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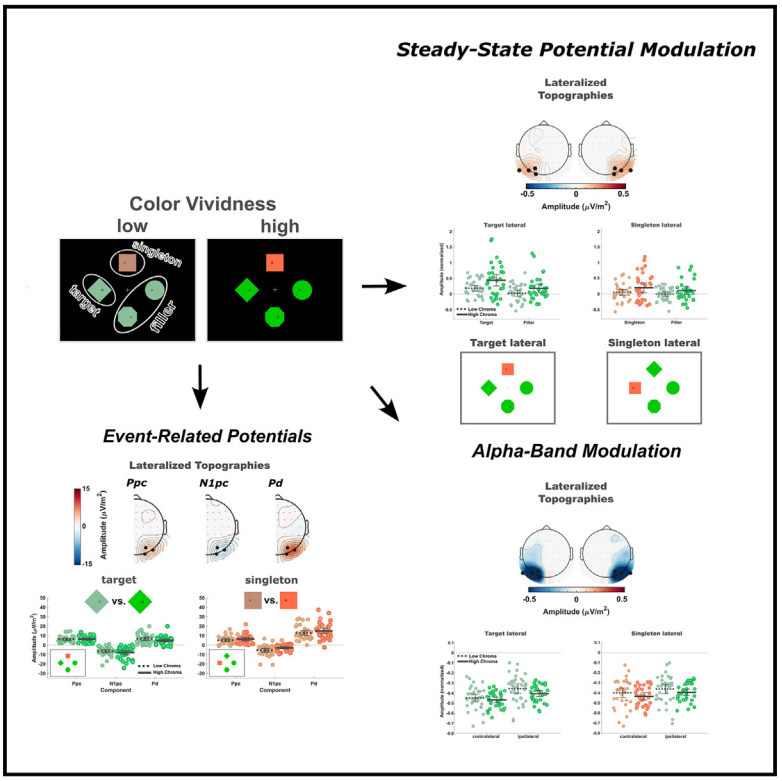
The consequences of color chromaticity on electrophysiological measures of attentional deployment in visual search

Graphical abstract



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In brief

Cognitive neuroscience; Sensory neuroscience

Highlights

- Investigated role of color vividness in visual search
- Concurrently measured ERPs, alpha band, and SSVEP amplitude modulations
- Color vividness affected attentional deployment as reflected in SSVEP but not ERP or alpha
- Suggests complementary neural responses across different processing stages

Forschack et al., 2025, iScience *28*, 112252
April 18, 2025
https://doi.org/10.1016/j.isci.2025.112252

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The consequences of color chromaticity on electrophysiological measures of attentional deployment in visual search

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https://doi.org/10.1016/j.isci.2025.112252

SUMMARY

We investigated to what extent color vividness of visual items influences how humans prioritize information in a search task. For this, color chromaticity was manipulated over two search experiments. While recording the electroencephalogram, participants searched for a shape of certain color among three other shapes, when it emerged from a stream of flickering gray placeholders. Each location was tagged with a specific frequency evoking the steady-state-visual-evoked potential (SSVEP) allowing to track attentional deployment on multiple items. Color vividness boosted SSVEP amplitudes independent of item type, i.e., targets or distractors, while leaving other measures of attentional deployment—event-related potentials and alpha-band amplitudes—mostly unaffected. Interestingly, relative modulation of target and distractor SSVEP amplitudes was comparable between experiments suggesting similar attentional deployment. The results highlight that attentional deployment to search items depends on low-level stimulus features that need to be controlled to allow for inferences about capture or suppression of individual items.

INTRODUCTION

The deployment of selective attention during visual search is a fundamental cognitive process crucial for our ability to extract task-relevant information amidst potential distractibility in cluttered visual scenes. The current study investigated how humans prioritize visual information that is relevant to the task when multiple items are present in the visual field. Previous studies have reported that the presence of a salient, unique distractor—a singleton—does not necessarily deteriorate task performance as one would expect from bottom-up theories suggesting attentional capture by salient stimuli.[1–3] That is, behavioral interference by the presence of singletons might be absent or could turn into benefits.[4–8] Conceptually, this paradoxical effect can be explained as adaptive attentional resource allocation based on the task relevance of the stimuli as reflected on a so-called priority map.[9] For instance, when searching for a green circle, the position corresponding to a green circle will receive the highest priority, or weight, on that map. However, if participants have learned that a singleton distractor will consistently appear as a red square, the weight assigned to this singleton may be suppressed relative to non-singleton distractors (called fillers; see proactive suppression hypothesis[10]). Alternatively, "filler" nontargets could be upweighted if they contain a target-defining feature, e.g., the color green, by global feature-based attention.[7] Both hypotheses can explain the absence of behavioral costs in the presence of singletons, based on *top-down goals* influencing early visual processing of the singleton or target stimulus features, respectively.

In many conceptualizations of priority maps, however, stimulus priority is not just influenced by top-down goals but also by *bottom-up stimulus strength*, e.g., stimulus contrast.[11–16] Thus, brighter stimuli result in larger weights on the priority map. Although most previous studies investigating visual search equated the luminance (brightness) of the stimuli in search arrays, other stimulus parameters like color chromaticity (vividness) or color hue were typically not controlled, which makes it difficult to evaluate potential effects of stimulus salience across studies. Indeed, it has been suggested that the saliency of targets and singleton distractors might affect target facilitation and distractor rejection as measured by reaction times and event-related components.[4,8,17] Bottom-up views suppose that any sufficiently salient stimulus will capture attention; but this would seem to be incompatible with the core proposition of the proactive suppression view, namely that expected singletons are suppressed on the level of feature maps.[6] In line with the former view, we have reported a rapid increase of neural activity in human early visual cortex when a salient singleton occurred in a frequency-tagged stream of gray placeholders, as measured by the steady-state visual evoked potential (SSVEP[5,18]). This finding was corroborated in primates, where increased multi-unit activity was found when the singleton was presented in the measured receptive field compared to when non-salient fillers were presented at the same location.[19] Thus, enhanced processing of a salient stimulus appears to be an obligatory step in the allocation of attentional resources. However, it is currently unclear how color hue and chromaticity

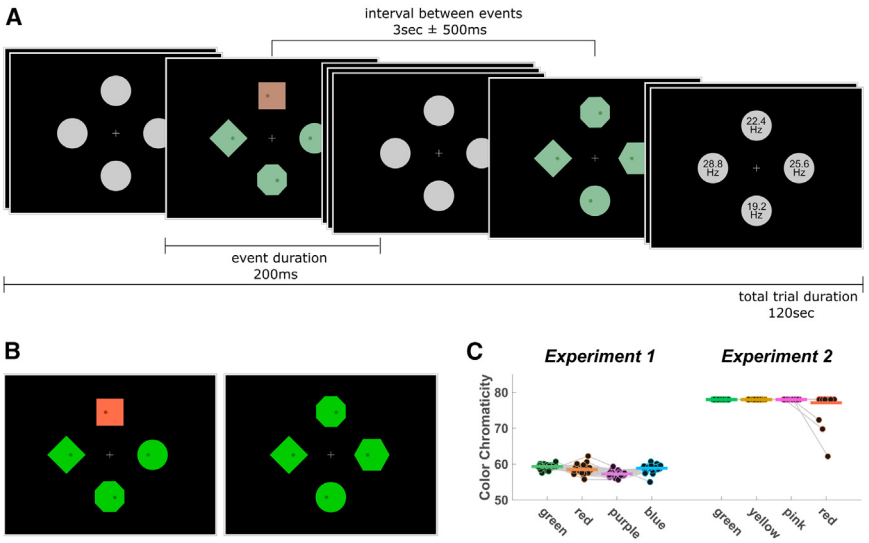

Figure 1. Task design of both experiments

An exemplary trial of experiment 1 in (A).

(B) Examples of two high chroma search arrays of experiment 2 for comparison with the search arrays in A for experiment 1. Apart from the different color chromaticities, the experimental design of both experiments was identical. For illustrative purposes, differences between the colors of the two experiments were exaggerated and do not reflect the actual colors as they appeared in the laboratory.

(C) Chromatic intensity of the colors used in the two experiments. Circles represent individual chroma values, while horizontal bars show the color specific median across each sample. Note that displayed colors differ from the colors presented in the experiment as the Propixx has a much larger gamut than the standard RGB space.

contribute to the "salience" of a stimulus and what role both factors play in preventing attentional capture by singleton distractors.

The current study thus aimed to delineate the effect of stimulus saliency operationalized by color chromaticity on search performance and neural processing of search array items in a typical four stimulus display. Color chromaticity/chroma, or colorfulness, can be independently parameterized from perceptual color space like the CIE L*a*b* space.[20,21] Small chromaticity values result in less colorful or greyish colors, while higher values increase the color content.[22–24] Thus, given a constant luminance, colors of different hues (like green, red, blue, etc.) are less salient when chroma is low than when it is high. Color chromaticity was manipulated over two experiments, while subjective luminance perception was controlled by heterochromatic flicker isometry,[25] and the color hue of all search array items was fixed (see Figure 1). Using a frequency-tagged visual search design akin to Forschack and colleagues,[5] participants searched for a predefined shape of a certain color among three other shapes of the same color when the search array emerged from a stream of flickering isoluminant gray placeholders. In some of the search arrays, one filler was substituted with a color singleton (e.g., a square of a different salient color, see Oxner et al.[26] This critical condition enabled the assessment of how stimulus salience affects the control of distracting information. Behaviorally, this effect was quantified as the reaction time difference between trials with a singleton present and those with a singleton absent (i.e., comprising only target and filler stimuli) and tested between high and low chromatic search arrays. In parallel, SSVEP amplitudes were analyzed relative to the pre-stimulus gray placeholders to evaluate attentional deployment to the different stimulus categories (target, singleton, filler) and across stimulus salience conditions. In contrast to components of the event-related potential (ERP) (see in the further text), SSVEP responses are specific to the tagged stimulus position and originate in early visual areas including V1, V2, V3d/v, and V4v,[27] the latter of which was shown to be especially sensitive to color contrast[28] of visual input and perceptual color content.[29,30] Should stimulus salience indeed impact bottom-up attentional capture, we anticipated greater SSVEP amplitudes after search array onset for high compared to low chromatic stimuli.

