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Time matters: Feature-specific prioritization follows feature integration in visual object processing

Berit Brummerloh, Matthias M. Müller *

Department of Psychology, Leipzig University, Neumarkt 9-19, 04109, Leipzig, Germany

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ABSTRACT

Objects represent a fundamental selection unit of visual attention. However, at odds with the integrated competition account, our recent study demonstrated that attentional facilitation of constituent features does not spread automatically within an object, but instead depends on the specific task relevance of each feature. Here, we employed a novel experimental design, allowing simultaneous electrophysiological measurements of the allocation of attention to two distinct features (rotation and color) within one object (a square) during both trial-wise and block-wise cued shifts of attention. This was possible through the presentation of a square that evokes two distinct steady-state visual evoked potentials (SSVEPs) for its rotation and its color changes, respectively. Given the continuous oscillatory nature of SSVEPs, we were able to investigate the time course of neural activity in the early visual cortex of the human brain when subjects attended to one of the two features, compared to when the whole object was attended. This approach enabled us to uncover feature-based mechanisms of attention within one object, as well as their interaction with object-based mechanisms. Both behavioral and electrophysiological results indicate a biphasic process composed of an early transient integration of the constituent object features, followed by sustained mechanisms of feature selection with amplification of the to-be-attended feature, followed temporally by suppression of the to-be-ignored feature.

1. Introduction

Objects represent – along with locations and features – one of the fundamental selection units of visual attention (see e.g. Duncan, 1984; O'Craven et al., 1999; Scholl, 2001). A key prediction of object-based attention is the mandatory integration of all constituent features of an object, regardless of their task relevance (see Duncan, 1984; O'Craven et al., 1999). This integration is suggested to result from object features not competing with one another for the same processing resources (see Allport, 1971). Accordingly, task-irrelevant features may be processed automatically and at no cost when attention is directed to any feature of the same object. However, the capacity of the visual system is limited and the amount of information in typical visual scenes exceeds the amount of visual information that can be processed at a given moment (Desimone and Duncan, 1995). Therefore, visual attention normally acts as a cognitive filtering mechanism in order to select only behaviorally relevant information for processing.

In stark contrast to the integrated competition account, some recent studies have shown that attentional facilitation of constituent object features does not spread automatically across an object, but depends on the specific task relevance of each feature (Brummerloh et al., 2019; Freeman et al., 2014; Nobre et al., 2006; Wegener et al., 2014). Moreover, cognitive processing of object constituent features was also shown to be dependent on each feature's task relevance (Serences et al., 2009; Woodman and Vogel, 2008). These results indicate that object-based processing might resemble well known neural mechanisms of feature-based attention under certain circumstances (Maunsell and Treue, 2006).

Recently, Xu (2010) conducted a functional magnetic resonance imaging (fMRI) study in order to explain the seemingly conflicting results between the integrated competition hypothesis (Duncan, 1984) and findings that are in favor of task-relevant feature-specific priority in object processing (see above). In her study, Xu examined under which conditions object-based processing occurs. In three experiments, the processing of a task-irrelevant feature (shape) was examined while subjects were asked to attend to another feature (color) of the same object, which was manipulated in terms of its encoding demand. Processing was evaluated by measuring fMRI responses from a brain area involved in shape representation. Results indicated that object-based processing of task-irrelevant features of an attended object does exist but varies in its

* Corresponding author.
E-mail address: m.mueller@uni-leipzig.de (M.M. Müller).

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magnitude depending on the encoding demand of the task-relevant feature of the object and occurs only transient. This finding clearly suggests the existence of neural competitive interactions that are dependent and time-limited, but given the temporal sluggishness of the BOLD response, the exact time course of such effects remains unresolved.

A number of previous studies investigated the time course of neural interactions and dynamics in spatial-based (see e.g. Hopf and Mangun, 2000; Müller, 2008; Müller et al., 1998), object-based (see e.g. Serences et al., 2004; Ward et al., 1996) and also feature-based (see e.g. Andersen and Müller, 2010; Schoenfeld et al., 2007) attention. Some studies also integrated temporal neural dynamics of spatial-based attention in combination with object-based (see e.g. Egeth and Yantis, 1997; Yantis and Serences, 2003) and feature-based (see e.g. Hayden and Gallant, 2005; Hopf et al., 2004; Liu et al., 2007) attention. Nevertheless, up until present day, research that has considered temporal neural dynamics of feature-based attention in object processing is limited.

Schoenfeld et al. (2014) conducted a magnetoencephalography (MEG) study in which they examined the timing and sequencing of the activation of feature-specific cortical areas of task-relevant and task-irrelevant features within an object-based attention task. They demonstrated that attention to the task-relevant feature (motion or color) of the attended object (one of two superimposed moving dot arrays) resulted in increased activity in the respective feature-specific cortical area starting at around 150 ms after motion onset. This activation was followed, after approximately 60 ms, by an enhanced activity in the feature-specific cortical area of the task-irrelevant feature (color or motion). These results were interpreted as the neural basis for the binding of object constituent features into a unified perceptual construct. However, the study did not directly compare the magnitude of activity increase evoked by the task irrelevant compared to the task relevant feature dimension, and in what time scale those magnitudes did eventually deviate from each other based on feature specific processes. Furthermore, while moving dot arrays are indeed widely accepted as forming objects that are useful to study object-based attention - at least since the seminal work of Valdes-Sosa et al. (1998) - moving dot arrays still lack classical “objecthood” compared to “real” objects such as houses, faces or geometric figures, which are observed in everyday life (see e.g. O'Craven et al., 1999).

Our recent electroencephalographic (EEG) study sought to overcome such limitations by using a familiar single object, i.e., a rotating square, that periodically changed color to elicit distinct steady state visual evoked potentials (SSVEPs) for each feature, respectively (Brummerloh et al., 2019). We found facilitation of the to-be-attended feature and competitive interactions when both features (rotation and color) of the square became task-relevant. Our results were therefore in line with recent studies supportive of feature-specific facilitation within object processing (see above).

However, given that we cued our subjects before trial onset, our previous study did not conclude whether this facilitation was generated through amplification of the task-relevant feature only, or if it was accompanied by a suppression of the task-irrelevant feature. Furthermore, we were unable to extract temporal neural dynamics of attentional allocation to one of the features due to the pre-trial cueing.

Therefore, we have developed our methodology into an attentional shifting paradigm, by presenting the color changing, rotating square while subjects first attended to central fixation and then were cued to shift attention to either rotation, color or the entire object (i.e., rotation and color). Given the continuous oscillatory nature of SSVEPs, as has been well observed in previous studies (see Andersen and Müller, 2010; Forschack et al., 2017; Fuchs et al., 2008; Müller et al., 1998), we were able to analyze the time course of SSVEP amplitudes to uncover neural temporal dynamics of feature-based attention in object processing in the early visual cortex in near real time.

