variable for follow-up analyses. To see how the pupil responded to psychologically "bright" and "dark" digits, the authors split the reported lightness values at the median and plotted them. The synesthetes showed a pupillary constriction to digits they perceived as bright and dilation to digits they perceived as dark. Active control participants did not show that effect. In a subsequent block, only the synesthetes were shown the colors they reported perceiving as colored discs. Their pupillary responses were similar. The authors also found that the differences in pupillary responses between light and dark perceptions (with digits) were only slightly delayed in their onset to the perception of a colored disc, and therefore the color perception accompanying a digit is unlikely to be effortful or a retrieved association, but occurs rather automatically.

Strengths:

The authors employed a well-controlled and designed quasi-experiment comparing color-grapheme synesthetes to non-synesthetes and showed convincingly that the color perceptions accompanying graphemes alter the physical perception of brightness. They also made a reasoned attempt to ruled out the possibility that color associations are occurring effortful via retrieved associations.

The follow are questions which I had asked in a first round of reviews, and which were answered adequately by the authors:

(1) Are the pupillary responses among synesthetes, which objectively do not seem to match the degree of physical stimulation entering the retina, in any way maladaptive for eye functioning? I understand the constriction/dilation of the pupil to not only benefit visual acuity but also to protect the retina from damage. Are synesthetes at any risk of retinal damage due to over-dilation of the pupil to brighter stimuli? Or are these effects of a magnitude that is too small to matter? As reported in arbitrary units, it was hard to know how large these effects were in terms of measurable changes in dilation (e.g., millimeters).

(2) Likewise, is the automatic synesthetic merging of two percepts something that could be learned such that natural synesthetes and "artificial" synesthetes would look similar? For example, if a group of non-synesthetic participants were to learn a color-grapheme association to automaticity, would you expect their pupillary responses to the graphemes look similar to the synesthetes? If so (or if not), what would this tell us anything about the phenomenology of synesthesia?

(3) Do the synesthetic perceptions of digit graphemes merge in a sensible way? For example, if a synesthete sees a particular color with the digit 1, and a different color with the digit 9, what do they perceive when they see 19? or 1-9, or 1 9? Is there color blending, or an altogether different color perception?

https://doi.org/10.7554/eLife.110390.2.sa1

Author response:

The following is the authors’ response to the original reviews.

> ***eLife Assessment***
>
> *This study used pupillometry to provide an objective assessment of a form of synesthesia in which people see additional color when reading numbers. It provides convincing evidence that subjective color ratings are matched by changes in pupil size that recapitulate brightnessmediated changes when exposed to the real color. The work provides a valuable contribution to the literature on both synesthetic perception and the use of pupillometry to probe perception and related psychological processes.*

We were pleased to learn that our manuscript was of interest to the reviewers and the editor. We thank the reviewers for their useful feedback and have addressed all their comments in the revised version. We here give the most prominent changes as quotes.

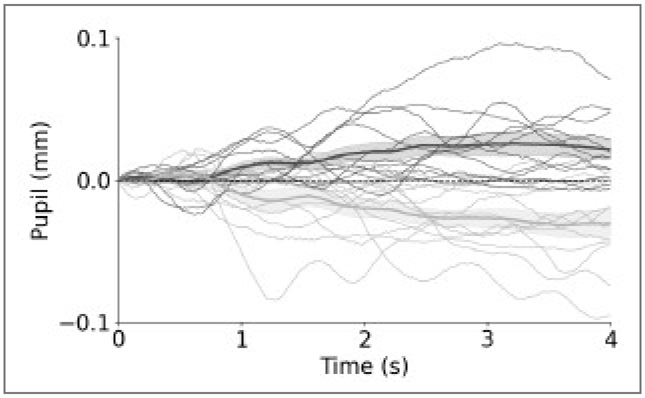
We thank all reviewers and for their very helpful input.

> ***Public Reviews:***
>
> ***Reviewer #1 (Public review):***
>
> *Summary:*
>
> *Knowing that small pupil-size variations accompany brightness variations (even when these are illusory), the authors asked whether pupil constrictions would accompany the synesthetic perception of a brighter color (compared with a darker one), induced by the presentation of a blackwhite character. This grapheme-colour synesthesia is only experienced by a few participants, sixteen of whom were enrolled in this study. The results reliably showed that a relative pupil constriction would "betray" the perception of a brighter color in these participants, while no such effect would be observed in control participants who were asked to report a color in association with each grapheme, even though they did not perceive any.*
>
> *Strengths:*
>
> *The main strength of the study lies in its combination of psychophysics (brightness ratings) and pupillometry, which allowed for showing clear-cut results.*
>
> *Weaknesses:*
>
> *Some relatively minor weaknesses concern the ancillary analyses, which tackle secondary questions and are not entirely convincing.*
>
> *(1) The linear mixed model approach is a powerful way to identify important variables, but it does not clarify whether the key factors are between-subject or between-trial variations. Some variables are inherently defined at a subject level (e.g., PA scores), others are not. I would strongly recommend an alternative visualisation of the results to examine inter-individual variability.*

Visualizing the highly idiosyncratic effects is indeed challenging. Addressing R1's point 4 and a point brought up by R2, we updated all figures to now visualize pupil size in millimeters instead of arbitrary units. Furthermore, we added a supplementary figure (supplementary figure 4) that visualizes pupil size change without demeaning (please see reply to point 4).

To get a better grasp of the interaction between lightness and coupling strength, we further included the supplementary figure 5 that splits by lightness and coupling strength in synesthetes.

