Attentional Facilitation of Constituent Features of an Object Does Not Spread Automatically along Object-defining Cortical Boundaries

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Abstract

■ The integrated object account predicts that attention is spread across all features that constitute one object, regardless of their task relevance. We challenge that prediction with a novel stimulation technique that allows for simultaneous electrophysiological measurements of the allocation of attention to two distinct features within one object. A rotating square that flickers in different colors evoked two distinct steady-state visual evoked potentials (SSVEPs) for rotation and color, respectively. If the integrated object account were true, we would expect identical SSVEP amplitudes regardless of what feature participants attended. We found greater SSVEP amplitudes for the to-be-attended feature compared with the to-be-ignored feature. SSVEP amplitudes averaged across both features were significantly reduced when participants attended to both features, which was mirrored in behavioral costs, implying competitive interactions or a division of attentional resources. Surprisingly, this reduction in amplitude was mainly driven by the SSVEP amplitude elicited by color changes. In conclusion, our results challenge the integrated object account and highlight the extent to which color is "special" within feature space. ■

INTRODUCTION

Visual attention is an important cognitive filtering mechanism to select behaviorally relevant information for processing, given that the amount of information in typical visual scenes exceeds the limited processing capacity of the visual system (Desimone & Duncan, 1995). Object-based attention is one of the key visual selection mechanisms with the key prediction of a mandatory integration of all features that constitute an object, regardless of their task relevance (O'Craven, Downing, & Kanwisher, 1999; Duncan, 1996). The integrated object account was challenged in recent studies. Whereas Freeman, Macaluso, Rees, and Driver (2014) used stimuli that were spatially separated, and participants attended to one object at one location with features either grouped or segmented from the object at the opposite hemifield, Wegener, Galashan, Aurich, and Kreiter (2014) used a Posner-like behavioral cueing design, in which participants were cued either to one object or to a particular feature of an object. Comparably, both studies reported a global sensory gain effect as predicted by feature-selective attention (Treue & Martínez Trujillo, 1999) but failed to find object-based integration. One limitation of these studies is their spatial confound, that is, feature grouping across space. In everyday life, attention to one object is not confounded with spatial separation of the features that define the object. A further limitation of the study by Wegener et al. (2014) is

that it uses only behavioral measurements, without considering any of the underlying neural processes of feature processing and integration. Another study, which challenges the integrated object account and was able to overcome the aforementioned limitations, was conducted by Nobre, Rao, and Chelazzi (2006), who used a feature-specific negative priming paradigm. Behavioral and electrophysiological results revealed the existence of inhibitory processes at the single feature level within objects, which lead to a modulation of brain activity during early stages of perceptual analysis. However, in that study, only the inhibition of irrelevant features, and not the possible amplification of relevant features, was in the focus.

This study aims to gain a more comprehensive understanding of basic neural mechanisms involved in object-based attention and the allocation and distribution of attentional resources to object constituent features. In particular, we were eager to rule out any spatial attention confound. Besides, we utilized EEG data as an objective electrophysiological measurement of early visual processing in the human brain, which allowed for a simultaneous analysis of neural responses to both task-relevant and task-irrelevant features throughout the period of feature selection. We presented our participants with an outlined rotating square that changed color at a certain frequency (Figure 1). Both rotation and color changes evoked a distinguishable steady-state visual evoked potential (SSVEP; see Figure 3), which allowed for the direct measurement of attentional resource allocation in the early visual cortex in response to the two constituting features that were

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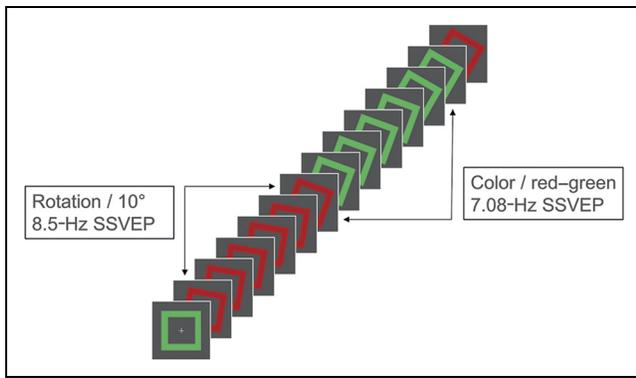
Figure 1. Schematic representation of the stimulation. The square rotated in jumps of 10° of a circle, evoking an SSVEP at 8.5 Hz. Simultaneously, color changed from red to green at a rate of 7.08 Hz. For target events, see text. Each image represents two frames of screen refresh.

not spatially separated. Participants were instructed in different blocks to attend to either color, rotation, or both and to detect target events within the relevant feature dimension. In the baseline or reference condition, participants were instructed to attend to the fixation cross on the screen and to detect targets that appeared at the fixation cross.