Further complementary neural measures of stimulus processing and suppression from the ERP and visual alpha oscillatory activity were analyzed. While for the lateralized ERP the so-called N1pc (N1 posterior, contralateral) component has been found to reflect target processing,[4,5,18,31–34] both the Pd (distractor positivity) component and increased alpha-band amplitudes have been argued to reflect distractor suppression[35–44] (but see[4,5,18,45–47]). Thus, we expected an N1pc to the target to accompany enhanced target SSVEP and reduced alpha-band amplitudes, whereas a Pd to the singleton should coincide with a reduced singleton SSVEP and increased alpha-band amplitudes.

RESULTS

Behavior

The comparison between low (LC) and high chroma (HC) groups did not reveal a significant reaction time difference ($t < 1$, see Table 1) and 3.2 times more evidence in favor of the null hypothesis (i.e., there is no difference).

Participants' reaction times did not differ significantly between conditions where the target appeared alone or with a singleton for both chroma groups, backed up by moderate evidence in favor of the null hypothesis (Table 1). Thus, singleton presence was not associated with behavioral costs (Figure 2). Consistent with a decline in visual performance for targets presented along the vertical meridian, both groups showed slower reaction times for targets presented at vertical positions (i.e., DLTV trials) compared to targets presented at lateral positions (i.e., TLDV or TL trials), replicating previous studies.[4,5,48,49] However, the difference between TL and DLTV trials in the low chroma group was not significant, which might be due to the relatively small effect size ($d = 0.17$) given the experiments sample size potentially increasing the likelihood of rejecting a true effect.

Table 1. Behavioral performance

Group	Conditions	Mean (ms)	STD (ms)	Range (ms)	df	*t*-value	p_{fdr}	Cohens-d	BF_{01}/BF_{10}
LC	TLDV vs. DLTV	−16	35	−103–48	34	−2.64	***0.037***	0.25	3.6
LC	TL vs. DLTV	−11	41	−85–78	34	−1.52	0.21	0.17	***1.9***
LC	TLDV vs. TL	−5	32	−115–65	34	−0.93	0.36	0.09	***3.7***
HC	TLDV vs. DLTV	−22	28	−79–34	32	−4.54	***0.0002***	0.4	331.1
HC	TL vs. DLTV	−18	32	−69–83	32	−3.12	***0.006***	0.31	10
HC	TLDV vs. TL	−4	31	−72–89	32	−0.82	0.42	0.08	***3.9***
LC	Average (TLDV & TL)	640	55	541–812	66	0.71	0.48	0.17	***3.2***
HC		631	52	517–724					

Average differences of reaction time with the standard deviations (STD) and sample ranges between the main experimental conditions and for both groups, respectively. TLDV—target lateral, distractor vertical; DLTV—target vertical, distractor lateral; TL—target lateral only; LC—low chroma; HC—high chroma. Final row of the table shows the group comparison for averaged TLDV and TL conditions. Bayes factors (BF) are reported in favor of the alternative hypothesis if fdr-corrected *p* values indicate a significant effect (i.e., $p < 0.05$) and in favor of the null-hypothesis otherwise. For better visibility, Bayes Factors in favor of the null hypothesis and significant *p* values were printed in italic, bold font.

Event-related potentials

As depicted in Figure 2B, pronounced Ppc, N1pc, and Pd components were evident in the difference waveforms (contralateral minus ipsilateral) to lateralized stimuli, i.e., pooled across targets and singletons. All components had focal scalp distributions over the contralateral occipital scalp *(see topographical insets of* Figure 2B*)*. These components were very similar to those recorded in our previous studies and seem to be at least partly, driven by a difference in the slopes of the cardinal contra- and ipsilateral waveforms.[5,18,31,32,34,50] Average component amplitudes that were extracted based on individual peaks of the lateralized potential are shown in Figure 3 (see also Table S1) and were submitted to a repeated measurements ANOVA and conditions-wise contrasts to test for the effects color chromaticity (high or low) and the type of lateralized stimulus (target or singleton).

The repeated measurement ANOVA on pooled target (TLDV + TL) and singleton (DLTV + DL) lateral conditions for the N1pc amplitude revealed an interaction *lateralized stimulus* x *chromaticity* ($F(1,66) = 5.6$, $p = 0.021$, $\eta^2_G = 0.024$) and a significant main effect of *lateralized stimulus* ($F(1,66) = 15.6$, $p = 0.0002$, $\eta^2_G = 0.067$; *chromaticity* was not significant: $F(1,66) = 0.8$, $p = 0.37$, $\eta^2_G = 0.007$). The interaction can be explained by the relatively small N1pc amplitude elicited by the singleton in the high chroma group resulting in a significant difference to the N1pc to the target in the low chroma condition ($t(66) = 3.6$, $p_{fdr} = 0.0018$, $d = 0.87$). The planned post-hoc comparisons of the N1pc amplitudes to target and singletons revealed a significant difference for high chromatic ($t(66) = -4.3$, $p_{fdr} = 0.0008$, $d = 0.9$) but not low chromatic stimuli ($t(66) = -1.2$, $p_{fdr} = 0.31$, $BF_{01} = 3$).

The rmANOVA for the Pd amplitude only showed a significant main effect of *lateralized stimulus* ($F(1,66) = 78.4$, $p < 0.0001$, $\eta^2_G = 0.28$), while the interaction ($F(1,66) = 2.8$, $p = 0.1$, $\eta^2_G = 0.01$) and the main effect of *chromaticity* were not significant ($F(1,66) = 0.1$, $p = 0.8$, $\eta^2_G < 0.001$). As expected, Pd amplitudes were larger for singletons than targets regardless of their chroma (*low chroma*: $t(34) = 6.4$, $p_{fdr} < 0.0001$, $d = 1.1$; *high chroma*: $t(32) = 6.3$, $p_{fdr} < 0.0001$, $d = 1.3$). The same was true when comparing singleton and target evoked Pd across chromatic conditions (*sing_low* vs. *targ_high:* $t(66) = 5.5$, $p_{fdr} < 0.0001$, $d = 1.3$; *sing_high* vs. *targ_low*: $t(66) = 4.7$, $p_{fdr} < 0.0001$, $d = 1.1$).

The Pd amplitude effects were in contrast to the earlier positivity that was present in all conditions and experiments. None of the factors of the Ppc rmANOVA revealed a significant effect (*interaction*: $F(1,66) = 1.8$, $p = 0.18$, $\eta^2_G = 0.005$); *lateralized stimulus:* $F(1,66) = 0.5$, $p = 0.48$, $\eta^2_G = 0.009$; *chromaticity*: $F(1,66) = 1.1$, $p = 0.31$, $\eta^2_G = 0.01$) speaking for a potential that emerges independently from the later Pd.

Item color chroma did not show an effect on component latencies (all $p_{fdr} > 0.11$), which might suggest that previously found saliency induced N1pc latency shifts were related to relative salience differences within a given search item. Here, as color chroma was identical between items of a specific search array, there were no relative salience differences across experiments.

SSVEP amplitude modulation

From previous studies, we expected enhanced SSVEP amplitudes for both, target and singleton stimuli (relative to prestimulus baseline), and according to our hypothesis this enhancement should be more pronounced for high chromatic stimuli. Figure 4A shows the SSVEP amplitude modulation in the time window 200 ms–450 ms after search array onset relative to prestimulus baseline for the cardinal conditions (lateral target and singleton) and the different chromatic search displays. SSVEP amplitudes were either enhanced or did not differ relatively to prestimulus baseline.

The *lateral stimulus (target/singleton, filler) x condition (target, singleton) x chromaticity (low, high)*-ANOVA of the average amplitude values revealed a significant main effect of *condition* ($F(1,198) = 24.73$, $p < 0.0001$), and *lateral stimulus* ($F(1,198) = 34.18$, $p < 0.0001$), as well as an interaction of *lateral stimulus* x *condition* ($F(1,198) = 7.35$, $p = 0.007$), indicating that target SSVEP enhancement relative to fillers was more pronounced as compared to singleton distractor SSVEP enhancement, which was corroborated by the planned comparisons given in Table 2.