Another possible reason for conflicting results within the field of object processing (besides encoding demand as suggested by Xu (2010)) is stimulus presentation time, a potentially critical experimental parameter factor that may affect integrated feature processing or facilitation of the task-relevant feature. In fact, closer inspection of presentation times in several studies is suggestive of its relevance. As detailed in Table 1, studies with very short stimulus presentation times supported the integrated competition hypothesis (Duncan, 1984; O'Craven et al., 1999; Schoenfeld et al., 2014), while longer presentation times tended to support the view of feature-specific priority in visual object processing (Brummerloh et al., 2019; Freeman et al., 2014; Wegener et al., 2014). The only exception to this trend is a study by Nobre et al. (2006), presenting stimuli for only 150 ms but indicating feature-selective processes within objects. However, in this study a feature-specific negative priming paradigm was used, and, thus not the effects during the (short) presentation of the prime stimuli were in the focus. Since the prime and probe were delayed by more than 1000 ms, this adaptation interval probably allowed for the facilitation of long-term, feature-specific processes.

If presentation time was a critical factor, in our shifting paradigm, we would first expect transient feature integration, as predicted by the integrated competition hypothesis, followed by a sustained feature-selective process allowing perceptual prioritizing of the task-relevant feature. In one of our recent studies, in which we investigated neural temporal dynamics in a feature-based attentional shifting design, we reported a biphasic neural process consisting of amplification of the to-be-attended feature preceding suppression of the to-be-ignored feature (Andersen and Müller, 2010). If feature-based mechanisms follow feature integration, we would expect a similar temporal relationship between amplification and suppression during feature selection.

When it comes to attentional shifts, several studies report differences in shifting time between random trial-by-trial cueing and sustained cueing, i.e., constant cueing within an entire block (see e.g. Eimer, 1994; Hillyard et al., 1998; Mangun, 1995; Zopf et al., 2004). Contrary to block designs, trial-by-trial cueing involves additional cognitive processes such as identification and processing of the cue itself, which can result in delayed feature selection. Furthermore, some attentional processes seem to require rather sustained environments to allow the brain to adapt to a specific task. Studies that exemplify this need for a sustained environment are those that investigate the split of the attentional spotlight. Under conditions of longer stimulation and block-wise instructions, it is clearly demonstrated that the attentional spotlight can be divided into disparate locations (Müller et al., 2003), while short presentation times and trial-by-trial cueing suggest that the attentional spotlight has an

Table 1
Stimulus presentation times in studies of visual attention, examining feature processing within objects.

	indication	presentation time of stimuli
Duncan (1984)	integrated competition	experiment 1: Ø 79.2 ms (individually adjusted) experiment 2: $\frac{2}{3}$ 80 ms, $\frac{1}{3}$ 60 ms experiment 3: $\frac{1}{2}$ 70 ms, $\frac{1}{2}$ 80 ms experiment 4: $\frac{1}{2}$ 70 ms, $\frac{1}{2}$ 80 ms
O'Craven et al. (1999)	integrated competition	experiment 1: 675 ms experiment 2: 375 ms
Schoenfeld et al. (2014)	integrated competition	300 ms
Nobre et al. (2006)	task-relevant feature-specific priority in object processing	150 ms prime plus 1150 ms probe
Wegener et al. (2014)	task-relevant feature-specific priority in object processing	3200 ms plus 1000 ms response window
Freeman et al. (2014)	task-relevant feature-specific priority in object processing	2000 ms
Brummerloh et al. (2019)	task-relevant feature-specific priority in object processing	3500 ms

unitary beam (Heinze et al., 1994).

Taken together, these studies suggest that time is a crucial factor in many attentional settings. When it comes to feature-selective priority in visual object processing, this also seems to be the case. Therefore, our shifting design with frequency tagging of the object constituent features is a prime method to uncover the underlying temporal neural dynamics. To look further into the effect of this process, our subjects were divided into two different experimental designs: half were instructed to shift attention in a random trial-by-trial fashion, whereas the other half was instructed block-wise.

2. Material and methods

2.1. Participants

In total we recorded 50 young adults with normal color perception and normal or corrected-to-normal visual acuity that were either assigned to the block design or trial-by-trial cueing version of the experiment (see 2.2. and 2.3.). Out of all 50 subjects, 6 participated in both versions of the experiment, resulting in 28 recordings per version (trial-by-trial: 6 males, 1 left-handed, mean age 22 years (SD = 3.64, range 18–31)/block: 5 males, 1 left-handed, mean age 23.82 years (SD = 4.4, range 18–33)). Due to the novelty of our experiment, an estimation of the effect size and thereby an *a priori* power analysis was not feasible. However, a *post hoc* power analysis of both versions of the experiment will be reported subsequently (see 2.4. and 3.1.). All subjects received class credits or financial reimbursement (8 € per hour) for their participation and gave informed consent prior to testing. The study was approved by the local ethics committee (University of Leipzig) and was conducted in compliance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

2.2. Stimuli and tasks

Identical to our previous experiment (Brummerloh et al., 2019), we provided our subjects with an outlined square, rotating clockwise every 118 ms in steps of 10° of a circle (thereby driving an SSVEP at 8.5 Hz), and changing color from red to green every 176 ms (thereby driving a different SSVEP at 5.67 Hz) (see Figs. 1 and 3).

Stimuli were presented on a 19-inch CRT monitor at a resolution of 640-by-480 pixels, a color depth of 32 bits and a refresh rate of 85 Hz, all viewed at a distance of 80 cm. The side-length of the outer edges of the square corresponded to a visual angle of 6°, while the inner edges

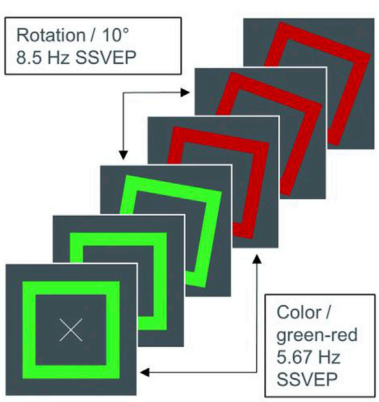

Fig. 1. Schematic representation of the stimulation. The square rotated in steps of 10 degrees of visual angle resulting in a frequency of 8.5 Hz while simultaneously changing color between red and green at a frequency of 5.67 Hz. Events were periods of speeded rotation and some blue added to the colors. The “X” in the middle of the screen is changing into an “R”, an “F”, or a “B” after about 1750 ms in each trial to cue the shift of attention to rotation, color, or both. The trial continued for 3000 ms. Note: Not to scale.

corresponded to a visual angle of 4°. Luminance of red and green was individually adjusted to the luminance of the gray background (3 cd/m^2) by means of heterochromatic flicker photometry (Wagner and Boynton, 1972).