On the basis of the integrated object account (Schoenfeld, Hopf, Merkel, Heinze, & Hillyard, 2014; Katzner, Busse, & Treue, 2009; O'Craven et al., 1999), attending to one feature of the square results in the perceptual integration of the to-be-ignored feature. As a consequence, SSVEP amplitudes should not differ as a function of feature-based attention; that is, SSVEP amplitudes should neither differ when one feature is attended compared with being ignored nor differ when one feature is attended compared with both features being attended. The same prediction would also follow from spatial-based attention (Posner, 1980) because the entire object is located in the "attentional spotlight" when participants performed the task. If, however, greater facilitation of the task-relevant feature was observed compared with the task-irrelevant feature (measured via SSVEPs), this would clearly contradict the predictions from object- and spatial-based accounts. Furthermore, on the basis of the integrated object account, one would not expect any interference between object constituent features. Accordingly, behavioral performance, as well as neural responses for all three feature conditions ("attend rotation," "attend color," and "attend color and rotation"), should be similar. Any other result, especially with respect to the condition when both features need to be attended, would go against the integrated object account.

METHODS

Participants

G*Power was employed to perform an a priori power analysis to estimate the minimum sample size required to achieve adequate statistical power. On the basis of a large effect size of $\eta^2 = 0.5$ in a pilot study, G*Power predicted the need for a sample size of at least 18 participants for the planned three-factor repeated-measures ANOVA to analyze SSVEP amplitude differences (applying the necessary nonsphericity correction and assuming an α error probability of 5% and a power of 95%).

In our experiment, we recorded 32 young adults with normal or corrected-to-normal vision. Data from two participants had to be excluded because of extremely noisy data, that is, exclusion of more than 50% of all trials during preprocessing, leaving 30 participants in the sample (four men, two left-handed; mean age = 21.3 [ranging from 18 to 35] years). For a behavioral control experiment, 18 participants from the original experiment participated again.

All participants received class credits or financial reimbursement for their participation and gave informed consent before the application of electrodes. The experiment was conducted in compliance with the Code of Ethics of the World Medical Association (Declaration of Helsinki) and the local ethics committee (University of Leipzig).

Stimulus Material and Tasks

Participants observed a rotating outline of a square. Rotation of the square occurred in steps of 10° of a circle every 118 msec, thereby driving an SSVEP at 8.5 Hz. Simultaneously, the color of the square alternated between red and green every 141 msec, thus driving a different SSVEP at 7.08 Hz (see Figures 1 and 3).

Stimuli were presented on a 19-in. CRT monitor set to a resolution of 640 × 480 pixels, a color depth of 32 bits, and a refresh rate of 85 Hz and were viewed from a distance of 80 cm. The side length of the outer edges of the rectangle corresponded to a visual angle of 6°, and the inner edges corresponded to a visual angle of 4°. Red and green were individually set to be isoluminant with heterochromatic flicker photometry (Wagner & Boynton, 1972).

Participants were instructed block-wise to attend either to color changes or to rotation, or to both, and were asked to detect target events within the relevant feature dimension. In the baseline or reference condition, participants were asked to attend to the fixation cross and detect targets there. Blocks appeared in a randomized order. Before each block, the instruction for either "attend color," "attend rotation," "attend color and rotation," or "attend fixation cross" appeared in German in the center of the screen until participants started the next block by pressing the spacebar. Thereafter, the instruction would disappear, and the stimulus was presented for 3500 msec, followed by an interval with no square. Here, the fixation cross was displayed in the middle of the screen for varying lengths of time between 1250 and 1750 msec. Each block contained 26 trials, and the entire experiment consisted of 20 blocks (see below).

Rotation targets were defined through an acceleration of rotation speed of the rectangle for 353 msec. Color targets were defined through a discoloration, that is, some blue that was mixed into red and green, for 424 msec (speed of rotation acceleration and amount of blue depended on the individually adjusted difficulty of the tasks; see below). In addition, the bars of the fixation cross changed length minimally in very short intervals of 35, 47, or 59 msec, in the baseline or reference condition "attend fixation cross" (changes in length and duration depended on individually adjusted difficulty; see below). Participants were instructed to respond to targets in the cued feature/location by pressing the spacebar upon detection while ignoring such changes in the uncued property ("distractors"). For the combination task ("attend to color and rotation"), targets were defined as simultaneous changes in color and rotation, and distractors were defined as changes in only one of these properties. In the baseline or reference condition, targets were defined as a shortening of one of the bars of the fixation cross, whereas lengthening was defined as a distractor. The earliest onset of targets and distractors was 353 msec after stimulation onset. Either none, one, or two events could occur in a single trial. To allow for an unambiguous assignment of responses, the appearance of subsequent targets or distractors was separated by at least 1059 msec.

Although the constituent object features share the same space, that is, the square, it might be theoretically possible that participants adopted a strategy to attend to isolated locations of the square, such as one of the corners, to perform the task. In a behavioral control experiment (completed by participants from the original experiment), we controlled for such strategies by changing some physical properties that would make it impossible to solve the task with a purely spatial attentional selection. In general, the principal experimental settings, namely, stimulus material, tasks, individually adjusted difficulty of the tasks, and procedure, remained the same. However, for the color task, targets appeared at random in one of the four sides of the square, and rotation included irregular, incremental jumps of 70°. These manipulations required participants to attend to the whole object to complete both the rotation task and the color task. Blocks assessing the baseline/reference condition, that is, "attend fixation cross," were excluded in the control experiment.