Stimulus chromaticity generally boosted SSVEP amplitude modulations as evident by a significant main effect of *chromaticity* ($F(1,66) = 5.28$, $p = 0.025$) while exerting no modulatory effect on the other conditions as none of the interactions were significant (*chromaticity x condition:* $F(1,198) = 2.55$, $p = 0.11$;

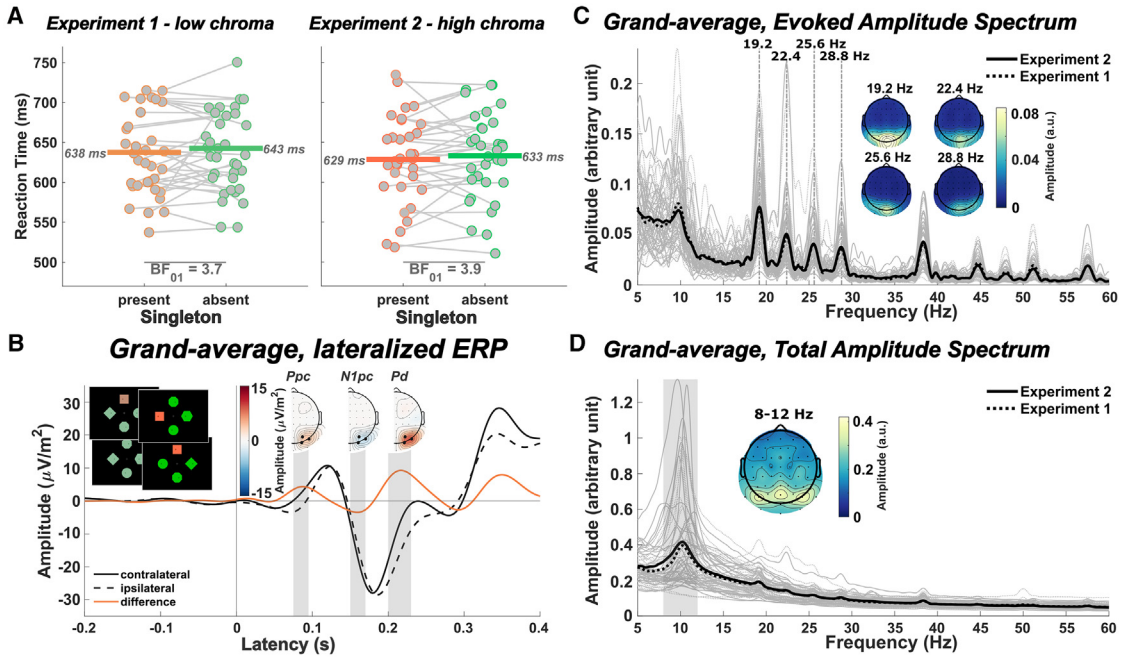

Figure 2. Behavioral performance results and event-related potentials and spectra that guided the selection of time windows, frequency bins, and electrode clusters

(A) Reaction time comparison for both chroma groups and singleton present versus absent trials. Horizontal (colored) bars show the average reaction time across the sample and condition. BF_{01} represents the Bayes Factor in favor of the null hypothesis.

(B) Grand-average ERP averaged across both experiments for pooled lateralized stimulus conditions (left/right target and singleton trials as depicted in the search display insets). Topological maps were calculated for the respective time windows indicated by the gray-shaded background on the lateralized potential given in orange and indicate the electrode cluster used for subsequent ERP analyses.

(C) Evoked spectrum showing SSVEP response(and their harmonics) for both experiments and pooled for all stimulus conditions based on a broad parieto-occipital cluster of electrodes: {"POz"; "O1"; "PO3"; "PO7"; "Oz"; "O2"; "PO4"; "PO8"}.

(D) Total spectrum showing Alpha-band response (8–12 Hz) for both experiments and pooled for all stimulus conditions based on a parieto-occipital cluster of electrodes: {"POz"; "PO3"; "PO7"; "PO4"; "PO8"}. Single subject spectra are given in light gray lines.

chromaticity x lateral stimulus: $F(1,198) = 1.96$, $p = 0.16$; *chromaticity x condition x lateral stimulus:* $F(1,198) = 0.54$, $p = 0.46$). Nevertheless, descriptively, high chromatic color targets showed a 26% higher SSVEP amplitude increase than low chromatic color targets (see Table 3*, upper part*). For both singleton and filler stimuli this chroma effect was around 13 to 15%. Interestingly, however, there was at least two times more evidence that enhancement of target and singleton relative to filler or target relative to singleton (corrected for filler modulation) were comparable (Table 3, *lower part*) between the chromaticity groups than that this measure would differ. This suggests that relative attentional deployment to single search array items is similar between differently salient search displays in which color chromaticity of their elements is controlled.

Modulation of alpha-band activity

Contra- and ipsilateral alpha-band amplitudes were reduced relative to baseline following both lateral targets and singletons, and this reduction was significantly greater over contralateral than ipsilateral scalp sites for all conditions and both chroma groups (Figure 4B; Table 4), which was corroborated by the significant main effect of *laterality* ($F(1,198) = 188.77$, $p < 0.0001$). The finding that alpha-band amplitude reduction was greater contralateral following both targets and singletons—evident as a significant interaction *condition x laterality* ($F(1,198) = 20.71$, $p < 0.0001$) and the main effect of *condition* ($F(1,198) = 29.57$, $p < 0.0001$), replicates our previous studies and is consistent with attention being shifted to both types of stimuli.[4,5,18,47,51–53] Planned comparisons showed that this lateralized amplitude difference was greater following targets than singletons for low as compared high chromaticity colors (Table 4), qualifying the three-way interaction of *condition x laterality x chromaticity* ($F(1,198) = 3.7$, $p = 0.056$).

Apart from that, color chromaticity did not affect alpha-band amplitudes significantly as neither the main effect of *chromaticity* ($F(1,66) = 1.71$, $p = 0.2$) nor any of its (1-way) interactions with *laterality* ($F(1,198) = 2.88$, $p = 0.09$) or *condition* ($F(1,198) = 0.02$, $p = 0.89$) became significant. However, there was a trend toward a bigger alpha lateralization (i.e., the difference between contra- and ipsilateral electrode clusters) for low compared to high chroma targets (see Table S2, uncorrected $p = 0.025$). Furthermore, the difference between lateralization due to targets versus singletons tended to be larger for low compared to high chromaticity colored items (uncorrected $p = 0.049$). Together this may point to a flooring effect of alpha-band amplitude reduction after highly salient input (i.e., colors of high chromaticity). However,

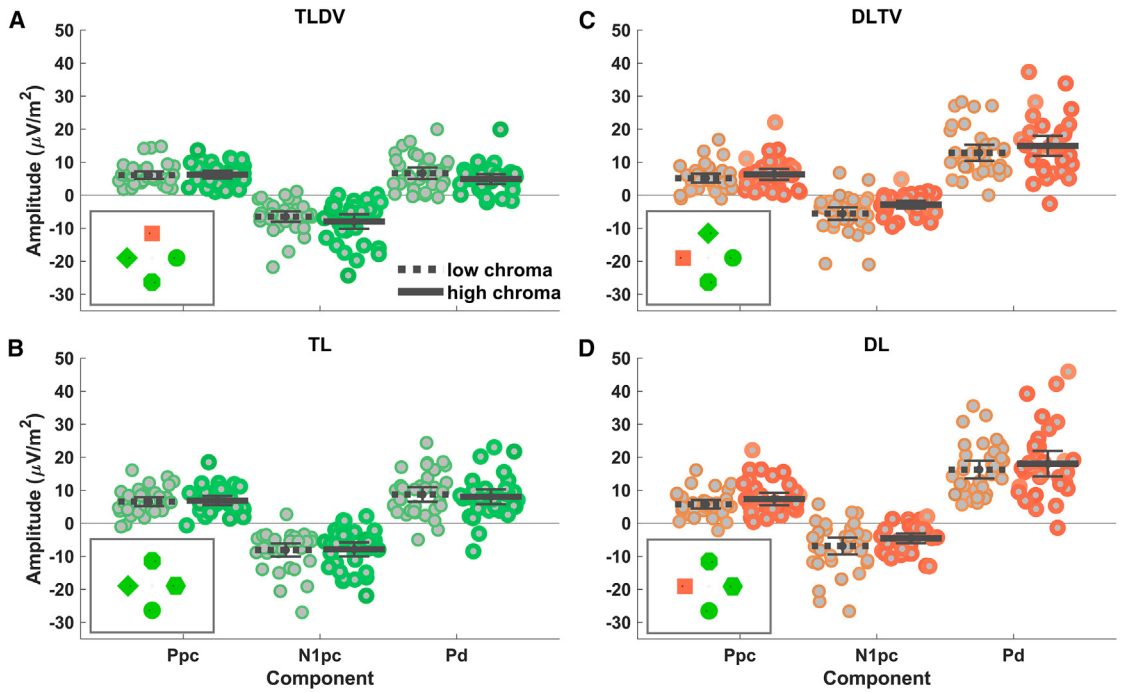

Figure 3. Event-related component amplitudes by stimulus type and color chromaticity

Three difference ERPs (i.e., contra-minus ipsilateral) to the green target and singleton distractors of varying color are shown for both experiments and the conditions, respectively: "target lateral—distractor vertical (TLDV)," "single target lateral (TL)," "distractor lateral—target vertical (DLTV)," and "single distractor lateral (DL)." Group average values are given by horizontal black dashed or solid lines as well as corresponding 95% confidence intervals of a t test against zero. Dots represent single subject values. Diagram insets show illustrative search display examples for lateralized targets (A and B) and lateralized singleton (C and D) items with (A and C) and without (B and D) a singleton or target on the midline, respectively.

the current study misses a comparison to a condition with even more salient items to convincingly show the upper boundary of neural excitability as measured by alpha-band amplitude reduction.