Subjects were instructed to attend to the “X” in the middle of the screen and to detect target events there (see below) until the “X” changed into another letter (fixation cross task). After a jittered time window between 1500 and 2000 ms (mean 1750 ms), subjects were cued to shift attention to either rotation (here the “X” changed into an “R”), or to color changes (here the “X” changed into an “F” = “Farbe” in German), or to both features simultaneously (here the “X” changed into a “B”) and were asked to detect target events within the relevant feature-dimension. Half of the subjects was cued in a randomized trial-by-trial fashion, whereas the other half was instructed to shift attention in a block-wise manner, i.e., the shifting cue was the same for each trial within each block (see below). After the cue, trials continued for 3000 ms. In a control condition for both versions of the experiment, the letter did not change and subjects had to maintain attention at the point of fixation and to detect targets here for the entire trial. This condition was introduced to further control for cue expectancy effects (additional to the time jittered presentation). Each trial was followed by an interval between 1250 ms and 1750 ms with no square, but with the “X” continually displayed in the middle of the screen, which allowed the subjects to blink.

During the fixation cross task, the bars of the “X” changed length minimally for 176 ms (changes in length depended on individually adjusted difficulty – see 2.3.). Fixation cross targets were defined as a shortening of one of the bars, while a lengthening was defined as a distractor. Rotation targets were defined through an acceleration of rotation speed and color targets through some blue that was mixed into red and green (speed of rotation and amount of blue depended on the individually adjusted difficulty - see 2.3.). Both target types (rotation and color) lasted for 353 ms and occurred in the last time window of 3000 ms only. This was also true for trials in which subjects maintained attention to fixation. Subjects were instructed to respond to targets in the cued feature or location by pressing the spacebar, and were instructed to ignore changes in the uncued property (defined as ‘distractors’). For the combination task, i.e., “attend to rotation and color”, targets were defined as simultaneous changes of rotation and color, and distractors were defined as changes in only one of the properties.

The earliest onset of any event at the fixation cross occurred 353 ms after stimulation onset and for the square this was 353 ms after the cue. In each of the two time windows, i.e., before and after the cue, either none, one or two events could occur in each trial (resulting in overall 0 to 4 events per trial). To allow for an unambiguous assignment of responses, subsequent targets or distractors were separated by at least 706 ms between disappearance of the first and appearance of the next event.

2.3. Experimental procedure

Prior to EEG recordings, two or more blocks of training were performed. In the trial-by-trial design version, all four conditions (“attend rotation”, “attend color”, “attend rotation and color” and “attend fixation cross”) were included in random order in each block. In the block design, in contrast, each block contained one condition only. Thereby, in the block design, two or more training blocks had to be performed per condition. During the training blocks, difficulty was adjusted per subject until each reached a stable performance of at least 80% of hits, and less than two false alarms in each condition. The training started with a relatively easy setting, i.e., targets in the rotation task were rotating in steps of 35° (i.e., acceleration to 350% of the ongoing rotation), and 30% of blue (out of full blue) was added to red and green, respectively, in the color task. In the fixation cross task, the bars changed length by 15%. The difficulty was then increased (in rare cases of very low performance despite the relatively easy setting at the beginning, difficulty was decreased) stepwise until subjects reached a performance between 80 and 90% of hits and less than two false alarms in two consecutive training blocks. To guarantee that rotation and color tasks were identical in difficulty, performance was equalized on the individual level for those two tasks. The criterion was set to a maximum difference in hit rates of 5% between the two tasks in the training blocks. The combination task, i.e., "attend to rotation and color", was only practiced twice. In here, the difficulty was not adjusted but adopted from the two single tasks, i.e., "attend rotation" and "attend color", and training was performed only to familiarize subjects with the task.

After the adjustment procedure, 600 trials were recorded in both versions of the experiment, resulting in 150 trials per experimental condition as well as in the control task (i.e., maintain attention at fixation), respectively. Two thirds of the trials contained no targets or distractors after the cue, while one third of trials contained one or two events after the cue. The same was true for events in the pre-cue period. In the trial-by-trial design, trials were presented in 15 blocks of 40 trials each, in which trials were presented in randomized order. In the block design, the experiment was presented in 20 blocks of 30 trials each, and blocks were presented in randomized order. Each trial lasted 4.75 s on average with an inter-trial-interval of about 1.5 s (see 2.2.), resulting in a block duration of 4.14 min in the trial-by-trial design, and 3.1 min in the block design.

2.4. Analysis of behavioral data

Responses given within 200 to 1000 ms after target or distractor onsets were defined as hits or false alarms, respectively. The sensitivity index d' was calculated as a measure of performance (Stanislaw and Todorov, 1999). d' was then compared between the three experimental conditions, i.e., "attend rotation", "attend color", and "attend rotation and color", via a repeated-measures ANOVA. Given the hypothesized importance of time as a variable of feature processing within objects (see section 1.), this analysis was performed with a second within-subject factor (besides the experimental condition), namely time window in which the events appeared. This factor was subdivided into three different time windows: 1) the first 1000 ms after the cue, 2) the window between 1000 and 2000 ms, and 3) between 2000 and 3000 ms after the cue. There was no temporal overlap of events at the borders of the time windows. In addition, the design version (i.e., trial-by-trial and block wise cueing) was included as a between-subject factor in this analysis. When Mauchly's test indicated that the assumption of sphericity had been violated ($p \leq .05$), degrees of freedom were corrected using Greenhouse-Geisser (G-G) estimates of sphericity.

Provided that we found a significant interaction of the two within-subject factors in this ANOVA (i.e., "experimental condition" and "time window"), indicating that differences between experimental conditions depend on the time window where the events appeared, three further repeated-measures ANOVAs were performed, one for each of the three time windows (separately for trial-by-trial and block wise cueing). These three ANOVAs were Bonferroni corrected to counteract the problem of multiple comparisons. Bonferroni corrected *post hoc* tests were executed to identify details of the differences.

Besides the sensitivity index d', we also analyzed reaction times of the responses. Importantly, as an inherent characteristic, reaction times to rotation targets were always slower compared to those for color targets. This is due to the fact that rotation targets could only be detected after the square had been observed to rotate faster, i.e., after 118 ms, whereas color targets could be detected immediately. Given this, reaction times were not compared between attentional conditions.

Finally, behavioral data were compared between the two versions of the experiment in order to prove that performance did not differ between trial-by-trial and block design. In this step, d' values as well as reaction times were compared between the two design types. Given that we tested for the null hypothesis, for this comparison, Bayes factors for dependent-group designs were computed (Rouder et al., 2009) via Gaussian quadrature, using the function ttestBF from the R package BayesFactor v0.9.12–2 (Morey et al., 2018). A non-informative Jeffreys prior was placed on the variance of the normal population (Jeffreys, 1961), while a Cauchy prior with a width of $\sqrt{\{2\}}/2$ was placed on the standardized effect size (Morey and Rouder, 2011; Morey et al., 2011; Rouder et al., 2012). Jeffreys (1961) categorization for the grade of evidence was used for the interpretation of Bayes factors.