Procedure

Before EEG recordings, two or more blocks of training were performed for each condition and the difficulty was adjusted per participant until each reached a stable performance of at least 80% of hits and less than two false or blind alarms. Therefore, participants started their training with the same relatively easy setting; that is, targets in the rotation task were rotating in steps of 30°, and

30% blue (out of full blue) was added to red and green, respectively. For the fixation cross task, the bars changed length by 6% for a duration of 59 msec. The difficulty was then increased stepwise until participants reached a performance between 80% and 90% of hits and less than two false or blind alarms in two consecutive training blocks. Furthermore, the rotation and color task performance were equalized per participant to guarantee that both tasks were identical in difficulty. The criterion was set to a maximum difference in hit rates of 5% between the two tasks. The combination task, that is, "attend to color and rotation," was given twice to familiarize participants with the task. The difficulty was not adjusted here but adopted from the two single tasks, namely, "attend to color" and "attend to rotation."

After the adjustment procedure, 520 trials of the task were recorded. Half of the trials contained no targets or distractors, whereas the other half contained one or two events. Trials were presented in 20 blocks of 26 trials, each lasting around 2 min. Each condition was assessed in four of the 20 blocks. Given that events were possible in the square and in the fixation cross during blocks assessing the baseline/reference condition (and not only in the square as in the three other conditions), we recorded eight blocks for this condition, because as outlined below, only trials without any event were subjected to electrophysiological analysis. After each block, participants received feedback for their antecedent performance.

EEG Recording and Analysis

Brain electrical activity was recorded from 64 Ag/AgCl electrodes mounted in an elastic cap at a sampling rate of 256 Hz using an ActiveTwo Amplifier (BioSemi). During recording, data were referenced to the Common Mode Sense electrode. Four electrodes, placed at the canthi of both eyes (horizontal EOG) and below and above the right eye (vertical EOG), recorded eye movements and blinks throughout the experiment. The EEGlab toolbox (Delorme & Makeig, 2004) and custom MATLAB scripts (The MathWorks, Inc.) were used for offline data analysis. First, data were epoched from 0 to 3500 msec relative to trial onset. Only trials without any targets or distractors were included in the analysis to avoid any potential influence of events and subsequent decisional or motor processes. The analysis time window spanned between 500 and 3500 msec (the beginning of each trial was discarded to exclude the visual evoked response to stimulus onset). For this time window, diverse types of artifacts were identified, and contaminated trials were excluded, or data were interpolated with an automated procedure. First, data were detrended to correct for linear drifts; subsequently, trials containing blinks or eye movements were rejected based on a threshold procedure. In the next stage, the "statistical control of artifacts in dense array EEG/MEG studies" (Junghöfer, Elbert, Tucker, & Rockstroh, 2000) was applied: On the basis of the statistical parameters of

the data, channel data were interpolated, or in the case of noise contamination of at least 10 neighboring data channels, trials were excluded. On average, 3.32 channels were interpolated per trial ($SD = 1.55$), and an average of 13.4% of the trials ($SD = 6.5\%$) was excluded from the analysis. Data were then rereferenced to average reference and averaged for each participant and each experimental condition separately.

Afterward, base-to-peak SSVEP amplitudes were quantified as the absolute Fourier coefficients for the two separate stimulation frequencies. In contrast to traditional data analysis approaches in SSVEP research, a weighted combination of electrodes—instead of the data from single or several individual electrodes showing the greatest response to rhythmic stimulation—was used for the SSVEP analysis of this study. This weighted combination of electrodes has been derived from a method combining and extending existing multivariate source separation methods, termed "rhythmic entrainment source separation" (RESS; Cohen & Gulbinaite, 2017). On the basis of a generalized eigendecomposition of SSVEP signal and reference covariance matrices, channel weights were constructed that maximize the SSVEP signal representation (signals at the SSVEP frequency) over non-SSVEP signals (i.e., signals for frequencies neighboring the SSVEP frequency). From this generalized eigendecomposition, the channel weights with the largest eigenvalue (i.e., maximizing the SSVEP signal representation) were selected and served as a spatial filter (RESS filter). A single time course (RESS component) was extracted, by multiplying channel time courses with this spatial filter, and then analyzed. Crucially, RESS filters are constructed based on data from all experimental conditions and are thus unbiased. Using this method, "electrode picking" is avoided, and thereby, the issue that the specific selection of electrodes may differ by individual, flicker, and experimental condition is minimized. Furthermore, the signal-to-noise ratio of the narrow-band steady-state response in the frequency domains is maximized by this method.[1]

To examine the dissimilarity of the two resulting RESS components and thereby analyze whether the two distinct SSVEPs (at 8.5 Hz [rotation] and at 7.08 Hz [color]) are based on different topographical distributions, the Global Map Dissimilarity index was calculated (Murray, Brunet, & Michel, 2008; Lehmann & Skrandies, 1984). The true index of dissimilarity was then statistically tested against an empirical zero distribution, which was generated by a permutation test based on 5000 permutations, using Monte Carlo procedures.

SSVEP amplitude values based on the RESS component of each of the two frequencies were then extracted for all conditions and participants. For an analysis of the effects of feature-based attention to certain features within one object, first, standardized amplitude modulations for the three attentional conditions were calculated by dividing SSVEP amplitudes of a respective "attend-to-square" condition by the SSVEP amplitudes of the baseline/reference condition. The quotient was multiplied by 100, and then

100 was subtracted from the resulting value, leading to a change in SSVEP amplitudes in percentage relative to the baseline/reference condition. Second, calculated amplitudes were compared across attentional conditions using repeated-measures ANOVA testing. This was carried out for both frequencies separately as well as averaged across the two frequencies. In the case of violation of the assumption of sphericity, indicated by Mauchly's test ($p \leq .05$), degrees of freedom were corrected using Greenhouse–Geisser estimates of sphericity. Finally, Bonferroni-corrected post hoc tests were applied to identify details of the differences.