Furthermore, as this review and response will be publicly available, Author response image 1 provides participant-mean traces per lightness bin in addition to the overall means and hopefully makes the stability/variability of effects visually clearer (in addition to the strip plots that attempt this for the average response).



Author response image 1.

We hope that these additional visualizations make the effects of interest more transparent. Ultimately, however, the LME figure likely provides the information best, albeit at the cost of complexity.

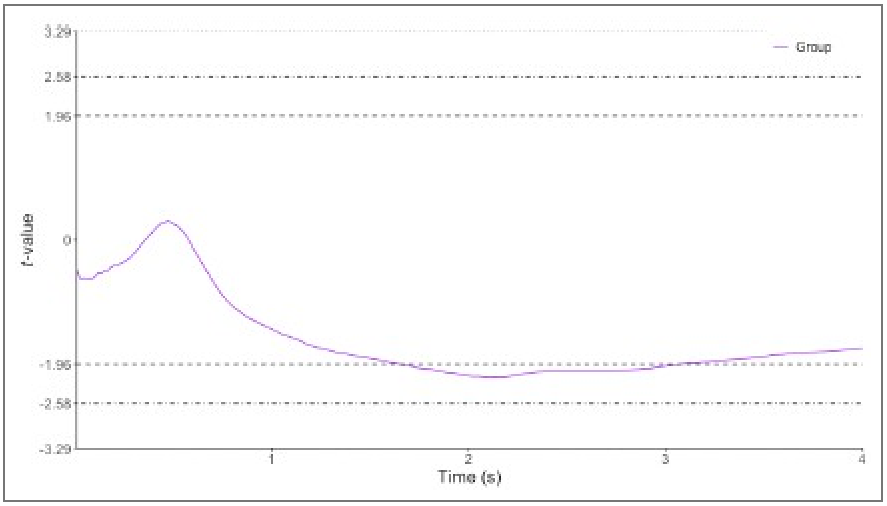
> *(2) It is not clear why taking the first derivative of pupil size in Figure 5 would isolate the effect of arousal, eliminating those of luminance and contrast changes (in fact, one could argue for the opposite, since arousal effects are generally constant for extended periods of time while contrast effects are typically more local and transient).*

First, please note that the results in 2.3.1 cannot be explained by task or context effects such as luminance and contrast: the exact same active color reporting task (same task and context) was presented to synesthetes and non-synesthetes.

Indeed, the reviewer is correct that the first derivative does not eliminate other concurrent pupil-driving effects, that was expressed wrongly in our original text. Indeed, any stimulus-locked effect, such as the luminance and contrast effects, but also the effort effect will reflect similarly in the derivative measure.

We did take the derivative because pupil responses driven by other non-trial related activity, such as increasing tiredness or excitement over the course of trials differ almost by necessity between participants, thus creating variability. However, these effects are most likely happening at a slower timescale and thus show less in the derivative measure. Accordingly in past research, we previously found clearer response-locked effects in the past when using a derivative measure (Douze et al., 2025; Ten Brink et al., 2024). This way, we also hoped to get rid of such variability that happens between participants for this between participant analysis.

Even if we were to use the same baseline corrected analysis, we would arrive at the same conclusion: we here directly compared baseline-corrected pupil sizes by taking individual differences into account (using a LME). In other words, we tested for the same question, but not relying on the derivative. We thus compared baseline-corrected pupil sizes using over-time LMEs. Group (active control vs. synesthete) gained significance between ~1.7s and 3s, aligning with the derivative-based result.



Author response image 2. **t-values of a per-time point LME predicting pupil response from group (synesthete/active control) Group reached significance.**

In sum, we deem the derivative more powerful/more appropriate in this context, but the interpretation of findings does not hinge on that analysis choice (as can be seen in the Author response image 2).

We corrected the claims on the derivative as a measure cleaning out other effects that indeed was oversimplified as it stood. We now write:

“Mental effort presents in task-evoked pupil dilations, yet other factors simultaneously affect the pupil, such as luminance and contrast changes at trial onset, as well as slower trends across the session (e.g., fatigue). To reduce the influence of these slower, non-trial-locked fluctuations while retaining the trial-evoked dynamics, we calculated the first derivative of the pupil time course to assess the velocity of pupillary changes (Butterworth filter, 18 Hz, order 3, 2.5 Hz lowpass, following our previous works [60, 61]).”

Douze, B. T., Ten Brink, A. F., Dijkerman, H. C., & Strauch, C. (2025). Pupil responses objectively index pharmacologically altered tactile sensitivity. Cortex, 193, 90-104.

Ten Brink, A. F., Heiner, I., Dijkerman, H. C., & Strauch, C. (2024). Pupil dilation reveals the intensity of touch. Psychophysiology, 61(6), e14538.

> *(3) It is a pity that responses to physical brightness modulations were only measured in the synesthete group, not in controls, as this would have allowed for ruling out differences in pupil reactivity across the two populations.*

The reviewer is correct that this would allow additional comparisons, but argue that light responses in healthy control samples are very well documented and stereotypical. For instance, Bergamin & Kardon (2003) provide very systematic latency estimations, for low-luminance change stimuli in the realm of about 320ms that can accelerate to about 250ms for very strong luminance changes. Our relatively small luminance increments should thus be expected in this range. Indeed, this also well describes the response latencies we observed in synesthetes when exposed to the colored disks. While there is no detailed information about participants in Bergamin & Kardon (2003), data from previous studies shows very similar pupil light response profiles in a healthy student control population that matches our synesthetes well demographically (Strauch, Romein et al., 2022 Figure 2a, exact same lab as for the present study; Koevoet et al., 2025 Figure 3a). See also the further responses, baseline pupil size in millimeters across groups did not differ.