DISCUSSION

The current study investigated the effect of salience in a visual search display (i.e., item color vividness) upon electrophysiological measures of attentional resource deployment, which is central for understanding the interplay of automatic, stimulus-driven (i.e., bottom-up) and goal-oriented (top-down) processes. To this end, SSVEP amplitude modulations of low color chroma search displays in experiment 1 were compared with high color chroma search displays presented in experiment 2. High chroma generally exerted an increased SSVEP amplitude modulation as compared to baseline that was most pronounced for targets (26% enhancement) and to a lesser extent for filler and singleton distractor stimuli (13–15% enhancement). Consistent with attentional deployment to the target, the ERP exhibited an N1pc component in both experiments as well as a contralateral reduction of alpha-band amplitude after search display onset. A similar pattern emerged for lateralized singleton distractors: there was above-baseline and above-filler SSVEP amplitude enhancement, as well as alpha-band amplitude reduction and a singleton-evoked N1pc, all indicating attentional resource allocation to the singleton distractor. Interestingly, and differing from the SSVEP results, there was no general chroma effect on the ERP components and alpha measures, discussed in detail further. Behaviorally, the two experiments replicate a large body of literature by showing that the presence of the singleton distractor did not deteriorate task performance as reaction times were similar between singleton present and absent trials. As expected, high color chroma had no effect on reaction times compared to low chroma search displays, due to the titration procedure equating task demands between experiments (i.e., the luminance of the to-be-discriminated dot within the target item).

The absence of behavioral costs from singleton presence is consistent with the idea that top-down goals may regulate stimulus-driven (i.e., bottom-up) processes that would otherwise deteriorate task performance.[5,26,54–59] How this interaction between bottom-up stimulus features and top-down goals is implemented neurophysiologically is currently still a matter of debate, and especially the question whether or not processing of highly salient distracting information can be suppressed without the initial deployment of attention has spurred a lot of research by many different groups in the past years.[9,60,61] In the current study, salience of *all* items was manipulated by changing their chromaticity values by the same amount. As SSVEP amplitude modulations are known to closely track the time course of attentional deployment[27,46,47,62–70] and being a marker of attention-driven early neural (sensory) gain control,[71–74] we expected them to be larger for high than low chroma

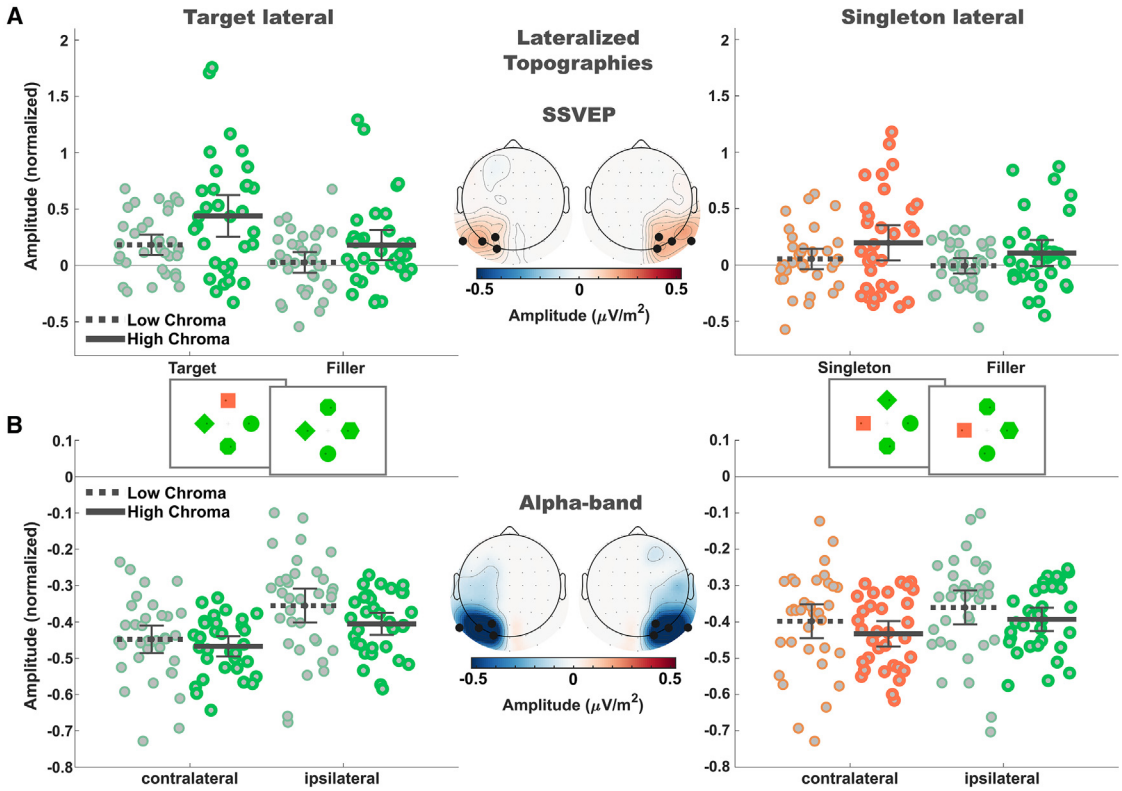

Figure 4. Steady-state visual evoked potential and alpha-band amplitudes by stimulus type and color chromaticity

(A) Baseline-normalized (−500 to −200 ms) SSVEP amplitudes averaged across the time window 200 to 450 ms after search display onset for target (left, TLDV + TL) and singleton lateral (right, DLTV + DL) conditions and low and high chromatic colors. Grand mean amplitudes together with 95% confidence intervals are indicated by horizontal dotted or solid lines and whiskers and dots represent individual amplitudes, respectively. Lateralized topographies show the difference between right versus left stimulus (target and singleton) presentations averaged across all conditions and groups for the same time window. (B) Same as (A) but for alpha-band amplitudes. Diagram insets show illustrative search display examples for lateralized targets and lateralized singleton items with and without a singleton or target on the midline.

colors. Consistent with our previous findings,[5,18] SSVEP amplitude modulations provided clear evidence for attentional deployment to all salient stimuli in the high chroma experiment (i.e., target, singleton distractor, and filler), which is predicted by stimulus-driven theories of attention,[2,19,54,56,57,75] but inconsistent with a mechanism of pre-attentional suppression prior to a singleton distractor.[5,38] Reduced color chromaticity of the stimuli in experiment 1 resulted in smaller SSVEP amplitude modulations compared to high chroma displays for the task-relevant stimulus (i.e., the target) and fillers (see Table 3, *upper part*), but not for the singleton distractor (although no conclusive evidence for equality was reached). This underlines that low-level stimulus features may affect automatic attentional capture during visual search, while not necessarily deteriorating task performance. As we and others could demonstrate previously, the capacity of behaviorally regulating the consequences of attentional capture most likely depends on the availability and usage of proactive target templates.[4,26,37,76–78] Thus, increased stimulus saliency potentially increases neural representation of stimulus features in early visual processing stages that might

Table 2. SSVEP amplitude modulation for the low (LC) and high chroma (HC) group and target (TLDV + TL) and singleton lateral (DLTV + DL) condition

Group	Comparison	Mean	STD	Range	df	*t*-value	p_{fdr}	*Cohens-d*	BF_{01}/BF_{10}
LC	**Target vs. Filler**	0.16	0.28	−0.71–0.83	34	3.29	***= 0.007***	0.56	15.05
	Singleton vs. Filler	0.06	0.23	−0.48–0.68	34	1.53	= 0.134	0.26	***1.90***
	Target vs. Singleton (Filler corrected)	0.10	0.32	−0.60–0.91	34	1.78	= 0.100	0.31	***1.33***
HC	**Target vs. Filler**	0.26	0.38	−0.29–1.54	32	3.97	***= 0.002***	0.70	76.11
	Singleton vs. Filler	0.09	0.21	−0.30–0.58	32	2.53	***= 0.025***	0.45	2.87
	Target vs. Singleton (Filler corrected)	0.17	0.37	−0.52–1.26	32	2.59	***= 0.025***	0.46	3.20

Pairwise t-tests were multiple comparisons corrected by false discovery rate. Conventions as in the previous table.

Table 3. SSVEP amplitude modulation comparing the low (LC) and high chroma (HC) group for target (TLDV + TL) and singleton lateral (DLTV + DL) conditions

Group	Comparison	Mean	STD	Range	df	*t*-value	p_{fdr}	*Cohens-d*	BF_{01}/BF_{10}
LC	**Target lateral**	0.18	0.27	−0.23–0.68	66	−2.59	***= 0.018***	−0.63	4.04
HC		0.44	0.52	−0.33–1.76					
LC	**Filler lateral**	0.01	0.24	−0.56–0.68	134	−2.59	***= 0.018***	−0.44	3.73
HC		0.14	0.35	−0.45–1.29					
LC	**Singleton lateral**	0.05	0.26	−0.57–0.63	66	−1.64	= 0.105	−0.40	***1.28***
HC		0.20	0.44	−0.37–1.18					
LC	**Target vs. Filler**	0.16	0.28	−0.71–0.83	66	−1.30	= 0.549	−0.31	***1.97***
HC		0.26	0.38	−0.29–1.54					
LC	**Singleton vs. Filler**	0.06	0.23	−0.48–0.68	66	−0.60	= 0.549	−0.15	***3.44***
HC		0.09	0.21	−0.30–0.58					
LC	**Target vs. Singleton** (Filler corrected)	0.10	0.32	−0.60–0.91	66	−0.85	= 0.549	−0.21	***2.94***
HC		0.17	0.37	−0.52–1.26					

Filler refers to the search item contralateral to the target or singleton. Pairwise t-tests were multiple comparisons corrected by false discovery rate. Conventions as in the previous table.

be tied to a modulation on feature saliency maps[61] in the service of guiding attention to likely target locations.