Behavioral Data

Responses occurring between 200 and 1000 msec after target or distractor onset were classified as hits or false alarms, respectively. To examine behavior across attentional conditions, the sensitivity index d' (as a measure of performance) and the response criterion c were calculated (Stanislaw & Todorov, 1999) and compared between the three attentional conditions, namely, "attend to color," "attend to rotation," and "attend to color and rotation," using a repeated-measures ANOVA. Bonferroni-corrected post hoc tests were executed to identify the details of those differences.

To test for and exclude the possibility that participants adopted a spatial strategy to perform the respective task, we directly compared performance (d' values) between the EEG experiment and the behavioral control experiment. Given that we have hypothesized a confirmation of the null hypothesis, that is, no behavioral differences between the two experiments, Bayes factors for dependent-group designs were computed (Rouder, Speckman, Sun, Morey, & Iverson, 2009) via Gaussian quadrature, using the function *ttestBF* from the R package BayesFactor v0.9.12-2 (Morey et al., 2018). A noninformative Jeffreys prior was placed on the variance of the normal population (Jeffreys, 1961), whereas a Cauchy prior with a width of $\sqrt{2}/2$ was placed on the standardized effect size (Rouder, Morey, Speckman, & Province, 2012; Morey & Rouder, 2011; Morey, Rouder, Pratte, & Speckman, 2011). Jeffreys's (1961) recommended categorization for the grade of evidence was used for the interpretation of Bayes factors.

RESULTS
Electrophysiological Data (SSVEPs)

Figure 2 shows the topographical distribution of SSVEP amplitudes (top) and channel weights of RESS filters of the SSVEPs (bottom). As in a previous study (Müller et al., 2006), color changes elicited a maximum response at occipital electrodes. Rotation was linked to a broader temporal–parietal distribution, which was significantly different from the color distribution (dissimilarity index $= 0.85$, $p_{\text{Monte-Carlo}} \leq .001$)
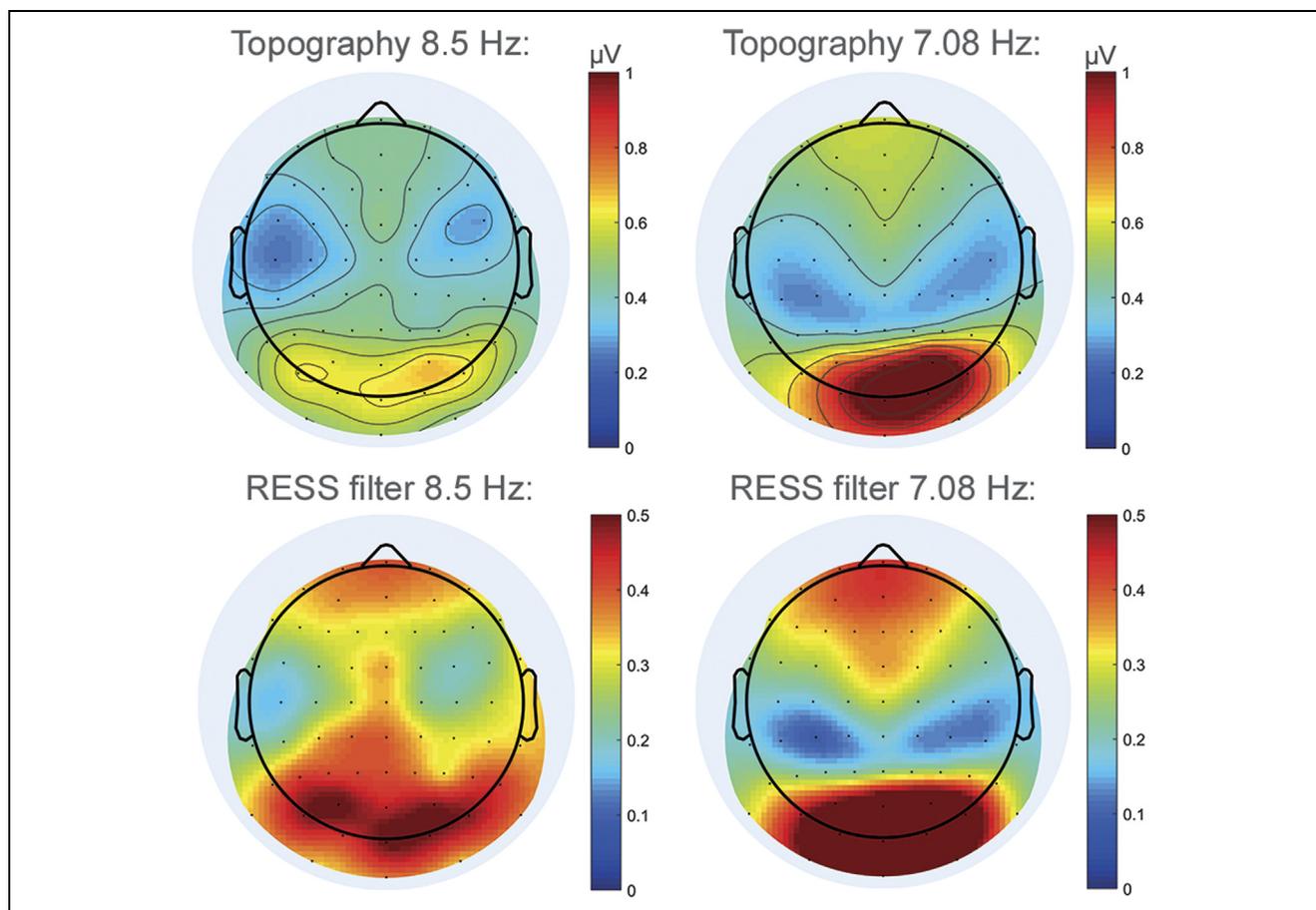
Figure 2. Topographical distributions of grand mean SSVEP amplitudes (top) and channel weights of RESS filters of the SSVEPs (bottom), averaged across all participants and all experimental conditions. SSVEP topography and RESS filter for rotation (8.5 Hz) on the left and for color changes (7.08 Hz) on the right. Take note of arbitrary units for channel weights of the RESS filters.