Together, we can safely conclude that pupil light responses in synesthetes are not different from pupil light responses in controls. We agree with the reviewer that this is a sensible point to also make in the manuscript:

“Specifically, pupil size first responded significantly to physical luminance after 330 ms (see Supplementary Figure 7 for per-timepoint LME; in line with response latencies of similar control populations, see Bergamin & Kardon [52], Koevoet et al. [40], and Strauch et al. [53]), but only responded significantly to synesthetic lightness at about 870 ms (see also Figure 3c vs e and Figure 4 for per-timepoint LME)”.

Bergamin, O., & Kardon, R. H. (2003). Latency of the pupil light reflex: sample rate, stimulus intensity, and variation in normal subjects. Investigative Ophthalmology & Visual Science, 44(4), 1546-1554.

Koevoet, D., Naber, M., Strauch, C. & Van der Stigchel, S. Presaccadic Attention Shifts Up-and Downwards: Evidence From the Pupil Light Response. Psychophysiology 62, e70047 (2025).

Strauch, C., Romein, C., Naber, M., Van der Stigchel, S., & Ten Brink, A. F. (2022). The orienting response drives pseudoneglect—Evidence from an objective pupillometric method. Cortex, 151, 259-271.

> *(4) Another concern is with the visualisation of the pupil traces in Figure 3 (main results); these were heavily pre-processed (per-participant demeaned), losing any feature besides the effect of interest and generating the unrealistic expectation that perception of dark/bright colors generate a net dilation/constriction of the pupil - whereas perception-related modulations of pupil size are always relative and generally small compared to the numerous other effects registered in pupil size. It would be far better to see the actual profiles, preserving the unfolding of dilations and constrictions over time, especially since these are further analysed in Figures 4 and 5.*

Indeed, the expectation that any dark synesthetic experience would lead to pupil dilation whereas any bright synesthetic experience would lead to constriction is not warranted – it would only do that relative to the counterfactual of not having that experience.

Many factors affect the pupillary signal at the same time, and often differently across individuals (think of tiredness etc.), making merely baseline corrected traces seemingly noisy. Our visualization highlights that there is a systematic part to that variation that lies in the synesthetic brightness experience.

Visualizing the effects of idiosyncratic experiences, varying within and between participants is challenging. For the theoretical insight brought about through our paper in Figure 4 (synesthesia being sensory in nature), demeaning is favorable in our opinion as it isolates the effect of interest in visualization. However, for methodological reasons and to better show effect sizes etc., there is certainly use in additional transparency. We now thus provide non-demeaned traces in the supplementary material as the reviewer suggested and also refer to these in the main manuscript. Furthermore, all figures are now provided in millimeters, with all pupil related analysis being rerun and updated to this end (without qualitative changes to the results). This should further rectify possibly inflated expectations about the absolute size of effects and allows to put effects into perspective across studies. We now added:

“Pupillary data were transformed from arbitrary eyelink units to millimeters using a conversion factor obtained with an artificial eye (see Hayes & Petrov, 2016).”

Hayes, T. R., & Petrov, A. A. (2016). Mapping and correcting the influence of gaze position on pupil size measurements. Behavior research methods, 48(2), 510-527.

> *Impact:*
>
> *Despite these weaknesses, and especially if they are adequately addressed in the review, this work is likely to improve our understanding of synesthesia, providing a new tool to quantify the subjective sensations; an interesting potential extension would be using pupillometry for tracking changes over time of the synesthetic experiences, opening up the possibility to evaluate the importance of learning for this peculiar experience.*

We were happy to read our manuscript was evaluated this positively and hope that our replies can address the remaining smaller concerns and make findings more transparent to the readers.

> ***Reviewer #2 (Public review):***
>
> *Synesthesia is a neurological condition where stimulation of one sensory channel leads to involuntary, automatic, and consistent experience of another, unrelated percept. For example, Sir Francis Galton (1880, Nature) famously described the robust tendency of some individuals (synesthetes) to associate numerals with a distinct color. Ever since, synesthesia has continued to attract a broad interest in the cognitive neurosciences in light of its implications for the study of domains such as perception, consciousness, and brain connectivity, among others.*
>
> *Strauch, Leenaars, and Rouw measured pupil size in a group of 16 grapheme-color synesthetes and two matched control groups. The participants were presented with gray digits - that is, visual stimuli having identical physical properties in terms of brightness. Each participant subsequently rated the corresponding evoked color and brightness: unlike controls, synesthetes did so in a very consistent and reliable fashion. Accordingly, this was also shown in their pupils: despite the same objective luminance, digits associated with brighter percepts caused their pupils to constrict, and digits associated with darker percepts caused their pupils to dilate more than controls. These results highlight how crossmodal correspondences are deeply rooted in synesthetes, and put forward pupillometry as a particularly appealing biomarker for some phenomenological experience (at least those grounded in "brightness").*
>
> *Further strengths of the technique are its temporal resolution and its responsiveness to several constructs. Across several tasks, the authors show, for example, that responses to synesthetic light are somewhat slower than responses to real light (i.e., they are likely mediated), but at the same time faster than responses to mental imagery. The role of mental imagery can also be reasonably dismissed when considering the second feature of pupil size: its responsiveness to mental effort and cognitive load. The pupils tend to dilate with demanding, challenging tasks, and this was the case when control participants were asked to report the color of a digit for which they did not consistently experience a synesthetic association. The same task was, instead, seemingly effortless for synesthetes, again speaking in favor of the automaticity of number-color correspondences in their case.*
>
> *Overall, the findings by Strauch, Leenaars, and Rouw are highly significant for the field and likely to be impactful. The strength of their evidence, when accounting for the relatively small sample size and the inherent variability of both phenomenology (color perception and subjective reporting) and physiology (pupil size), is adequate and sufficiently convincing.*

We were glad to read this overall very positive assessment of our work and thank the reviewer for the additional non-public suggestions for improvements.