However, it might be possible that performance and velocity differences, or the absence of any differences, between the two designs are not caused by the designs themselves, but rather by the difficulty of the rotation or color targets. The difficulty of the rotation and color targets was adjusted individually for each subject as described above (see 2.3.) and the difficulty level could differ between the two experimental designs. To explore this alternative explication for the presence or absence of performance and velocity differences between the two experimental designs, and to examine if both designs had the same difficulty, configurations of the rotation and color targets were compared between the two designs via Bayes factors for dependent-group designs (see above).

2.5. Electrophysiological recording and analysis

Brain electrical activity was recorded noninvasively via 64 individual Ag/AgCl electrodes mounted in an elastic cap, with measurements recorded at a sampling rate of 256 Hz using an ActiveTwo Amplifier (BioSemi, Amsterdam). Data were referenced to the CMS-electrode ("Common Mode Sense", see https://www.biosemi.com/faq/cms&drl.htm) during recording. Lateral eye movements were monitored via two electrodes placed at the canthi of both eyes (horizontal electrooculogram), and vertical eye movements and blinks were monitored via two electrodes placed below and above the right eye (vertical electrooculogram). The EEGlab toolbox (Delorme and Makeig, 2004) and custom Matlab scripts (The MathWorks, Natick, MA) were used for offline data analysis. First, data were epoched from −1500 to 3000 ms relative to the onset of the cue, i.e., the change of the "X" into "R", "F" or "B". Only these trials were included in the final analysis, whereas trials in which subjects maintained attention to fixation were excluded from the final analysis.

Furthermore, only trials without any events after the cue entered the EEG analysis, in order to avoid potential influence of events and subsequent decisional or motor processes. Importantly, smaller changes in the fixation cross were not expected to elicit an equally huge event related potential (ERP), which would otherwise distort the ongoing SSVEP, so in the pre-cue baseline period, trials with and without events were both included. For the epoched time windows, diverse types of artifacts were identified, and contaminated trials were excluded, or data were interpolated with an automated procedure. First, linear drifts were corrected via detrending. Subsequently, trials containing blinks or eye movements were rejected based on a threshold procedure (blinks: adaptive threshold (mean = 179.4 μV, SD = 133.81) in vertical electrooculogram/eye movements: threshold of 25 μV in electrooculogram). Thereafter, the "statistical control of artifacts in dense array EEG/MEG studies" (Junghöfer et al., 2000) was applied and based on the statistical parameters of the data, channel data were interpolated or, in the case of noise-contamination of at least ten neighboring data channels, trials were excluded. Overall an average of 21.86% of trials (SD = 10.04) was excluded from the analysis and on average, 3.54 channels were interpolated per trial of those trials with interpolations (SD = 0.98). Data were then re-referenced to average reference and averaged for each subject in each version of the experiment and in each experimental condition separately.

Subsequently, analyses were executed separately for the two stimulation frequencies as well as for the trial-by-trial design and the block design. However, both frequencies and both designs were analyzed with an identical set of procedures. Base-to-peak SSVEP amplitudes were calculated by means of a Fourier transformation over a time window of 500 ms to 3000 ms after cue onset for the two stimulation frequencies (the first 500 ms after the cue were discarded to exclude the ERP to the cue). Bearing in mind individual variations in subjects' topographical distributions, we applied a 'best electrode' selection for further SSVEP

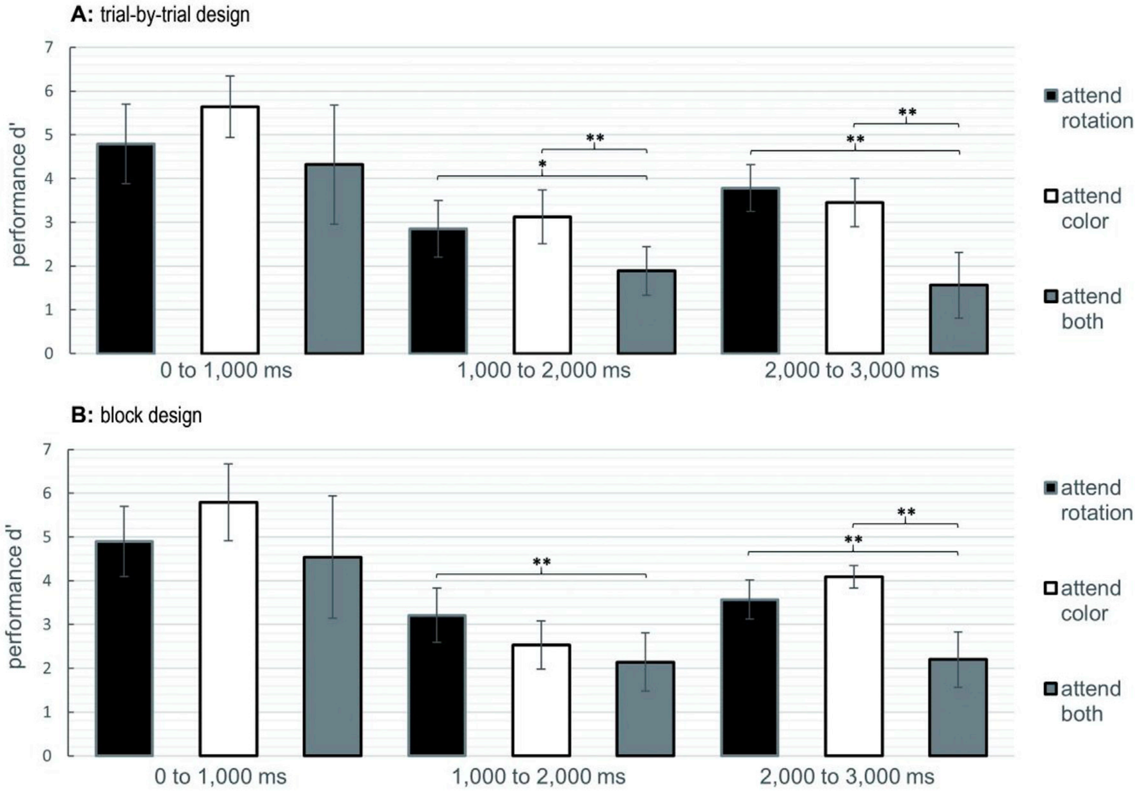

Fig. 2. Performance d' in the three different experimental conditions ("attend rotation", "attend color" and "attend both"), averaged across all subjects, separately for each design version (**A**: trial-by-trial cueing and **B**: block-wise cueing) and for each of the three temporally non-overlapping time windows in which events did appear (i.e., 0 to 1000 ms after the cue, 1000 to 2000 ms after the cue and 2000 to 3000 ms after the cue). Error bars represent the standard deviations of the means. $^{*}p \leq .05$ and $^{**}p \leq .01$ for Bonferroni corrected post hoc tests of the conducted repeated-measures ANOVAs.

analyses (Bekhtereva and Müller, 2017; see e.g. Fuchs et al., 2008; Gulbinaite et al., 2014; Malinowski et al., 2007).