indicating activation of different cortical neural sources in the visual cortex for color and for rotation (see Figure 2).

Figure 3 depicts the spectral power between 0 and 20 Hz for a broad occipital–parietal cluster. The resulting spectrum shows two decisive peaks, at 7.08 Hz (evoked by color changes) and 8.5 Hz (evoked by rotation).

SSVEP amplitudes averaged across both frequencies (8.5 and 7.08 Hz) were modulated by attention (sphericity
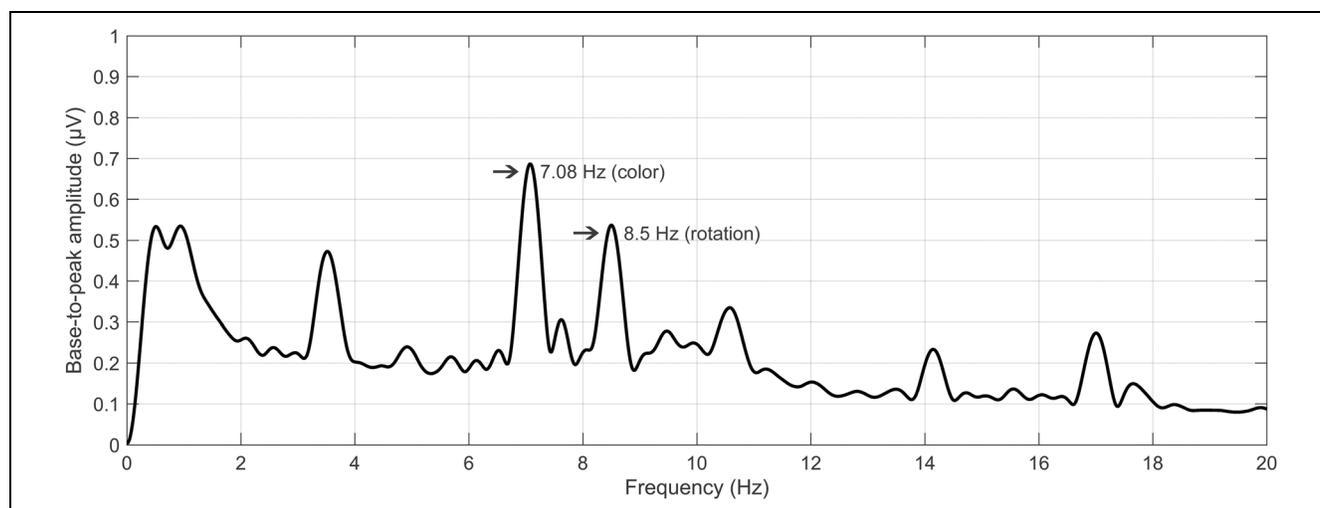
Figure 3. Grand mean spectral power across all participants, averaged across an occipital–parietal electrode cluster (electrodes: I1, Iz, I2, O1, Oz, O2, PO7, PO3, POz, PO4, PO8, P9, P7, P5, P3, P1, Pz, P2, P4, P6, P8, and P10).
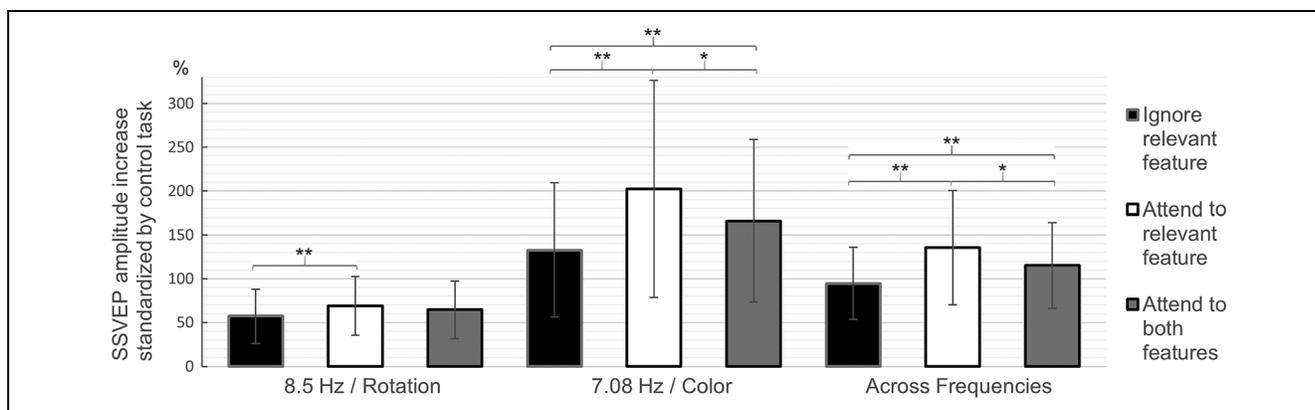
Figure 4. Grand mean SSVEP amplitude increase relative to baseline/reference measure ("attend fixation cross") in percentage for both frequencies as well as averaged across frequencies. Error bars represent the standard deviations of the means. $*p \leq .05$ and $**p \leq .01$ for Bonferroni-corrected post hoc tests.