In a recent combined SSVEP-fMRI study,[27] we showed that neural sources for the attentional SSVEP amplitude modulation seemed to be dependent on the selected feature dimension. When participants attended to color, V4 contributed significantly to the SSVEP amplitude enhancement. When they attended to a square and ignored a circle, it was primary visual cortex that contributed to the amplitude enhancement. This is a key finding, because the alternative would be that a number of early visual areas followed the on/off activation pattern with attention. This demonstrates that selective visual attention builds on a feature specific compartmentalized architecture,[30,79,80] and that attentional allocation in a visual search display seems to rely on the salience computations within each feature dimension that is relevant to the task. In the current study, the salience of search items was manipulated by changing their color vividness. This was achieved by defining color in the standard CIEL*a*b* color space that is perceptually uniform as color values in this space scale with subjective color experience of human observers.[21,81] This uniformity in perception does not necessarily map onto the subcortical neural contrasts based on the cone excitation input of the retina.[20,82] Thus, it is currently unclear, which portion of the reported effects could be possibly explained by the contribution of neural responses of subcortical origin. It is far beyond the scope of the current study but it would be an interesting avenue if future studies' experimental designs would incorporate biological color spaces to test the impact of biological subcortical computations on neuroimaging measures (like ERP, neural oscillation, or fMRI) commonly used to study human behavior during visual search. Nevertheless, the target SSVEP amplitudes were largest for both low and high chroma colors as compared to non-target stimuli suggesting top-down attentional deployment to the task-relevant stimulus.

Despite the smaller SSVEP signals for low chroma stimuli most likely reflecting reduced stimulus-driven attention, we found an N1pc to both the target and singleton distractor. Consistent with a larger target than singleton SSVEP amplitude, the target N1pc was larger than the singleton N1pc for high chroma colors indicating that the task-relevance of the stimulus could be captured by both measures. However, target N1pc amplitudes were of similar size between the two chroma groups, while target SSVEP amplitudes were larger for high than low chroma colors. This indicates that the N1pc as a lateralized measure does not capture stimulus-driven attention directly and challenges the idea that stimuli that are more salient automatically receive more top-down attention. Instead, the N1pc has been widely regarded as attentional engagement with the target in the process of individuating it from contextual and potentially distracting information.[83,84] This implies a processing stage beyond the

Table 4. Alpha-band amplitude lateralization for the low (LC) and high chroma (HC) group and target (TLDV + TL) and singleton lateral (DLTV + DL) condition

Group	Comparison	Mean	STD	Range	df	*t*-value	p_{fdr}	*Cohens-d*	BF_{01}/BF_{10}
LC	**Lateralization Target**	−0.09	0.06	−0.27–0.01	34	−9.02	***<0.00001***	−1.55	67463550.29
	Lateralization Singleton	−0.04	0.05	−0.13–0.08	34	−4.96	***<0.0001***	−0.85	1113.95
	Lateralization Target vs. Singleton	−0.05	0.07	−0.24–0.11	34	−4.82	***<0.0001***	−0.83	762.74
HC	**Lateralization Target**	−0.06	0.05	−0.17–0.04	32	−7.38	***<0.00001***	−1.30	627895.31
	Lateralization Singleton	−0.04	0.04	−0.19–0.01	32	−5.45	***<0.0001***	−0.96	3730.31
	Lateralization Target vs. Singleton	−0.02	0.07	−0.16–0.17	32	−1.92	*=0.064*	−0.34	1.05

Pairwise t-tests were multiple comparison corrected by false discovery rate. Conventions as in the previous table.

mere guidance toward likely target locations. Thus, the N1pc may reflect the effort in resolving competition between task-relevant stimuli (targets) and non-target—but still salient—distractors and can be evoked by distractors, too, as long as these stimuli are difficult to disambiguate.[85] Therefore, a distractor evoked N1pc will be reduced/absent when competition is low, i.e., non-targets are easier to disambiguate (high chroma stimuli) and greater in highly competing contexts, i.e., non-targets are difficult to disambiguate from the target (low chroma stimuli). In line with these predictions, the singleton evoked N1pc was smallest when color contrast was high (experiment 2) compared to when color contrast was low (experiment 1, where all colors were more similar to the isoluminant gray point). Interestingly, the singleton-evoked N1pc was largest for the low chroma singleton in experiment 1, while there was no significant SSVEP amplitude enhancement for the singleton after the presentation of the search display, which could point to a more difficult target feature disambiguation. In contrast, there was a pronounced SSVEP amplitude modulation after a high chroma singleton in experiment 2, while the corresponding N1pc amplitude was considerably reduced. This pattern suggests that both measures might represent complementary but independent aspects of attentional deployment[86–90]: While the SSVEP seems to be sensitive to salience changes of a specific stimulus as well as its task relevance, the N1pc may signify the effort to identify the target features among multiple stimuli.[4,78] Computationally, such attentional engagement might be implemented by an attention map that integrates information from the subordinate feature maps to localize one or more targets and then projects an enhancement signal back down to earlier processing stages at the appropriate location.[13,91] Remarkably, this attention map would allow recurrent excitation between the early sensory processing and the task-relevant items on the expense of the irrelevant items. Thus, although the singleton distractors of the current study were salient color hue singletons,[60] their positions could be strategically ignored (down weighted), thereby preventing inappropriate capture (see also in the studies by Gaspar et al., Jannati et al., and Liesefeld et al.[37,92,93]).

Pd amplitudes were, as expected, larger when evoked by the singleton distractor compared to the target, stressing its role in attentional (re)orienting due to salient and potentially distracting visual information.[60] The missing effect upon Pd amplitudes of singleton chroma corroborates earlier findings that show the singleton-evoked Pd to be independent of stimulus saliency.[4,17] Furthermore, the current results show that the Pd can emerge together with electrophysiological signs of attentional capture (i.e., a preceding N1pc, enhanced SSVEP, reduced alpha-band amplitudes; see[4,5,18,31,55,56,78]) but it seems to be independent of their modulation by color salience (irrespective of whether a target or singleton was presented). Together with the N1pc as marker of attentional engagement, this sharpens the suggestion of Pd's potential role in being part of a general feature disambiguation process in the service of identifying the target.[4,5] This process may not act on early visual processes or the level of concrete features[61] but is most likely implemented at a later (or higher order) processing stage.[5,13,18] It should be noted that the color of the singleton distractors was NOT fixed in each experiment, but one of three equal-chroma colors was selected randomly on a trial-by-trial basis (similar to Oxner et al., 2024a). Nevertheless, these varying color singletons evoked prominent Pd components (see also in the study by van Moorselaar et al.[94]) furthering the proposal of the Pd signifying higher order processes (e.g., release of attention after attentional engagement[78]) and not acting on the level of feature suppression.[95]

Regarding the early lateralized positive deflection in the time range of 80–150 ms,[60] the current results clearly qualify this positivity to be different from the Pd. In fact, while the Pd amplitude was sensitive to whether a lateral target or singleton was presented, neither stimulus type nor color salience affected that early positivity. Whether this positivity posterior contralateral (Ppc) indicates a sensory imbalance,[40,96–98] a dishabituation after less frequently occurring stimuli,[5,18,99] or a general priority signal[100–103] remains to be shown.

Finally, contralateral alpha-band amplitudes to targets and singletons were always lower compared to ipsilateral amplitudes suggesting the absence of any active stimulus suppression but the processing of task-relevant or singleton distractor stimuli. This view matches with the hypothesis of alpha reflecting neural excitability in the service of preparing for upcoming task-relevant (amplitude decrease) or task-irrelevant (amplitude increase) events[104,105] (but see Pietrelli et al.[106]) or as a consequence of stimulus salience or attentional selection.[45,46,107–110] In line with that, alpha-lateralization to the target was more pronounced for low (experiment 1) than high color salience (experiment 2) search displays, which seemed to be mirrored by the increased attentional deployment to high chroma *fillers* as suggested by the SSVEP amplitudes. Alternatively, participants might have exerted more top-down control to maintain focus on the target when stimuli were less salient, despite non-target stimuli were still distracting (see N1pc to the singleton). Put differently, to maintain task performance the visual system might have traded-off stimulus-driven and effortful guided processes as reflected by alpha-band lateralization. In contrast, alpha lateralization to the irrelevant singleton distractor was not affected by color salience of the search display (despite it being consistently more reduced contra-than ipsilateral to the high and low chroma singleton). Apart from that, the effect of color salience on alpha-band amplitudes appears neglectable, at least for the current between-subject design of search display salience (see also in the study by Forschack et al.[4]). Thus, alpha modulations do not seem to be related to the control of salient but irrelevant stimuli that could potentially interfere with the task (singleton distractor) but may indicate the consequences of attentional selection of the task-relevant search item (the target; see in the study by Gundlach et al.,[46,108]) on the expense of its contralateral competitor (always a filler of the same color) by possibly stabilizing the attentional focus.[111]