Given the core finding of our most recent study that features can be selectively attended within objects (Brummerloh et al., 2019), which is in line with some other recent studies (see Xu, 2010)), we focused on the time course of the attentional effects within this study. The time course of SSVEP amplitudes was quantified via a Gabor filter (Gabor, 1946) centered at the respective stimulation frequency (8.5 Hz for rotation and 5.67 Hz for color). These time courses were extracted from the individual best electrode (out of a broad occipital-parietal electrode cluster – see Fig. 4) showing the maximum attentional modulation (i.e., activity when the respective object feature was attended minus unattended) based on the Fourier transformation described above. This electrode selection was chosen to maximize the existing attentional effects based on two reasons: (1) generally smaller effects in shifting experiments compared to non-shifting designs (see e.g. Fig. 2c Andersen and Müller (2010) versus Fig. 1c Müller et al. (2006), showing smaller effects in the first case despite same analyses and same designs except being a shifting design in the first case), and (2) the necessity of relatively huge effects for being able to analyze SSVEP time courses. Bearing in mind that the feature-based attention effect within objects was already shown with the very same stimuli and tasks (Brummerloh et al., 2019), and the fact that we are focusing on the time course of the effects and not on the effect itself, this procedure seems legit in this case.[1] In addition, it should be noted that electrodes were chosen based on the difference between an object feature being attended versus unattended but the main analyses, as stated below, predominantly refer to the difference between an object feature being attended or unattended versus the whole object being attended. The determination of the occipital-parietal electrode cluster from which the individual best electrodes were chosen was performed in order to limit the effects to early visual attentional processes (see e.g. Fuchs et al., 2008).

Gabor filters had a frequency resolution of ±1 Hz full width at half maximum, resulting in a time resolution of ±220.6 ms. This is the reason we changed the stimulation frequencies (needed to be separated by at least 2 Hz for this analysis) compared to our previous study (Brummerloh et al., 2019). Note that all references to time points of SSVEP amplitudes refer to the Gabor-filtered data and are therefore affected by the temporal integration of the filter (±220.6 ms). To characterize the attentional effect in terms of feature-selective SSVEP amplitude modulations, SSVEP time courses were normalized by subtracting the amplitudes determined for attending to both features from each data point. This was done for both conditions (i.e., when the respective feature was attended or unattended) separately. This allowed us to directly contrast representations of each feature when attention was allocated to the whole object as opposed to when attention was allocated to either of the two features within the object. Another advantage of this normalization is the included removal of the ERP to the cue (which should be identical in all experimental conditions - see Fig. 6 for the unnormalized time courses) from the SSVEP time courses. For statistical analysis of SSVEP amplitude time courses, we performed one-tailed t-tests against zero for each sampling point in the time range from −500 until 3000 ms relative to cue onset. Significant differences were corrected for multiple comparisons via a cluster correction procedure based on Monte Carlo simulations (see Maris and Oostenveld, 2007). Only clusters that had a summed t-value greater than the maximum summed t-values of 95% of 5000 random permutations were interpreted as significant amplitude modulations. The onset of amplitude increase or decrease was defined as the first significant

[1] We discussed that matter with a number of EEG experts on several conferences where we presented parts of this experiment. All of them reassured us that this approach is legit to extract the time courses of our effects.

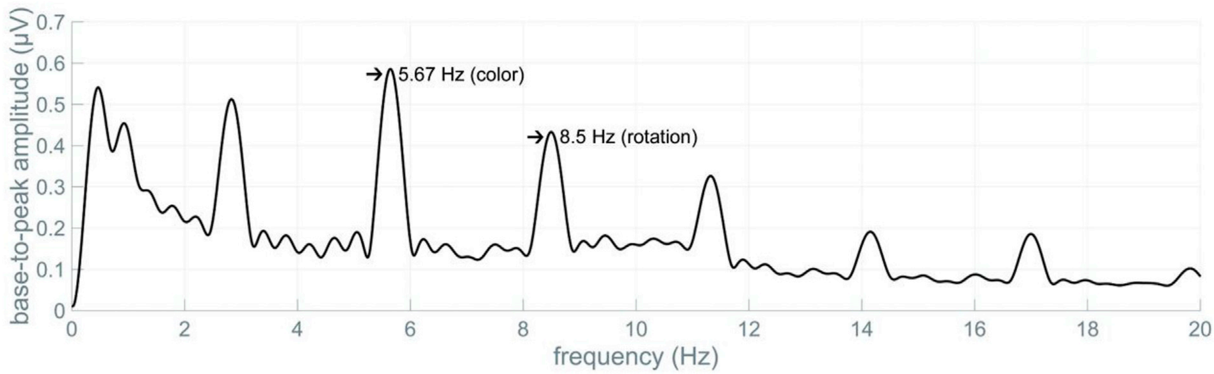

Fig. 3. Grand mean spectral power across all subjects (trial-by-trial design and block design) and across all experimental conditions ("attend rotation", "attend color" and "attend rotation and color"), averaged across an occipital-parietal electrode cluster (electrodes: I1, Iz, I2, O1, Oz, O2, PO7, PO3, POz, PO4, PO8, P9, P7, P5, P3, P1, Pz, P2, P4, P6, P8, P10 – see Fig. 4) from 500 to 3000 ms after the cue.