> ***Reviewer #3 (Public review):***

> *Summary:*
>
> *In the present study, the authors examined pupillary responses to uncolored stimuli (number graphemes) among number-color synesthetes and non-synesthetes. After seeing a digit, the synesthetes and active control participants were asked to indicate which color they perceived using three dimensions of hue, saturation, and lightness. The lightness values were the primary independent variable for follow-up analyses. To see how the pupil responded to psychologically "bright" and "dark" digits, the authors split the reported lightness values at the median and plotted them. The synesthetes showed a pupillary constriction to digits they perceived as bright and dilation to digits they perceived as dark. Active control participants did not show that effect. In a subsequent block, only the synesthetes were shown the colors they reported perceiving as colored discs. Their pupillary responses were similar. The authors also found that the differences in pupillary responses between light and dark perceptions (with digits) were only slightly delayed in their onset to the perception of a colored disc, and therefore, the color perception accompanying a digit is unlikely to be effortful or a retrieved association, but occurs rather automatically.*
>
> *Strengths:*
>
> *The authors employed a well-controlled and designed quasi-experiment comparing colorgrapheme synesthetes to non-synesthetes and showed convincingly that the color perceptions accompanying graphemes alter the physical perception of brightness. They also made a reasoned attempt to rule out the possibility that color associations are occurring effortfully via retrieved associations.*

We appreciate the positive assessment and useful suggestions for revision.

> *Weaknesses:*
>
> *There are some areas in which the implications of these findings could be elaborated upon. I had the following questions:*
>
> *(1) Are the pupillary responses among synesthetes, which objectively do not seem to match the degree of physical stimulation entering the retina, in any way maladaptive for eye functioning? I understand the constriction/dilation of the pupil to not only benefit visual acuity but also to protect the retina from damage. Are synesthetes at any risk of retinal damage due to over-dilation of the pupil to brighter stimuli? Or are these effects of a magnitude that is too small to matter? As reported in arbitrary units, it was hard to know how large these effects were in terms of measurable changes in dilation (e.g., millimeters).*

This is an interesting point. Some argue that pupil size changes in a mid-range mildly affect optics thus affecting detection performance, contrast perception, and depth of field (Eberhardt et al., 2022, Mathôt & Ivanov 2019, Ruuskanen, Boehler, & Mathôt, 2025), rather than serving a protective role for the retina (Mathôt, 2018). Indeed, any effects reported here were quite small. We agree with the reviewer that this can be made more accessible by reporting effects in millimeters. We thus now adjusted all figures accordingly and write in the methods section:

“Pupillary data were transformed from arbitrary eyelink units to millimeters using a conversion factor obtained with an artificial eye (see Hayes & Petrov, 2016).”

Note that even the largest effects here (those elicited by physical luminance change in block 2 for the synesthetes) only caused differences in pupil size of about 0.3mm. This lies below the maximal pupil dilations observable in response maximal effort (about 0.5mm), for instance, and substantially below the full range of pupil size changes elicited through strong luminance stimulation (several millimeters). We therefore deem the changes in pupil size as obtained in our study too minor to be practically maladaptive for optics/perception.

Eberhardt, L. V., Strauch, C., Hartmann, T. S., & Huckauf, A. (2022). Increasing pupil size is associated with improved detection performance in the periphery. Attention, perception, & psychophysics, 84(1), 138-149.

Hayes, T. R., & Petrov, A. A. (2016). Mapping and correcting the influence of gaze position on pupil size measurements. Behavior research methods, 48(2), 510-527.

Mathôt, S., & Ivanov, Y. (2019). The effect of pupil size and peripheral brightness on detection and discrimination performance. PeerJ, 7, e8220.

Mathôt, S. (2018). Pupillometry: Psychology, physiology, and function. Journal of cognition, 1(1), 16.

Ruuskanen, V., Boehler, C. N., & Mathôt, S. (2025). The Interplay of Spontaneous Pupil-Size Fluctuations and EEG Power in Near-Threshold Detection. Psychophysiology, 62(3), e70035.

> *(2) Likewise, is the automatic synesthetic merging of two percepts something that could be learned such that natural synesthetes and "artificial" synesthetes would look similar? For example, if a group of non-synesthetic participants were to learn a color-grapheme association to automaticity, would you expect their pupillary responses to the graphemes look similar to the synesthetes'? If so (or if not), what would this tell us anything about the phenomenology of synesthesia?*

We find this question most interesting. Likely, different synesthesia researchers wouldn't even fully agree on the most plausible answers to these questions. Training studies have shown that nonsynesthetes can be trained to associate particular colors to particular graphemes, as revealed in the synesthetic Stroop effect: interference effects of the learned color onto reporting the typeface color of the grapheme. The degree to which non-synesthetes can be trained to become similar to synesthetes is however still topic of debate.