How do these diverse effects on neurophysiological measures of attention fit to the behavioral effects in the studied search designs? The qualitative difference in the neurophysiological measures can neither be explained by differences in luminance of the search items nor by task demands as for both studies these parameters were matched inter-individually. Furthermore, the task was challenging as accuracy rates were titrated 75% correct responses for both experiments to facilitate top-down attentional control.[112] If participants would have relied more on

bottom-up processing than top-down control, the presence of the singleton distractor would most likely have resulted in behavioral costs as commonly reported for pop-out search (see for example Oxner et al.[78]). Yet, neither overall task performance changed across differently colorful search displays nor did distractor interference depend on a specific stimulus saliency. While the SSVEP is a stimulus-specific measure, lateralized potentials always reflect a compound signal of bilateral stimulus inputs (which is also true for alpha lateralization). Thus, featural item salience may only affect the lateralized ERP if low-level stimulus parameters like color chroma differ between the lateral inputs. As color chroma was equalized between the item types for each experiment in the current study, target N1pc amplitudes and, thus, attentional engagement in identifying the target did not differ between high and low chroma displays. Accordingly, SSVEP amplitude modulations to the target relative to the contralateral filler were very similar between the color vividness conditions, which corroborates the comparable behavioral performance (overall reaction times) between the low and highly salient search displays (Table 1, bottom row). While the singleton in experiment 2 captured more attention than in experiment 1 as indicated by a significant larger SSVEP modulation, there was also greater SSVEP enhancement to target and filler items (Table 3). Thus, the absent behavioral costs of a present singleton distractor might have emerged due to a similar reason in the two experiments, namely, comparable relative resource allocation between different item types and, potentially similar weight distribution on the priority map.[15,61,113] In a future study, it would be interesting to investigate whether bottom-up attentional capture could still be regulated by top-down (target template-) guided attention if only the relative salience of the singleton was increased. The current study demonstrates that attentional capture by salient (-enough) stimuli is obligatory and renders hypotheses suggesting pre-attentional suppression of irrelevant features unlikely.

To conclude, SSVEP, ERP, and alpha-band amplitudes reflect complementary but not interchangeable measures of attentional resource deployment. While both featural salience and items' task relevance may affect stimulus-specific SSVEP amplitudes, alpha-band lateralization is mainly affected by task relevance, while the ERP offers measures with sensitivities in detecting hemifield asymmetry (Ppc), attentional engagement (N1pc), and feature disambiguation (Pd). Attentional allocation in a visual search display seems to rely on the salience computations within each relevant feature dimension that might bias the competition between different search items. In line with these considerations, displays of low salience (experiment 1) showed generally smaller SSVEP amplitude modulations suggesting smaller priority weights on each stimulus location than in displays of high salience (experiment 2), however, with the effect of a similar inter-stimulus competition as feature salience was controlled between the respective search arrays. The joint consideration of complementary electrophysiological measures can help to better illuminate the neural implementation of attentional processes during visual search. Studies in the field of visual search should carefully consider color-defining parameters and precisely control the salience within the search array in order to avoid unexpected results that might be difficult to harmonize later on.

Limitations of the study

The current study aimed to investigate how parameters of a perceptually uniform color space, commonly used to define colors of search items, might affect neural measures of attentional deployment during visual search. However, and as mentioned in the discussion, subcortical cone opponency signals might have affected the current results, too. Unfortunately, we were not able to precisely quantify such subcortical contributions given our color sets for two reasons. First, we did not have a research-grade spectrophotometer available in our lab, which is required to quantify the spectral radiance of our projector in order to compute cone excitations. Second, cone contrasts are usually normalized by the background luminance of the screen incorporating cone adaptation to the input. However, it is an open question, whether the cones could instead be adapted to the flickering gray circles with our design, which would potentially lead to a different prediction about what mechanism would be stimulated.

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Norman Forschack (norman.forschack@uni-leipzig.de).

Materials availability

This study did not generate new materials.

Data and code availability

- All data (anonymized) reported in this paper will be shared by the lead contact upon request.
- This paper does not report original code.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

ACKNOWLEDGMENTS

We thank Romy Lempe and Jonas Jänig for their help in data recording. Furthermore, we are especially grateful to Jasna Martinovic for insightful discussions on how human color perception is implemented neurophysiologically. Research was funded by the Deutsche Forschungsgemeinschaft, grants MU 972/26–2, MU 972/29-1, and FO 1615/1-1.

AUTHOR CONTRIBUTIONS

Conceptualization, N.F., M.O., and M.M.M.; methodology, N.F., M.O., and M.M.M.; formal analysis: N.F.; investigation, N.F.; writing—original draft, N.F.; writing—review and editing, N.F., M.O., and M.M.M.; funding acquisition, N.F. and M.M.M.; resources, N.F., M.O., and M.M.M.; data curation: N.F.; visualization, N.F.; supervision, N.F. and M.M.M.

DECLARATION OF INTERESTS

The authors declare no conflict of interest.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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- EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS
- METHOD DETAILS
  - Apparatus and EEG recordings

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2025.112252.

Received: August 7, 2024
Revised: December 17, 2024
Accepted: March 17, 2025
Published: March 20, 2025

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Software and algorithms		
Psychophysics toolbox 3.0.15	http://psychtoolbox.org/	RRID:SCR_002881
Matlab R2017b	http://www.mathworks.com/products/matlab/	RRID:SCR_001622
neurodebian	http://neuro.debian.net/	RRID:SCR_004401
EEGLAB	http://sccn.ucsd.edu/eeglab/index.html	RRID:SCR_007292
RStudio 2023.06.0+421	https://posit.co/	RRID:SCR_000432

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Forty participants (28 female, mean age: 24.4; age range: 19 to 43 years) took part in Experiment 1 (low color chromaticity) and another 40 participants (30 female, 8 male, 2 diverse mean age: 24.8; age range: 20 to 33 years) in Experiment 2 (high color chromaticity). Four datasets had to be discarded from the sample of Experiment 1 because of excessive artifacts, and for one participant there were technical issues with saving the EEG data, leaving 35 participants for the final analyses. Six participants had to be excluded from all analyses of Experiment 2 for excessive artifacts and another one for missing EEG and behavioral data because of not finishing the experiment, leaving 33 participants for the final analyses. Based on our previous experiments,[5,18] power calculations assuming a beta error probability of 0.2 and an α error probability of 0.05 using G*Power[114] estimated that sample sizes of 34 participants are required for observing attentional modulation of SSVEP amplitudes in these designs. Participation was either compensated by class credits or financial reimbursement (10 € per hour). All participants had normal or corrected-to-normal vision. The study protocol was approved by the local ethics committee (2023.07.06_eb_207, Ethikbeirat der Universität Leipzig). Before starting, participants gave written informed consent and were informed about the nature of the experiment.

METHOD DETAILS

Apparatus and EEG recordings

Stimuli were presented through a ProPixx DLP Projector (VPixx Technologies Inc., Canada) having a resolution of 960-by-540 pixels and a refresh rate of 480 Hz. All stimuli were created with custom scripts using the Psychophysics toolbox 3.0.15[115,116] implemented in Matlab R2017b (The MathWorks, Natick, MA) running in a Linux Ubuntu environment (Version 16.04, xenial). Participants were seated in a dimly lit recording chamber at a viewing distance of 120 cm and responded on a standard QWERTZ computer keyboard, while EEG was recorded from 64 Ag/AgCl electrodes mounted in an elastic cap with an ActiveTwo Amplifier (BioSemi) at a sampling rate of 512 Hz with a low-pass filter of 102.4 Hz and stored for later offline analysis. Recording software was ActiView for Windows (version 9.02). Two electrodes were placed horizontally at the outer canthi of both eyes and vertically above and below the right eye to control horizontal and vertical eye movements and blinks.