violated: $\chi^2(2) = 22.3$, $p \leq .001$; Greenhouse–Geisser corrected: $\varepsilon = 0.64$; $F(1.28, 35.9) = 15$, $p \leq .001$, $\eta_p^2 = 0.35$). SSVEP amplitudes were significantly greater when the respective feature was attended compared with being ignored. Attending to both features simultaneously resulted in significantly reduced amplitudes compared with attending to only one feature (post hoc tests: attended vs. unattended feature, $p \leq .01$; attend to one vs. attend to two features, $p \leq .05$; ignore one feature vs. attend to both features, $p \leq .01$; see Figure 4).

When we analyzed SSVEP amplitudes separately for color and rotation, both frequencies were modulated by attention (8.5 Hz [rotation]: $F(2, 58) = 6.74$, $p \leq .01$, $\eta_p^2 = 0.19$; 7.08 Hz [color]: sphericity violated: $\chi^2(2) = 22.1$, $p \leq .001$; Greenhouse–Geisser corrected: $\varepsilon = 0.64$; $F(1.28, 35.9) = 11.4$, $p \leq .001$, $\eta_p^2 = 0.29$). Furthermore, SSVEP amplitudes were significantly greater when the respective feature was attended compared with being ignored. However, attending to both features simultaneously resulted insignificantly reduced amplitudes compared with attending to one feature for color (7.08 Hz) only and not for rotation (8.5 Hz; post hoc tests for 8.5 Hz [rotation]: attended vs. unattended feature, $p \leq .01$; attend to one vs. attend to two features, $p = .46$; ignore one feature vs. attend to both features, $p = .06$; post hoc tests for 7.08 Hz [color]: attended vs. unattended feature, $p \leq .01$; attend to one vs. attend to two features, $p \leq .05$; ignore one feature vs. attend to both features, $p \leq .01$; see Figure 4).

Behavioral Data

Unsurprisingly, given the preexperimental difficulty adjustment, task performance—evaluated by d'—did not differ significantly between rotation and color (rotation: mean = 4.99, $SD = 0.82$; color: mean = 5.11, $SD = 1.28$). However, when participants attended to both features, d' values were significantly reduced (mean = 3.07, $SD = 1.19$, $F(2, 58) = 47.9$, $p \leq .001$, $\eta_p^2 = 0.62$ (post hoc tests: rotation vs. color, $p \geq .99$; rotation and color vs. both

features each, $p \leq .001$). Regarding the response criterion c, we found no statistically significant differences between rotation and color (rotation: mean = 1.08, $SD = 0.45$; color: mean = 0.9, $SD = 0.5$). Identical to d', c values were significantly reduced when participants attended to both features (mean = 0.27, $SD = 0.54$, $F(2, 58) = 24.48$, $p \leq .001$, $\eta_p^2 = 0.46$ (post hoc tests: rotation vs. color, $p = .45$; rotation and color versus both features each, $p \leq .001$).

Behavioral Control Study

The performance (d') comparison between the EEG experiment and the behavioral control study resulted in substantial evidence in favor of the null hypothesis, according to the computed Bayes factors (rotation: $BF_{10} = 0.33 \pm 0.01\%$; color: $BF_{10} = 0.27 \pm 0.01\%$; both features: $BF_{10} = 0.27 \pm 0.01\%$; Jeffreys, 1961). Therefore, it is very unlikely that participants adopted a purely spatial attention strategy to perform the task in the EEG experiment, given that such a strategy was not possible in the behavioral control study.

DISCUSSION

Our study aimed to assess a basic prediction of the integrated object account, that is, the spread of attention and thus the processing of all object constituent features, regardless of their task relevance (O'Craven et al., 1999; Duncan, 1996). Similarly to previous studies, which used different methods (Freeman et al., 2014; Wegener et al., 2014; Nobre et al., 2006), our results questioned this strong prediction of the integrated object account. We demonstrate a clear, selective facilitation of the task-relevant feature compared with the to-be-ignored feature. When we averaged across both frequencies, we also found significantly reduced SSVEP amplitudes when both features became task relevant compared with the "attend to one feature" condition. The reduction in SSVEP amplitudes was mirrored in behavioral data with significantly reduced

d′ values when both features were attended compared with attending to one feature only. *c* Values were also significantly reduced when attention was allocated to both features compared with one feature only. However, upon closer inspection of the data, it was revealed that the SSVEP amplitude reduction was mainly driven by color, which may indicate that color behaves differently compared with other features (Duncan & Nimmo-Smith, 1996).