We now discuss as follows:

"Future studies could examine to what degree training a non-synesthete to associate specific colors to particular inducers (e.g., digits), can provide similar patterns of results as genuine synesthesia (Bor et al., 2014, Colizoli et al., 2012, Rothen & Meier, 2014). Could learning produce similar brightness-related pupil effects in non-synesthetes? Similarly, would effort-linked responses diminish with increased training duration? The perhaps most interesting question relates to response latencies: Would a trained participant ever be able to produce brightnessrelated pupil effects as fast as a synesthete?"

Bor, D., Rothen, N., Schwartzman, D. J., Clayton, S., & Seth, A. K. (2014). Adults can be trained to acquire synesthetic experiences. Scientific reports, 4(1), 7089.

Colizoli, O., Murre, J. M., & Rouw, R. (2012). Pseudo-synesthesia through reading books with colored letters. PloS one, 7(6), e39799.

Rothen, N., & Meier, B. (2014). Acquiring synaesthesia: insights from training studies. Frontiers in human neuroscience, 8, 109.

> *(3) Do the synesthetic perceptions of digit graphemes merge in a sensible way? For example, if a synesthete sees a particular color with the digit 1, and a different color with the digit 9, what do they perceive when they see 19? or 1-9, or 1 9? Is there color blending, or an altogether different color perception?*

This is a very interesting question indeed. While each synesthete will have their own specific expression of synesthesia, there are regularities in how a combination of digits evokes synesthetic color. First, if asked about the color of a specific digit, each digit keeps its own color, as the color of a digit is linked to the identity of the digit (Dixon et al., 2006). Context effects are however possible, in particular when context alters the interpretation of the digit (Myles et al., 2003). A particularly common context in a multi-digit number is a dominant first digit, spreading its color to the subsequent digits in the number. However, as the digit color is linked to digit identity, what does 'not' happen is a mixing of colors into a qualitatively new color; for example, a yellow "1" and blue "9" do not merge into a green "19".

Dixon, M. J., Smilek, D., Duffy, P. L., Zanna, M. P., & Merikle, P. M. (2006). The role of meaning in grapheme-colour synaesthesia. Cortex, 42(2), 243-252.

Myles, K. M., Dixon, M. J., Smilek, D., & Merikle, P. M. (2003). Seeing double: The role of meaning in alphanumeric-colour synaesthesia. Brain and Cognition, 53(2), 342-345.

Many thanks for the constructive assessment of our work.

> ***Recommendations for the authors:***
>
> ***Reviewer #1 (Recommendations for the authors):***
>
> *(1) I am not sure I'd use the term 'cross-modal' given that the case considered here (graphemecolor) is purely visual.*

The reviewer is absolutely right: the term 'cross-modal' has a historical background rather than reflecting an exact factual accuracy. The term is still commonly used however, as it readily reflects how the induced additional experience is always of a different (sub)type than the inducing experience. There is a cross-over between experiences that might occur within the same sensory modality, or even induce awareness of a particular concept. But key to synesthesia is the crossover experience as the inducer and concurrent are different (sub)types of experiences. For example, seeing a letter can evoke a synesthetic experience of seeing a color, or evoke awareness of a particular gender or personality of that letter, but does not evoke another letter. To remain consistent with literature, we refer to 'cross-modality' when explaining the link to previous literature, but generally switched to using 'cross-over experience':

"Therefore, synesthesia might provide a unique window into how the brain's constructive processes can generate additional, conscious content, in cross-over experiences, often across modalities, going all the way down to the level of sensory phenomenology."

We adjusted throughout the manuscript accordingly.

> *(2) I would not recommend focusing the introduction on the problem of qualia; this is a much more general and complex question than the one addressed in the study; the space of the introduction may be better used to present the actual object of study, giving a better picture of the synesthetic phenomenon and of previous work aimed at characterising it (behavioural, including PA scores and consistency measures, and neuroimaging). It is important to discuss how the pupillometric approach differs from the previously adopted neuroimaging techniques and what it can add to those.*

We agree that qualia is a very general and complex question. However, we respectfully disagree that this complex question is not the object of the study. What is remarkable about synesthesia is not the presence of an additional perceptual association per se, but the presence of a specific perceptual experience. As illustration, think of a test where an unconscious color association to the word 'banana' was tested. While a generic 'yellow' could semantically be linked and would likely be obtained in the (e.g. priming) experimental results, a follow-up question of picking on a color wheel the exact shade of yellow to this association, or describing the perceptual sensation of the color, would be non-sensical to the participants.

This sharply contrasts with the current study: synesthetes, but not non-synesthetes, indicate a perceptual sensation of additional colors, and subsequently indeed the sensory properties of this percept (experienced brightness) affects the objective reflection of this sensation (pupil size) in synesthetes but not in non-synesthetes. In our view, the presence of additional qualia is key in understanding what sets synesthetic apart from non-synesthete associations, including so-called cross-modal correspondences (unconscious consistent associations across modalities, common to us all). We even believe that the reported qualia is what makes synesthesia so interesting in the first place. We now more clearly explain this link to qualia better in the introduction.

"The most remarkable aspect of synesthesia is the subjective perceptual phenomenology of the induced colors, setting these sensations apart from color memory, thought, or amodal association. The contrast between synesthetes and non-synesthetes can thus offer an interesting doorway into examining qualia, the subjective perceptual phenomenology or first person (what's-it-like) perspective."