Experimental procedure and stimuli

The stimulation procedure and the task of both experiments was almost identical to our previous study.[5] There were four grey disks positioned at the vertical and horizontal meridian with a central fixation cross at a distance of 4.3° of visual angle; one above, one below, one left, and one right (see Figure 1). The left disk flickered at a frequency of 28.8 Hz, the bottom at 19.2 Hz, the top at 22.4 Hz, and the right at 25.6 Hz. "On" and "off" frames were interpolated to allow intermediate luminance values between background intensity and full luminance.[117] The four disks had diameters of 3.2° of visual angle (VA). The white (CIELab 1976 L*a*b*: 96, -0.0024, -0.0135) fixation cross had a bar length of 0.25° and bar width of 0.03° VA and was presented throughout a block of several trials (see below). Every block began with the flickering of the grey disks at all four positions and the simultaneous onset of the fixation cross. Search displays were formed at random intervals of 2500–3500 ms by the four disks changing color and shape for 200 ms. After that, the shapes turned back to the four grey disks (see Figure 1A). All shapes of the search array were area-matched to the disks, were randomly assigned to one of the four positions on a trial-by-trial basis, and appeared only once in a given search array. A search array could contain a square of 3.9° VA (diagonal), a diamond (45° tilted square), a circle (same size as placeholders), a regular hexagon of 1.7° VA side length, and a regular octagon of 1.3° VA side length. The duration of a block as depicted in Figure 1A was about two minutes. Overall, there were 26 blocks, each comprising 40 randomly presented search displays (i.e., trials). Blocks were separated by short, participant-paced breaks. Thus, over the entire experiment, 1040 search displays were presented. 760 of

these displays contained the target, which was either a green diamond or square (counterbalanced across and never changed for a given participant), and 280 trials contained the singleton without a target as in our previous study.[5] In 480 of the target arrays, the target appeared in one of the lateral positions (i.e., left or right), and at the top or bottom position in the remaining trials. 240 of the trials with a lateral target contained a color singleton distractor of varying color (see below) that appeared adjacent to the target (i.e., top or bottom, in the remainder article called *TargetLateralDistractorVertical* trials, TLDV), while 240 target lateral trials (TL) did not contain a singleton distractor. In 240 trials the singleton distractor was presented laterally with an adjacent target in the top or bottom position (DLTV), while 240 distractor lateral trials (DL) did not contain the target. The remaining 80 trials presented a single target or distractor in the top or bottom position (TV and DV) only accompanied by the task-irrelevant filler items (presented in green). These trials were included to reduce spatial expectation biases and were not part of the main analyses. In all search arrays, all items contained a dot with a diameter of 0.32° VA that was randomly located either 0.32° to the right or left of the item center. Participants were instructed to search for the target shape and to indicate the side of the dot (left or right) by pressing the left or right arrow button, respectively. No response was required in the target absent trials (i.e., DL and DV). Response hand was counterbalanced across participants and changed after 13 blocks.

Before the main experiment, participants matched four colors used in the experiment to a grey background (approximately 235 cd/m^2) having the same luminance as the grey disks by heterochromatic flicker photometry[25] in order to mitigate any luminance-driven saliency effects and differences between colors. The background during stimulus presentation was black (approximately 1.4 cd/m^2).

Furthermore, each participant underwent a training procedure, where dot luminance was varied for each search display to attain one out of five values. These values were adjusted relative to the individual isoluminant RGB values of the respective color (green and red) with a minimal luminance decrement of 0.15 RGB values (hard to see) and a maximal value of 0.45 (easy to see). Training was repeated until a proper fit of a Weibull function[118] on individual response rates for five different luminance decrements was reached (usually no more than three times, i.e., maximum training time roughly six minutes). During the experiment, dot luminance was chosen to match the individually modeled point estimate of 75% correct responses as in our previous studies.[5,18]

In Experiment 2, stimuli and procedures were identical to Experiment 1 except that color chromaticity was increased and distractor colors were adapted to fit color gamut of the projector for these higher chroma values (for matching exemplary search arrays compare Figures 1A and 1B). The basic colors used in Experiment 1 were green (CIELab 1976 L*C*h°: 68, 58, 148°) for the target and filler items, and red (68, 58, 58°), purple (68, 58, 328°), or blue (68, 58, 238°), of equal chroma, for the singleton item. Experiment 2 used the same green as Experiment 1 but with higher chroma for the target and filler items (68, 78, 148°). Singleton distractor colors were yellow (68, 78, 82°), pink (68, 78, 336°), or red (68, 78, 41°) of equal chroma. The average chromaticity of these colors as well as the variability across participants for both experiments, after matching color luminance with the grey placeholders, is given in Figure 1C and is reported in CIELab 1976 L*C*h° cylindrical space.

General preprocessing of electrophysiological data

Preprocessing of EEG data was performed offline using the same pipeline as in our previous studies.[5,18] Briefly, this procedure first applies the standardized early-stage EEG processing pipeline (PREP v0.55.3[119] Bigdely-Shamlo et al., 2015), followed by independent component analysis (ICA, adaptive mixture of independent component analyzers (AMICA)[120]) on continuous data. Independent components were then classified with the ICLabel classifier (v1.0.1[121]) to obtain seven classes of components (Brain, Muscle, Eye, Heart, Line Noise, Channel Noise, Other). Only components of the classes ''Brain'' and ''Other'' were retained in the data. In Experiment 1, on average (mean), 20.6 (5 SD) out of 56.1 (4 SD) components were rejected. Mean class probability of rejected, ''Brain'' and ''Other'' components was 0.68 (0.07 SD), 0.80 (0.04 SD) and 0.61 (0.05 SD), the mean percentage of data variance they accounted for was 65.6% (21.4% SD), 30.3% (20.1% SD) and 4% (3% SD), respectively. In Experiment 2, on average, 19.2 (4.2 SD) out of 58.9 (2.7 SD) components were rejected. Mean class probability of rejected, ''Brain'' and ''Other'' components was 0.67 (0.06 SD), 0.83(0.04 SD) and 0.63 (0.05 SD), the mean percentage of data variance they accounted for was 53.3% (22.4% SD), 36.4% (20.3% SD) and 7.7% (14.4% SD), respectively.

After that, high- and low-pass filters were applied (function "pop_firws" v2.1[122]; 1. step high-pass: low cut-off of 0.5 Hz, Kaiser window, maximum passband deviation: 0.001 and transition bandwidth: 1 Hz, resulting in filter order/length of 1856 data points; 2. step low-pass: high cut-off of 17 Hz, Kaiser window, maximum passband deviation of 0.0001 and transition bandwidth of 4.25 Hz, resulting filter order/length of 606 data points estimated by the *pop_firwsord* function).

Epochs ranging from -1500 to 1500 ms relative to search display onset (t=0) were cut from the continuous channel signals, from which the individual epoch mean (across time points) was subtracted to remove the direct current offset. To ensure that all further analyses are based on trials where participants did see the search display and were fixating, epochs exceeding an adaptive channel threshold and containing blinks or eye movements (exceeding a potential threshold of 30 μV[123]) within the time window of -350 to 350 ms were discarded after manually reviewing the alleged artifactual epochs in both experiments. As we were focusing on early visual processing and covert attentional deployment after search display onset, overt orienting could, thus, be excluded. The following mean number of trials per condition for each subject remained for the analyses of Experiment 1: 206 (19 SD) TLDV, 203 (18 SD) DLTV, 207 (19 SD) TL, 207 (14 SD) DL, and Experiment 2: 213 (9 SD) TLDV, 209 (14 SD) DLTV, 212 (10 SD) TL, 208 (11 SD) DL. The resulting data were transformed to reference-free current source densities (CSDs) by computing the surface Laplacian.[124]

For further analyses, the EEGLAB toolbox (v2021.1), custom MATLAB scripts (The MathWorks, 9.10.0.1851785 (R2021a) Update 6), and RStudio (2023.06.0+421 "Mountain Hydrangea", R version 4.3) were used.

QUANTIFICATION AND STATISTICAL ANALYSIS

Behavioral analysis

Trials with responses faster than 400 ms or slower than 1000 ms were excluded. To calculate the effect of singleton interference on target reaction times, the reaction times on *target lateral – distractor vertical* (TLDV) and *target lateral* (singleton absent, TL) trials were compared, excluding *distractor lateral – target vertical* (DLTV) trials because of the previously reported decline in visual performance for stimuli presented along the vertical meridian as compared to the horizontal meridian.[5,18,48,49] If the presence of task-irrelevant color singletons did not capture attention, we expected no differences in reaction times between singleton present and absent trials or even benefits from singleton presence. We expected chroma effects on behavioral performance to be unlikely because discriminating dot laterality within the target was orthogonal to the chroma manipulation and dot luminance was individually titrated for every participant to equate task demands between the two experiments. Trials with a distractor alone at the left or right position were pooled together as distractor lateral (DL) trials and were not part of the behavioral analyses because no response was required.

Statistically, reaction times were compared with paired two-sided t-tests and corrected for multiple comparisons by false discovery rate.[125] Tests for equality were achieved by Bayes Factor (BF) testing employing a standard JZS prior of $\sqrt{2}/2$[126] as implemented by Bart Krekelbergs (Bayes Factor Matlab package: https://github.com/klabhub/bayesFactor). Evidence in favor of the null hypothesis (NH, i.e., equality) instead of the alternative hypothesis (AH) is indicated by a $BF_{01} > 3$.[127,128] Effect sizes are reported as Cohen's d_s[129] for contrasting two groups or conditions and as η^2_G (generalized eta squared[130]) for analyses of variances (see below).