A novelty in our design lies in the fact that we did not use overlapping, competing (Ciaramitaro, Mitchell, Stoner, Reynolds, & Boynton, 2011; O'Craven et al., 1999; Duncan, 1996), or spatially separated (Freeman et al., 2014) stimuli but instead one coherent object that needed to be attended to in order to solve any of the tasks. In addition, we focused on both the inhibition of task-irrelevant features, such as in Nobre et al. (2006), and the amplification of task-relevant features concurrently. Furthermore, we included a condition in which participants were asked to attend to two features. Thus, our design mimics everyday requirements, which demand the extraction of one or more behaviorally relevant features from a single object. Therefore, our results significantly extend previous studies (Freeman et al., 2014; Wegener et al., 2014; Nobre et al., 2006) by demonstrating feature-selective dominance without spatial confounds, and even more importantly, our results demonstrate reduced cortical facilitation when two features are task relevant (mainly driven by the color-driven SSVEP), mirrored in reduced *d′* values. This clearly indicates that attending to two features was more difficult than attending to only a single feature. Again, this is at odds with common predictions of object-based attention, given the classical finding of better dual-judgment performance within one object (Duncan, 1984). Our results also suggest that attention to two features results in a less conservative response criterion (see *c* values). Whereas response criteria for single-feature conditions were relatively conservative, the response criterion was rather neutral when attending to both features simultaneously (Stanislaw & Todorov, 1999).

Considering the above results in greater detail, it is apparent that reduced SSVEP amplitudes resulting from attending to two features were mainly driven by the SSVEP that was evoked by color changes. Against the background of prior research, this finding seems not at all surprising prima facie, because on the one hand, different features are often described as behaving differently and, on the other hand, color has been described as behaving differently to all other features within the field of feature-based attention within objects (Duncan & Nimmo-Smith, 1996). Therefore, one could conclude that the described feature interference within objects is accounted for by color-based selective attention only and is not generalizable across features. However, in the study by Duncan and Nimmo-Smith (1996), color was associated with reduced competition and reduced interference, and not the opposite, as observed here. Results are therefore difficult to explain by the known "special" role of color.

However, generally smaller SSVEP amplitudes evoked by rotation (see Figure 3) could explain smaller differences between conditions. It is worth noting that the pattern is descriptively the same in color- and rotation-based feature-selective attention here. Nonetheless, future research should evaluate the generalizability of the demonstrated effects to other features.

One explanation for our finding of reduced SSVEP amplitudes in the two-features task might be related to competitive interactions, as postulated by both the biased competition account and normalization models of attention (Reynolds & Heeger, 2009; Desimone & Duncan, 1995). Competitive interactions arise when stimuli compete for processing resources (i.e., due to spatial proximity), even in the absence of attention. Competitive interactions were measured in our baseline/reference condition when participants attended to the fixation cross. Attending to only one feature resulted in the release of that feature from competitive interactions. Interestingly, the release of suppression was limited to the to-be-attended feature without attentional incremental grouping (Roelfsema, 2006) via neural integration between visual areas along object-defining boundaries. Attending to both features, however, resulted in competition for processing resources between the two, leading to reduced SSVEP amplitudes. This explanation follows that which was raised by Freeman et al. (2014). They even claimed that competition becomes much stronger when features form a grouped object, as was the case in this study. As a result of competition, attentional resources needed to be divided between both features, thus resulting in reduced SSVEP amplitudes and behavioral costs, as we have demonstrated in previous studies (Walter, Quigley, & Mueller, 2014; Keitel, Maess, Schröger, & Müller, 2013).

A further alternative explanation for our findings may be based on a sensory gain mechanism (Treue & Martínez Trujillo, 1999; Hillyard, Vogel, & Luck, 1998), which does not necessarily need competition. In this line of reasoning, attending to one feature allows assigning all attentional weights (Duncan & Humphreys, 1989) or resources to that feature. Attending to both features requires the distribution of attentional weights or resources between the two, which is particularly the case when both features are representatives of two different feature dimensions (Müller & O'Grady, 2000). Consequently, SSVEP amplitudes decrease compared with those of the single-feature condition, and behavioral costs emerge, because the amount of assigned resources per feature is reduced.

Whether or not competition is an essential neural mechanism cannot be answered with our design and is subject to future studies. However, both mechanisms, sensory gain and biased competition, would reasonably support a division of attentional resources between color and rotation. The result of significantly different activation patterns in our topographies between the two SSVEP signals clearly indicates the activation of different

cortical areas or networks, most likely related to color and motion processing.