We also improved the explanation of the synesthetic phenomenon, including a more detailed characterisation of behavioural measures (including consistency scores) and added neuroimaging studies. These changes have been incorporated into the text in response to previous comments (point 1- reviewer 1).

Please note that we have chosen not to include more detailed discussion of PA scores. Our results show a trend but do not allow for a conclusive interpretation on PA scores, and we feel that placing greater emphasis on this topic might therefore be confusing or even misleading. Still, it would be a very interesting topic for follow-up research to examine how alterations in characteristics of the synesthetic experience influence pupil responses.

The different synesthesia types all share the defining characteristics of an additional conscious and consistent experience. Synesthetes can verbally report their additional experience, and synesthetic sensations can be measured in behavioral paradigms such as the 'synesthetic Stroop' effect, or brain activation patterns in sensory cortex [15]. Furthermore, test-retest paradigms show how synesthetic, but not non-synesthetic associations are highly specific and consistent [16-18]. Thus, over the past decades, research has established synesthesia as a 'real' condition that can reliably be identified using behavior, neurophysiology, and neuroimaging [11, 13, 15–21]. The most remarkable aspect of synesthesia is the subjective perceptual phenomenology of the induced additional sensation, i.e., color in grapheme-color synesthesia. This sets synesthetic sensations apart from (color) memory, thought, or amodal association. Synesthesia can thus offer an interesting doorway into examining qualia, the subjective perceptual phenomenology or first person (what's-it-like) perspective.

We now discuss the pupillometric approach as it differs from the previously adopted neuroimaging techniques as follows:

“Compared to neuroimaging studies [12,15,51], pupillometry may offer a more direct window into synesthetic phenomenology, as the directionality between pupil light reflex and perceived brightness is straightforward. Finally, improved understanding of the underlying processes can be obtained by contrasting responses to perceived versus actual (physical) brightness, given that the pupil light reflex is a well-characterised reflex arc involving few inferential steps.

This adds to the explanation that was already present on how the current approach differs from previous techniques, and what it can add to those techniques:

"Instead, current paradigms capturing synesthesia employ objective measures, but fail to capture its phenomenology [16, 17, 21, 23]."

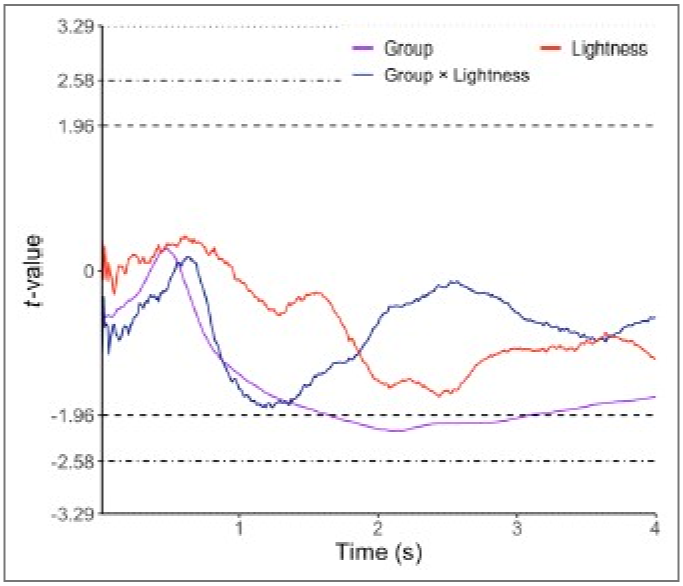
> *(3) There are a few typos and word repetitions.*

Many thanks – we identified typos and repetitions after another set of careful reads and hope to have eradicated them completely now.

> ***Reviewer #2 (Recommendations for the authors):***
>
> *I am overall very supportive of this work, but addressing the following points may enrich it further:*
>
> *(1) Paragraph 2.2.1. Here, models do not seem to compare synesthetes versus controls but rather assess the effects of interest separately in the two groups. The fact that experimental effects are significant in synesthetes, but not in controls, does not tell us much about differences between groups. Controls (e.g., Figure 3) do show a similar trend, albeit clearly smaller. There is one passage in which this issue appears to be tackled (page 10): "Critically, in an LME ran on synesthetes and controls and using only graphemes and the interaction of group and lightness as predictors, we found lightness to predict pupil size in synesthetes (t = -2.754, p = 0.006), but not controls (t = -1.134, p = 0.257)." But I am not sure that the reported statistics belong to the interaction - they seem to refer to the lightness effect within each group, not the difference.*

This is an important point, power for between-group comparisons is inherently limited for n = 16 per group (while still feasible for overall responses, things become trickier when less trials remain). A simple model of pupil ~ grapheme + group * lightness_scaled + (1 | participant) shows no significant interaction (despite one group showing the effect and the other not showing the effect significantly). The additional negative effect for group is in line with the effort-related effect reported later in the manuscript. Where does this leave us? Based on the lightness responses alone, the group difference can be characterized as a quantitative distinction, but the degree in which it is also a qualitative distinction cannot clearly be determined from current data. We revised the manuscript to make sure that such an interaction is not implied/ point to the absence of the significance of that interaction.

The sensory nature of synesthetic color is supported by within-synesthete analyses, where coupling strength parametrically modulates the lightness-pupil relationship in a theoretically predicted manner. Importantly, the effort-related findings provide a complementary and statistically robust group comparison: synesthetes and controls performing the identical colorreporting task showed significantly different pupil dilation rates, directly demonstrating that the two groups differ in how they access color information. Together, these two independent pupillometric signatures, one tracking perceptual quality, one tracking effort, converge on the same conclusion and mutually reinforce the interpretation that synesthetic color constitutes genuine sensory phenomenology.