Analysis of event-related potentials

To display cardinal and lateralized ERPs, epochs of 200 ms before to 400 ms after search display onset were extracted from the low- and high-pass filtered datasets (see above) and baseline corrected by the average current source density between -200 to 0 ms relative to search display onset (i.e., the average baseline value was subtracted from every datapoint of the epoch). Artifact free epochs were first pooled for target and singleton lateral conditions and averaged across the two experiments to calculate the grand-average, lateralized potential that guided the selection of time windows for ERP component amplitude extraction (the so-called collapsed localizer approach, see[78,131]). For the pooled epochs, the lateralization potentials (contralateral minus ipsilateral) were collapsed for a left and right hemispheric electrode cluster (left: PO7, PO3, O1; right: PO8, PO4, O2; see also[5]). Multiple pairwise t-tests for every data point in the baseline period were computed between contra- and ipsilateral waveforms to check for any systematic variation. None of the baseline tests exceeded the threshold for significance of $p_{fdr} < 0.05$. As can be seen from Figure S1, individual peak amplitudes of the lateralization potential could vary in terms of their peak latency. Extracting component amplitudes from a standard fixed time window for each participant would have necessarily underestimated these component amplitudes. Thus, based on the grand-average difference ERP, time windows for the N1pc (120 – 200 ms), and Pd (180 – 260 ms) were defined in which corresponding peak latencies were identified on a single-subject basis. Average lateralized potential amplitudes for a time window +/- 10 ms centered at the peak were calculated for every participant and condition. The Pd is sometimes quantified over a longer interval as a single component, spanning several cardinal peaks in the ERP (e.g., 100-300 ms [38]). We have noted in our own studies that the presence of the early part of the Pd lateralized potential might be independent of the stimulus type (i.e. target or singleton [5,18]), speaking therefore for a separate early component distinct from the Pd. Thus, based on the grand-average difference ERP, a third time window was defined around 50 – 130 ms in which peak latencies were identified for every subject. We will argue that this component reflects the so-called Ppc (positivity posterior contralateral) suggested to indicate a sensory imbalance of lateralized visual input[18,40,97,98] or a dishabituation to relatively rare events.[33,99] T-tests against zero were calculated for every component, condition, and experiment, which were multiple comparisons corrected by false discovery rate (fdr[125]). In Table S1, results of these tests are reported for each experiment and condition. All components were significant different from the pre-stimulus baseline (i.e. testing them against zero). Note however, that these tests were merely sanity checks of the amplitude extraction algorithm. The obtained ERP amplitudes were subjected to repeated measurements ANOVA and condition-wise contrasts tested the hypothesized influences of color chromaticity and stimulus type To test the effect of color chromaticity on the ERP and to compare components between the singleton lateral and the target lateral conditions, peak amplitudes were averaged for DLTV and DL, and TLDV and TL, respectively, and submitted to a repeated measures analysis of variance (rmANOVA) separately for each component with the factors of *condition (target, singleton)* and *chromaticity (low, high)*. Note: As the chromaticity cells of the design are not balanced, the full design was fitted by linear mixed effects modeling (*ERPamplitude ~ conditions * chromaticity + (1|participant:chromaticity)*). Model terms were then tested for significance by the Kenward-Roger approximation of the *F*-values (see also Forschack et al., 2022a). First, we expected to replicate the results from our previous study,[5] i.e., larger N1pc amplitudes for the target lateral than the singleton lateral condition, and vice versa for Pd amplitudes, which is following the view that these components reflect target and singleton distractor specific processes. As for the earliest component, we did not suspect any differences between conditions if it reflected the Ppc rather than an early Pd because lateralized sensory imbalances are identical across conditions for a given experiment (different shapes of equal luminance across color hues at horizontal positions). The Ppc, therefore, might also not be sensitive to chromaticity differences across the experiments as it is proposed to reflect sensory imbalances between the left and right visual hemifield. A similar logic applies to the hypothesis of

the Ppc resembling a dishabituation to rare events: as lateral target and singleton frequency was identical, we do not expect any difference between the stimulus conditions. Thus, the current study cannot discern between the sensory imbalance and dishabituation hypotheses regarding the Ppc. In contrast, the N1pc component has been shown to be modulated by the saliency of the target,[4,50] thus, high chromaticity targets might result in earlier or larger N1pc amplitudes. The Pd was shown to be unaffected by saliency manipulations,[4,17] thus, there should be no effect of chroma on the Pd amplitude.

Analysis of SSVEPs

To confirm the presence of stimulus-locked SSVEPs, amplitude spectra were calculated by means of discrete Fourier transformation across a time window starting one second before and ending one second after the pooled time-locking events after averaging high-pass filtered (see above), artifact free, detrended and zeropadded (15360 datapoints, frequency resolution = 0.03 Hz, centering the frequency bins on the tagging frequencies) epochs separately for the two chroma groups. Topological current source density maps were created for every tagging frequency and averaged across both groups to show that SSVEP signals originated over visual cortex.

To quantify SSVEP modulations early after search display onset, a time-resolved frequency analysis approach was employed. For this, averaged epochs ranging from -1500 to 1500 ms relative to search display onset were transformed to the frequency domain using fast Fourier transform (without zeropadding, thus, the full epoch length) and convolved with spectral Gabor kernels (temporal and spectral resolution: +/-158 ms and +/-1.4 Hz full-width-at-half-maximum) centered on the tagging frequencies to extract SSVEP amplitude time. This was done for each display condition. Because the main focus here, as in our previous studies[5,18] was on lateralized responses to laterally presented stimuli (and not the upper and lower visual hemifields), the SSVEP analysis was confined to the left and right flickering shapes. For statistical analyses, left (PO7;PO3;O1;P9) and right (PO8;PO4;O2;P10) lateralized electrode clusters contralateral to the respective stimulus (target/singleton/filler) positions were extracted and SSVEP amplitudes were averaged across the electrodes within each cluster in the time window 200 ms to 450 ms after search display onset. Note that a precise extraction/ separation of the tagging frequencies is ensured even with such a short window as the transformation was calculated on a larger window (3 seconds) and because of the temporal and spectral smoothing of the Gabor kernels (which is not possible to achieve with, e.g., a short-time windowed FFT). These stimulus-specific lateralized amplitudes were normalized relative to the prestimulus baseline (i.e., -500 to -200 ms) to account for amplitude difference due to the natural properties of the frequency spectrum (higher frequencies show lower amplitudes). After that, SSVEP amplitudes for left and right target/singleton/filler presentations were averaged. Note that the analysis time windows (baseline and post-search display onset) were separated by 200 ms from stimulus onset because of the temporal resolution of the Gabor filter that would, otherwise, have introduced temporal smearing of pre- and post-search display times when not separated. Furthermore, the analysis focused on perceptual and attentional processes before the earliest behavioral responses (i.e., ~520 ms, see Figure 2A). As in the ERP analysis, SSVEP amplitude modulations were statistically evaluated against prestimulus baseline and then averaged for DLTV and DL, and TLDV and TL, respectively, for each condition and group. Those values were submitted to a 2-by-2-by-2 rmANOVA (after fitting the full design by linear mixed effects modeling (*SSVEPamplitude ~ lateral stimulus * condition * chromaticity + (1|participant:chromaticity)*) with the factors of *lateral stimulus (target/singleton, filler)* and *condition (target, singleton)* and *chromaticity (low, high).* Planned comparisons tested the difference between target lateral (*TLDV + TL*), singleton lateral (*DLTV + DL*), and corresponding filler presentations and the chroma group differences by paired t-tests that were multiple comparisons corrected by false discovery rate. If SSVEP sources thrive on high chromatic stimuli (Experiment 2), we expected SSVEP amplitudes to be generally increased relative to stimuli of low chromaticity (Experiment 1). Furthermore, we expected to replicate the results of our previous study, esp. larger amplification of target stimuli compared to singletons and non-singleton filler stimuli.

Analysis of alpha band activity

First, amplitude spectra were calculated by means of discrete Fourier transformation like in the SSVEP analysis above with the only difference that the transformation was applied on single-trials and averaged thereafter to facilitate the detection of oscillatory components that are not strictly phase-locked to the search display onset. As can be seen from the resulting total amplitude spectrum in Figure 2D, both experimental groups showed a pronounced alpha-band response around 8–12 Hz and a parieto-occipital activity maximum in that frequency range.

Subsequent quantification of alpha-band amplitudes were based on single trials convolved with Gabor kernels centered at 8 to 12 Hz (in steps of 0.5 Hz) to obtain the total (i.e., both phase- and non-phase-locked oscillatory) alpha-band response. Importantly, Gabor filter width and electrode clusters were the same as in the analysis of the SSVEPs. To minimize spectral power phase-locked to search display onset, the Gabor filtered trial averaged signal (i.e., the evoked alpha band response) was subtracted. Differences in alpha-band amplitude were tested for the same averaged time window as for the SSVEP amplitudes, i.e., 200 to 450 ms relative to search display onset, between right and left clusters of electrodes contralateral and ipsilateral to the laterally presented target (*TLDV + TL*) or singleton distractor (*DLTV + DL*). These windowed averages were submitted to a within-subject repeated-measures ANOVA with the factors of *laterality* (contralateral, ipsilateral) and *condition* (target, singleton) and *chroma* (low, high). Planned post-hoc comparisons tested the alpha-band lateralization (contralateral minus ipsilateral amplitude) for the singleton lateral and the target lateral conditions by two-sided paired t-tests for each group. As written in the introduction, we expected increased alpha-band amplitudes contralateral to the singleton relative to ipsilateral electrode sides if the singleton had been suppressed.

As we have previously shown,[4,5,18,47] alpha-band amplitudes were suppressed below pre-stimulus baseline regardless which type of stimulus appeared at the lateral position (i.e., contra- and ipsilateral event-related desynchronization (ERD) of similar size both to target and distractor stimuli), which resembles the idea of alpha reflecting neural excitability as a spontaneous phenomenom[105,132,133] or as a consequence of stimulus salience or attentional selection.[45,46,107,134] Thus, we explored whether there is a larger alpha-band amplitude reduction after high than low chromatic stimuli if alpha reflects neural excitability due to stimulus salience. Alternatively, if alpha reflects the consequences of an attentional selection processes, there should be a larger lateralization after high than low chromatic input as it might be easier to select high chromatic stimuli. This was tested by independent two-sided t-tests of each lateralized electrode cluster (contra- and ipsilateral) and their difference between chroma groups.