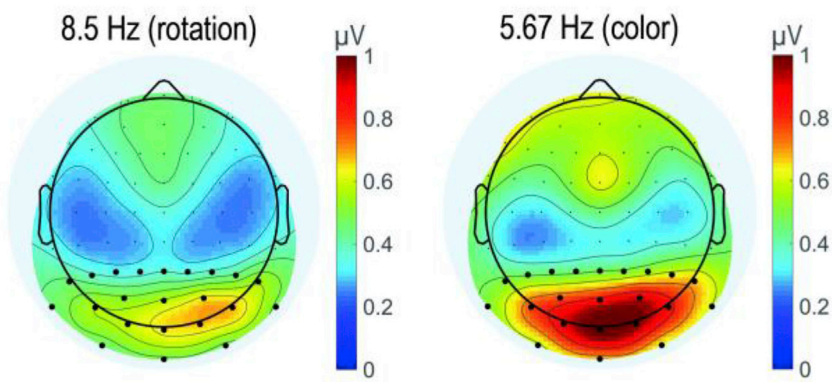

Fig. 4. Topographical distributions of SSVEP amplitudes averaged across all subjects (trial-by-trial design and block design) and across all experimental conditions ("attend rotation", "attend color" and "attend rotation and color") from 500 to 3000 ms after the cue. SSVEP topography for rotation (8.5 Hz) on the left, for color changes (5.67 Hz) on the right. Dots represent electrodes. Bold dots represent the broad posterior cluster from which the power spectrum of Fig. 3 was calculated and from which the individual best electrodes were chosen for the time course analyses of SSVEP signals.

sampling point after cluster correction. Sustainability of these effects was tested via a one-tailed *t*-test of the mean amplitudes from onset of amplitude increase or decrease until 2500 ms after cue onset against zero (the last 500 ms were discarded in order to exclude possible attentional drifts to trial end, and because the Gabor filter entered the inter-trial-interval without SSVEPs).

To visualize the attentional effects in all experimental conditions, SSVEP time courses were additionally extracted without the described normalization process (bearing in mind that these time courses entail the ERP to the cue). To statistically test neural dynamics in the first time window after cue onset, in particular to test if amplitudes were identical when the respective feature was attended or unattended (i.e., if features were integrated during this first time period), mean amplitudes of the "attend rotation" and "attend color" condition, from cue onset until the earliest amplitude increase, were compared via Bayes factors for dependent-group designs (see above).

A *post hoc* power analysis, based on the effect sizes of the described sustainability tests, was performed to compute the statistical power achieved (performed using G × Power software).

3. Results

3.1. Behavioral data

Hit rates and false alarm rates indicate that subjects were able to solve all three tasks ("attend rotation", "attend color" and "attend both") sufficiently and were attending to the instructed feature(s) in both experimental design versions (see Table 2).

The repeated-measures ANOVA analyzing d' differences, with the between-subject factor "design version" and the two within-subject factors "experimental condition" and "time window", revealed two main effects (condition: $F(2,108) = 31.03$, $p \le .001$, $\eta_p^2 = 0.37$, time: $F(1.63,87.79) = 128.9$, $p \le .001$, $\eta_p^2 = 0.71$ (sphericity violated: $\chi^2(2) = 13.86$, $p \le .05$, G-G corrected: $\varepsilon = 0.81$), as well as an interaction between the two within-subject factors ($F(2.73,147.4) = 4.59$, $p \le .01$, $\eta_p^2 = 0.08$ (sphericity violated: $\chi^2(9) = 44.95$, $p \le .05$, G-G corrected: $\varepsilon = 0.68$)). There was no interaction between any of those effects and the version of the experimental design (condition × design: $F(2,108) = 0.46$, $p = .63$, $\eta_p^2 = 0.01$, time × design: $F(1.63,87.79) = 0.64$, $p = .5$, $\eta_p^2 = 0.01$, condition × time*design: $F(2.73,147.4) = 1.37$, $p = .26$, $\eta_p^2 = 0.03$).

Based on the significant interaction between the experimental condition and the time window in which the events occurred, subsequently, additional repeated-measures ANOVAs were carried out for each time window separately. As listed in Table 2 and visualized in Fig. 2, the ANOVAs and the *post hoc* comparisons resulted in non-significant differences between the three experimental conditions within the first time window (0–1000 ms), for both trial-by-trial and block-wise cueing. In the second time window (1000–2000 ms), d' values in trial-by-trial cueing were significantly greater for rotation and color events in the single target condition compared to the dual target condition, while for block-wise cueing this was only true for rotation events. In the third time window (2000–3000 ms), for both experimental designs single color and rotation events revealed significantly greater d' values compared to when both features needed to be attended.

Results of the comparison between the two design types are detailed in Table 2. The respective comparison of performance (d') and reaction times resulted in substantial evidence in favor of the null hypothesis, according to the computed Bayes factors, indicating that task performance and speed is identical between trial-by-trial and block-wise cueing. One exception from this finding is the "attend both features" condition; the resulting Bayes factor from the comparison of d' in both

Table 2
Behavioral data and subsequent analyses across all subjects, separately for trial-by-trial and block design and for the three experimental conditions ("attend rotation", "attend color" and "attend both features"). Bold font denotes statistical significance ($p \leq .05$).

		attend rotation		attend color		attend both		ANOVA	post hoc tests	Bayes statistics
		mean	SD	mean	SD	mean	SD			
hit rate in %	trial	84.71	8.65	92.59	6.38	81.63	15.37			
	block	81.76	13.67	89.26	8.2	86.9	13.53			
false alarm rate in %	trial	10.97	5.83	7.21	5.41	15.74	6.47			
	block	10	6.09	8.12	6.35	13.25	7.5			
performance d' (0–1000 ms after the cue)	trial	4.79	1.82	5.64	1.4	4.32	2.72	$F(1.61,43.46) = 2.83$, $p = .24$, $\eta_p^2 = 0.1$ (sphericity violated: $\chi^2(2) = 7.23$, $p \leq .05$, G-G corrected: $\varepsilon = 0.81$)	rotation vs color: p = .14 color vs both: p = .12 rotation vs both: p ≥ .99	
	block	4.9	1.6	5.79	1.75	4.54	2.79	$F(1.53,41.23) = 2.77$, $p = .26$, $\eta_p^2 = 0.09$ (sphericity violated: $\chi^2(2) = 9.64$, $p \leq .05$, G-G corrected: $\varepsilon = 0.76$)	rotation vs color: p = .13 color vs both: p = .23 rotation vs both: p ≥ .99	
performance d' (1000 to 2000 ms after the cue)	trial	2.85	1.3	3.12	1.23	1.89	1.11	**$F(2,54) = 7.81$, $p \leq .01$, $\eta_p^2 = 0.22$**	rotation vs color: p ≥ .99 **color vs both: p ≤ .001** **rotation vs both: p ≤ .05**	
	block	3.21	1.24	2.53	1.1	2.14	1.33	**$F(2,54) = 8.15$, $p \leq .01$, $\eta_p^2 = 0.19$;**	rotation vs color: p = .06 color vs both: p = .62 **rotation vs both: p ≤ .01**	
performance d' (2000 to 3000 ms after the cue)	tiral	3.78	1.07	3.45	1.5	1.56	1.11	**$F(2,54) = 22.25$, $p \leq .001$, $\eta_p^2 = 0.45$**	rotation vs color: p ≥ .99 **color vs both: p ≤ .001** **rotation vs both: p ≤ .001**	
	block	3.57	0.9	4.09	0.52	2.2	1.26	**$F(2,54) = 28.95$, $p \leq .001$, $\eta_p^2 = 0.52$**	rotation vs color: p = .08 **color vs both: p ≤ .001** **rotation vs both: p ≤ .001**	
performance d'	trial	2.38	0.54	3.3	0.9	2.24	0.9			rotation: BF10 = 0.25 ± 0.01% color: BF10 = 0.25 ± 0.01% both: BF10 = 2.07 ± 0%
	block	2.51	0.86	3.14	1.1	2.76	1.03			
reaction time in ms	trial	638.68	60.44	543.14	50.08	642.97	68.73			rotation: BF10 = 0.21 ± 0.01% color: BF10 = 0.27 ± 0.01% both: $BF_{10} = 0.21 \pm 0.01\%$
	block	645.88	72.05	530.42	58.24	637.18	60.82			

Note: All time windows represent temporally non-overlapping onsets of respective events. trial = trial-by-trial cueing; block = block-wise cueing.

experimental design types was pointing towards existing differences here. However, this Bayes factor was so small that it would be categorized as "barely worth mentioning" according to Jeffreys (1961).