Author response image 3.

We now make this more explicit in the manuscript as follows:

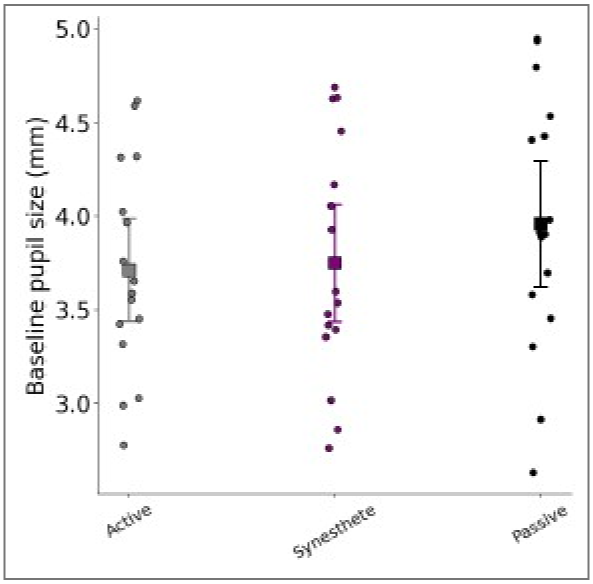
“We found significant modulations of pupil size by the lightness of the grapheme's synesthetic color - sustained and in the to-be-expected time window. Specifically, the pupil constricted more for brighter reported colors, and dilated more for darker reported colors, as predicted (Average pupil size 800-4000ms, t = -3.601, $p < 0.001$). In an LME ran for synesthetes and controls and using only graphemes and lightness as predictors, we found lightness to predict pupil size in synesthetes ($t = 2.844$, $p = 0.004$), but not controls ($t = 0.606$, $p = 0.544$). However, when taking group as interacting factor in a joint LME, there was no interaction of lightness and group ($t = -0.949$ $p = 0.342$).”

and

“For controls a separate model was run, now without the PA score as predictor (not assessed for controls). Neither lightness (t = -0.815, p = 0.415), coupling strength (t = 0.438, p = 0.661), nor their interaction gained significance (t = -1.058, p = 0.290; all for average pupil size between 800 ms and 4000 ms). Critically, we also ran a LME with the three-way interaction of coupling strength, group, and lightness (Wilkinson notation: pupil = grapheme + group + lightness * group + coupling strength * lightness * group + (1 | participant)). This analysis revealed a significant three-way interaction between lightness, coupling strength, and group (F = 3.86, p = .021), indicating that the lightness × coupling strength effect on pupil size was not equivalent across groups. Decomposing this interaction by group, the lightness × coupling strength slope was significant in synesthetes (t = 2.59, p = .010) but not in controls (t=-1.01, p=.311), suggesting that reported lightness and its coupling strength were more consistently related to pupil size in synesthetes than in controls. Note however, that this decomposition does not directly test whether the two slopes significantly differ from each other, however. Lastly, pupil size was marginally larger in controls than in synesthetes (t = 1.94, p = .062; see later sections for more in-depth analyses)”

> *(2) The authors choose to analyze pupil size in arbitrary eye tracker units. This is fine, although I would recommend assessing and reporting whether the average pupil size (e.g., during the baseline) is roughly comparable between groups. The size of the effects may be difficult to compare between groups in the presence of very different baseline pupil size.*

Please see Author response image 4 for Baseline pupil sizes per group in millimeters. There were no differences between groups.



Author response image 4.

*F*2, 45) = 0.707, *p* = 0.499 (One-way Anova).

We now write:

“Baseline pupil sizes did not differ between groups (*F*(2, 45) = 0.707, *p* = 0.499).”

We agree with the reviewer that millimeters are a more intuitive measure and updated all figures throughout manuscript and supplementary materials accordingly. We also briefly added to signal processing that this conversion was applied.

“Pupillary data were transformed from arbitrary eyelink units to millimeters using a conversion factor obtained with an artificial eye (see Hayes & Petrov, 2016).”

Hayes, T. R., & Petrov, A. A. (2016). Mapping and correcting the influence of gaze position on pupil size measurements. Behavior research methods, 48(2), 510-527.

> *(3) If I understand correctly, the main task counted 120 trials overall (12 per digit). It seems, however, that only 3 and 4 participants remained with at least 50 trials (or 25 per median split by lightness) after preprocessing. This appears to be quite a massive data loss: is there a reason behind it? Please also clarify: the overall percentage of discarded trials; whether the median split by lightness was computed on all responses or only on those of the remaining, valid trials.*

This is an important point for clarification indeed. The exclusion of participants in Figure 3 applies only to that particular visualization, not to the statistical analyses. The linear mixed effects models (LMEs) used all available valid trials from all participants, with no participant-level exclusions. The figure-specific threshold (≥25 trials per median-split bin) was applied purely for display clarity, as plotting participants with very few trials per bin would produce unreliable/noisy and thus visually misleading traces (as we note in the figure caption and point readers to Supplementary Figure 1, which shows the same visualization without any exclusions).

Since the paradigm required participants to repeat discarded trials until 120 valid trials were collected, all participants thus contributed exactly 120 valid trials to the analyses. There was therefore no data loss at the analysis level for the LME that is central to the claims of the manuscript (albeit more complex to grasp than the t-tests between bins).