Despite this, the question remains: How can our results be explained in light of previous studies that demonstrated neural coactivation for task-irrelevant features of an object (see Schoenfeld et al., 2014; O'Craven et al., 1999)? In addition, how is the reduction of SSVEP amplitudes in the "attend to color and rotation" condition related to common findings of additive effects during attention to feature conjunctions (see Andersen, Hillyard, & Müller, 2008) or in visual search as suggested by the guided search model (Wolfe, 1994)? Primarily, it must be noted that, in our study, SSVEP amplitudes were greater in the to-be-ignored condition compared with the baseline/ reference condition ("attend fixation cross") as well. This effect results from object- and/or spatial-based processes, which are not distinguishable in our study. This is because the fixation cross is not only a different object than the square but also at a different location. Nonetheless, differences in SSVEP amplitudes between the three feature conditions ("attend to color," "attend to rotation," and "attend to color and rotation") suggest distinct feature-selective processes, which ought to be absent within objects based on the integrated object account. The most obvious explanation for this observation, which deviates from some previous studies (see Schoenfeld et al., 2014; O'Craven et al., 1999), are fundamental differences between object identification tasks and tasks concerning the object constituent features themselves, which in turn increases task relevance of the features. Under conditions of object identification, as is the case in visual search or when objects are superimposed upon each other, spreading of cortical activation across all areas that are linked to the processing of a certain feature of that object (see Schoenfeld et al., 2014) is an essential process of incremental grouping (Roelfsema, 2006). As a consequence of these joint activities, neural activation (measured by EEG) increases and conjunction search or identification results in additive effects (Andersen, Müller, & Hillyard, 2015; Andersen et al., 2008). These additive effects might even be supported in the presence of other objects in the visual display, because the to-be-ignored objects or features of these objects needed to be suppressed (Desimone & Duncan, 1995); that is, attentional resources are withdrawn from the to-be-ignored object (features) and allocated to the to-be-attended object (features).

If, however, only one single object without competitor is present, all resources are allocated to the constituting features of that object, and task relevance of one feature results in the shifting of attentional weights (Duncan & Humphreys, 1989) toward that feature. Two task-relevant features within one object require the division of these weights (with or without competitive interactions), without the possibility to sequester additional resources from competing objects. In our experiment, this resulted in the reduction of SSVEP amplitudes. Not only did the relevance of the to-be-attended feature play a crucial role in

this study, but also the instruction to ignore distracting target events of the irrelevant feature, which most likely affected intentional inhibitory processes. Intentional inhibition might counteract any otherwise possibly existent spreading of attention to the task-irrelevant feature. Further work is needed to explore the differences between object identification tasks (in the presence of competing objects) and feature-specific tasks within one object (in which features with different task relevance are present in the absence of competing objects). In addition, future research is needed to examine the time course of inhibitory and excitatory feature-selective processes and their interaction as well as the interaction of feature- and object-based selective processes.

Furthermore, our behavioral results differ from those of previous research (see Duncan, 1984). In line with our EEG findings, performance decreased and response criteria became less conservative when participants attended to two features, compared with only attending to one feature within one object, whereas, for example, Duncan (1984) demonstrated no behavioral costs for attending to two features within one object (even when participants were presented with one single object without a competitor). It is worth mentioning that decision factors may differ between the single- and double-feature tasks. To guarantee attention to both features throughout the whole task in the respective condition, targets were defined as the simultaneous occurrence of rotation and color events only. Therefore, participants were asked to monitor two targets simultaneously here, and it was not possible to assess the accuracy for single features in the "attend to both features" condition. Consequentially, loss of accuracy in this condition might partly reflect the different decision factors (reflected in a less conservative response criterion) and/or the need to monitor two kinds of targets simultaneously, which makes this condition more difficult. Future research is needed to rule out this possible explanation for the observed behavioral results. However, these behavioral results are perfectly in line with our findings of reduced neural processing resources when two features are task relevant.

A possible explanation for this conflicting finding compared with previous studies might be given by the encoding demand of the task-relevant feature. This explanation is based on a series of experiments conducted by Xu (2010). In this study, participants attended to object colors, and the processing of task-irrelevant object shapes was examined by fMRI responses from a brain area involved in shape representation. Results indicated processing of the task-irrelevant feature (shape), that is, object integration, only at a low color-encoding load, whereas it was attenuated or even suppressed at a high color-encoding load. Xu concluded that the magnitude of object-based processing of task-irrelevant features of an attended object is determined by the encoding demand of the task-relevant feature. This premise would plausibly suggest that demand was lower in Duncan's (1984)

experiment compared with ours. In Duncan's experiment, participants were presented with a box varying in size (small or large) and position of a gap in its contour (right or left). Participants were asked to report afterward either the size or position of the gap. Apart from potential confounds of attentional processing with STM in Duncan's experiment, it is certainly conceivable that the described task is considerably less demanding than the target detection in our experiment, which also was individually adjusted in difficulty per participant.

Altogether, our results are at odds with purely object-based, as well as spatial-based, models of attention but offer empirical evidence for the importance of features as units of attentional selection. This is even then the case when the entire object, consisting of multiple features, is within the attentional spotlight. Thus, our results suggest that attentional selection of feature dimensions is a general mechanism of selective attention, which can operate independently of spatial- or object-based attentional selection. Obviously, when object constituent features become task relevant, resources must be divided between all features. This differs from commonly observed additive effects under conditions of object selection and identification.

Acknowledgments

Note

1. For a more detailed description of this method, see Cohen and Gulbinaite (2017).

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