To exclude the possibility that results of the performance comparison were caused by different adjusted difficulties in the two design types, we also compared the adjusted difficulties. On average, the ongoing rotation was accelerated to 261.79% (SD = 78.27) of its original speed in the trial-by-trial design and to 270% (SD = 64.29) of its original speed in the block design during rotation events. The computed Bayes factor for the comparison of those two values indicated substantial evidence in favor of the null hypothesis (BF10 = 0.23 ± 0.01%), indicating no difference in difficulty in this task between the two designs. For color events, on average 11.8% (SD = 8.05) of full blue was mixed into red and green in the trial-by-trial design, and 10.29% (SD = 6.02) in the block design. As for the rotation tasks, adjusted difficulty did not differ between design types for the color tasks, according to Bayes statistics (BF10 = 0.26 ± 0.01%)

3.2. Electrophysiological data

Fig. 3 illustrates the spectral power between 0 and 20 Hz for a broad occipital-parietal cluster (see bold locations in Fig. 4) averaged across all subjects and all experimental conditions. The resultant spectrum shows two decisive peaks at 5.67 Hz (evoked by color changes) and 8.5 Hz (evoked by rotation).

Fig. 4 shows the topographical distributions of grand mean SSVEP amplitudes for both stimulation frequencies. The topographical distribution of SSVEP amplitudes elicited by color changes appears to be more central and more distinct than the one elicited by rotation. However, both topographies exhibit maximal amplitudes in the area of the posterior electrode cluster, from which the individual best electrodes for the following analyses were chosen.

Fig. 5 depicts the normalized time courses of SSVEP amplitudes of both design versions of the experiment, separately for color (5.67 Hz) and

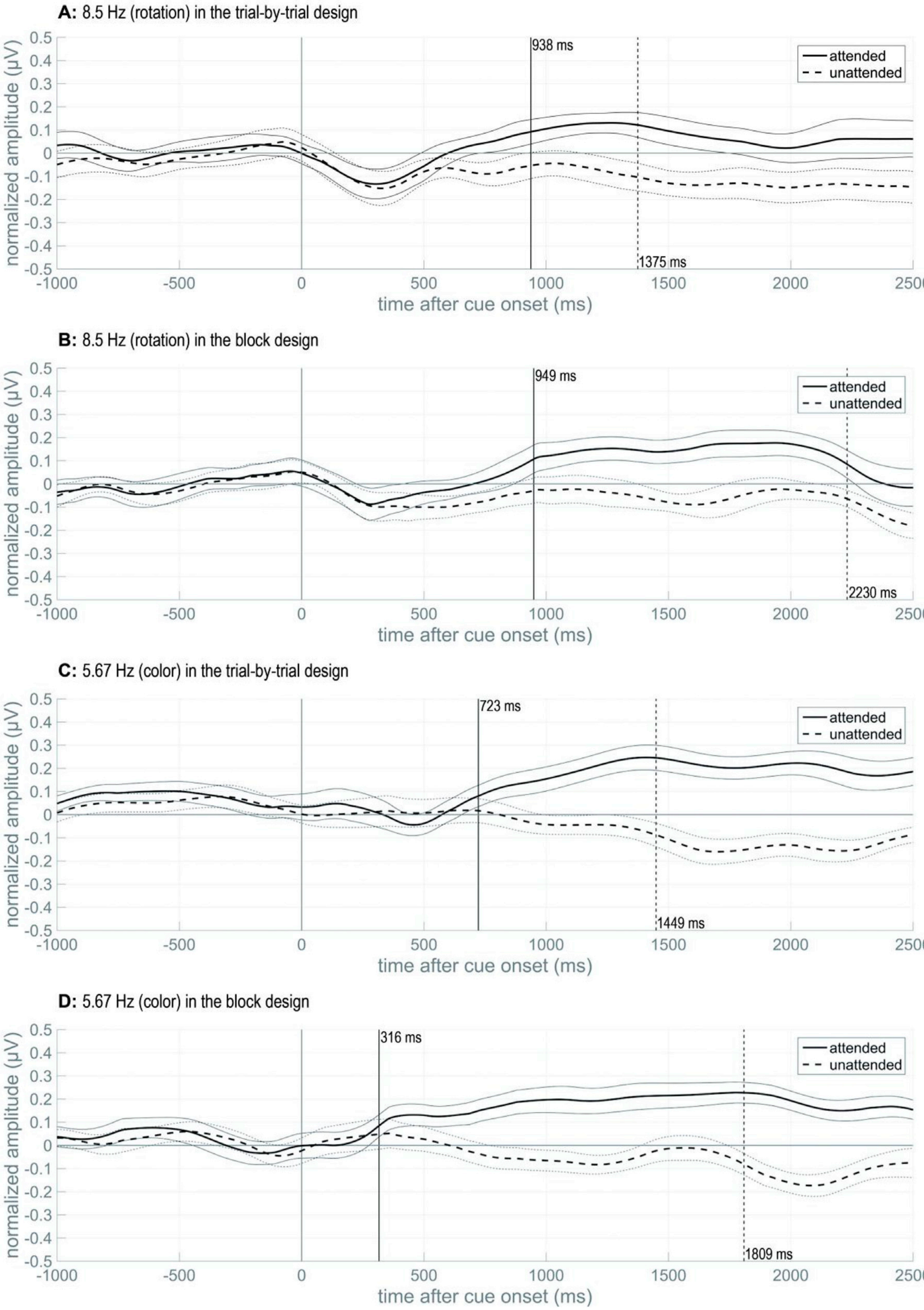

Fig. 5. Time courses of the SSVEP amplitudes normalized by subtracting the amplitudes of attending both features, i.e., the entire object, from each data point, respectively. (A) Rotation (8.5 Hz) with trial-by-trial cueing, (B) rotation (8.5 Hz) with block-wise cueing, (C) color (5.67 Hz) with trial-by-trial cueing, (D) color (5.67 Hz) with block-wise cueing. Solid lines represent when that feature was the to-be-attended feature, dashed lines when it was the to-be-ignored one, respectively. Thinner lines correspond to the standard errors of the mean. Vertical lines represent onsets of the significant differences from zero, revealed from the cluster corrected running t-tests ($p \leq .05$). Time-point zero indicates onset of the cue.