Why were there sometimes so little trials per brightness bin?

First, participants differed in how dark or bright (synesthetic or forced-report) colors were overall, meaning that differing proportions thereof would fall above or below the 0.5 cutoff that overall, well represented the sample (but not necessarily every single participant). Note that this median split was not performed per individual but across all color reports to allow an apples-to-apples comparison.

Second, participants often reported colors that differed in Hue and Saturation, but not Lightness. This is in line with synesthetes picking certain colors more often than others, as compared with non-synesthetes (Rouw & Root, 2019; Ward et al., 2025).

We now include a new Supplementary Figure that visualizes responses on the Hue and Saturation dimensions of HSL space for both synesthetes and controls; fully saturated reports appear on the outer edge. We refer to the supplementary figure in the caption of Figure 2 as follows:

"See Supplementary Figure 1 for color reports on the hue and saturation axes.”

Rouw, R., & Root, N. B. (2019). Distinct colours in the ‘synaesthetic colour palette’. Philosophical Transactions of the Royal Society B: Biological Sciences, 374(1787).

Ward, J., Maciel, S., Rouw, R., Simner, J., & Root, N. (2025). Synaesthesia is linked to differences in music preference and musical sophistication and a distinctive pattern of sound-color associations. Psychology of Music, 53(3), 453-473.

> *Minor points:*
>
> *(1) "Building on this evidence, we hypothesized that the cross modal color phenomenology in synesthesia can, if truly sensory in nature, could likewise be (...)" -> may need rephrasing (can/could).*

Many thanks, fixed.

> *(2) Caption of Figure 1: "Block 2 (synesthetes only): a colored disk and gray central patch, matching the average indicated color per digit, and the number and luminance of pixels of said digit were presented to assess externally triggered light responses." -> I find this sentence a bit hard to follow; perhaps consider rephrasing it.*

Agreed, we rephrased to:

Block 2 (synesthetes only): a colored disk was presented, colored according to the synesthete's average indicated color for that digit. At its center sat a gray patch matching the luminance and pixel area of the original digit from Block 1, together allowing assessment of externally triggered light responses.

> *(3) Figure 2 b: Consider truncating the y-axis to 1 if that improves the visualization.*

We adjusted the axis accordingly and added a bit more detail in the caption for the interpretation of the measure.

> *(4) Caption of Figure 3 points to "see Supplementary Figure 1", but it should probably be SF2.*

Many thanks for spotting, all references to supplementary figures have been checked and are corrected now.

> *Elvio Blini*
>
> ***Reviewer #3 (Recommendations for the authors):***
>
> *(1) As a minor comment, there are some terms that felt overused in the manuscript. For example, the words "extraordinary" and "exceptional" were used multiple times throughout. I believe I understand the authors to mean them in their descriptive sense (i.e., outside the realm of typical experience), but in context, those words make it seem like they are touting their own experiment as "exceptional" or "extraordinary," which I don't believe was their intention.*

We agree. We removed words such as exceptional and extraordinary when they do not directly refer to the sensation throughout the manuscript (which is indeed how we intended to use it). We hope that this removes unnecessary and convoluting hyperbole.

> *(2) It seemed counterintuitive to me that the color consistency score would be reverse-coded. In this case, the scores actually seem to indicate inconsistency, rather than consistency. Perhaps the raw scores can be inverted for a more intuitive interpretation that aligns with the terminology. I understand that they were following a previous publication in their method (Rothen et al., 2013).*

This manner of coding is counter-intuitive indeed. However, there are both logical and practical reasons to this approach. Importantly, this is indeed the standard way of reporting color consistency in synesthesia research (Carmichael et al., 2015; Eagleman et al., 2007; Root et al., 2025; Rothen et al., 2013). The calculation is based on a simple logic; a higher number reflects a larger distance in color space. An additional advantage is the clear and intuitive zero- reference: a score of zero implies choosing the exact same color. Finally, it intuitively reflects the distinction between synesthetes and non-synesthetes; there is by definition little variation across synesthetes (visualized at the bottom of the graph), then a 'cut-off line' (if consistency is used as diagnostic tool), and then the height of the range shows how large the range in consistency is, in that particular sample of non-synesthetes. In a way we therefore inherit a confusing definition/standard, but changing it would lead to new confusion instead. We now specifically clarify this in the caption as follows:

“Note that higher consistency is reflected in lower color distance, hence lower values [17].”

Carmichael, D.A., Down, M.P., Shillcock, R.C., Eagleman, D.M., Simner, J., 2015. Validating a standardised test battery for synesthesia: does the synesthesia battery reliably detect synesthesia? Conscious. Cogn. 33, 375–385

Eagleman, D.M., Kagan, A.D., Nelson, S.S., Sagaram, D., Sarma, A.K., 2007. A standardized test battery for the study of synesthesia. J. Neurosci. Methods 159 (1), 139–145.

Root, N., Chkhaidze, A., Melero, H., Sidoro -Dorso, A., Volberg, G., Zhang, Y., & Rouw, R. (2025). How “diagnostic” criteria interact to shape synesthetic behavior: The role of self-report and test–retest consistency in synesthesia research. Consciousness and Cognition, 129, 103819.

Rothen, N., Seth, A.K., Witzel, C., Ward, J., 2013. Diagnosing synaesthesia with online colour pickers: maximising sensitivity and specificity. J. Neurosci. Methods 215 (1), 156–160.

https://doi.org/10.7554/eLife.110390.2.sa0