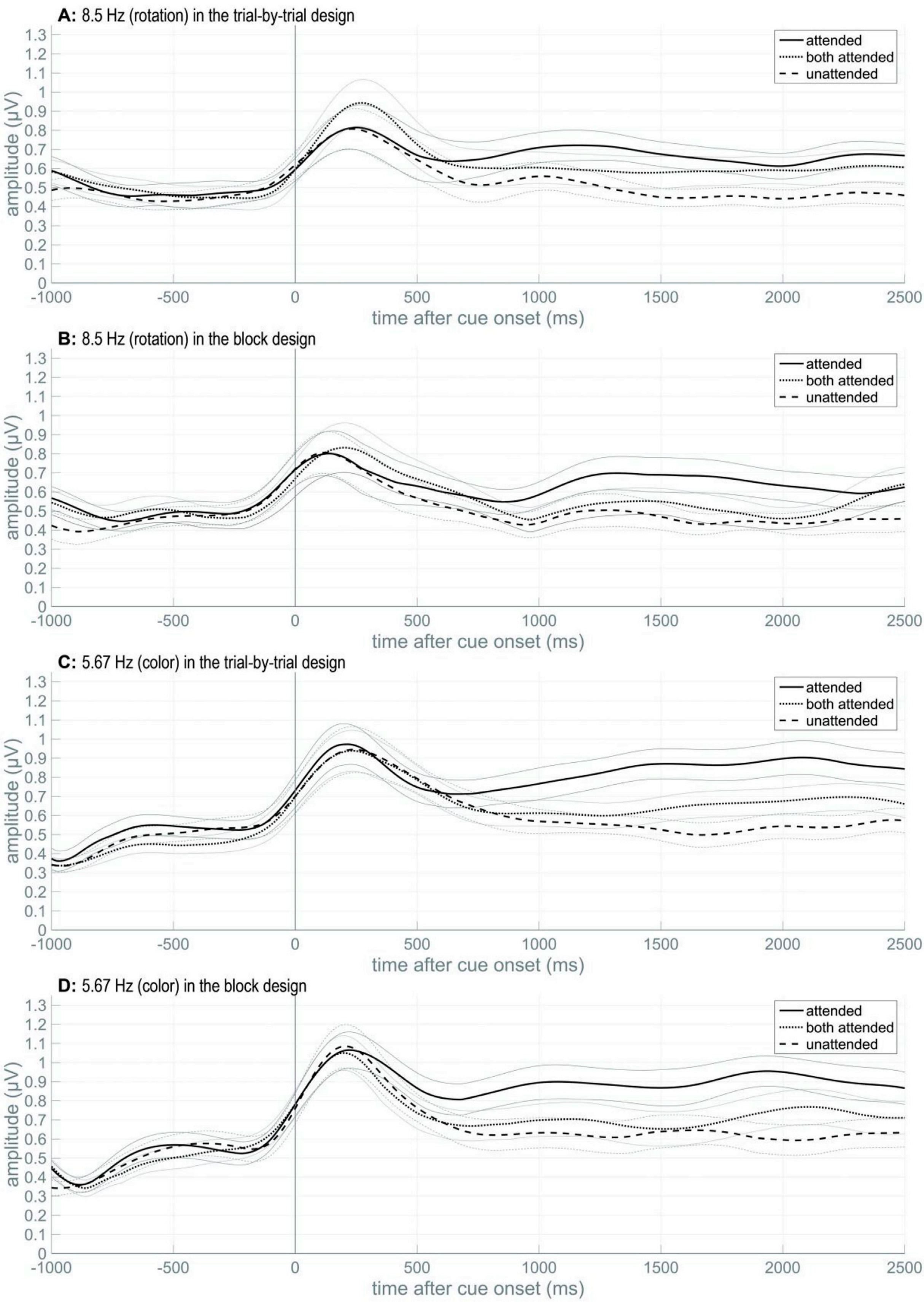

Fig. 6. Time courses of the unnormalized SSVEP amplitudes. (A) Rotation (8.5 Hz) with trial-by-trial cueing, (B) rotation (8.5 Hz) with block-wise cueing, (C) color (5.67 Hz) with trial-by-trial cueing, (D) color (5.67 Hz) with block-wise cueing. Solid lines represent when that feature was the to-be-attended feature, dashed lines when it was the to-be-ignored one, respectively. And dotted lines represent the condition where both features (i.e., the whole object) had to be attended. Thinner lines correspond to the standard errors of the mean. Time-point zero indicates onset of the cue.

for rotation (8.5 Hz), both when the respective feature was attended and when it was unattended.

In all cases, the to-be-attended feature elicits an SSVEP amplitude augmentation relative to when both features needed to be attended after a few hundred milliseconds (solid lines). Consequently, we found a significant increase of SSVEP amplitudes for all conditions (see below). Interestingly, the to-be-ignored feature maintains amplitudes fluctuating closely underneath the zero line, i.e., exhibiting more or less the identical SSVEP amplitude as if that feature was attended in the “attend both features” condition. Only after more than a second following the cue, the SSVEP amplitudes for the to-be-ignored feature decrease significantly below zero.

Table 3 lists the first time points of significant differences from SSVEP amplitude time courses against zero, representing onsets of amplitude increase or decrease, which derived from the cluster corrected running t-tests.

When we tested averaged SSVEP amplitudes from the onset of amplitude modulation to the end of the epoch (i.e., 2500 ms after cue onset), one-tailed t-tests confirmed the sustainability of all effects (increase: rotation trial-by-trial $(27) = 2.04$, $p \leq .05$, $d = 0.39$; rotation block $t\ (27) = 3.03$, $p \leq .01$, $d = 0.57$; color trial-by-trial $t\ (27) = 5.36$, $p \leq .001$, $d = 1.01$; color block $t\ (27) = 6.35$, $p \leq .001$, $d = 1.2$/decrease: rotation trial-by-trial $t\ (27) = -2.59$, $p \leq .01$, $d = -0.49$; rotation block $t\ (27) = -2.77$, $p \leq .01$, $d = -0.52$; color trial-by-trial $t\ (27) = -3.59$, $p \leq .001$, $d = -0.68$; color block $t\ (27) = -3.08$, $p \leq .01$, $d = -0.58$).

As predicted, trial-by-trial cueing resulted in much later onset times for the increase of the to-be-attended feature (Ø 831 ms) compared to block-wise cueing (Ø 633 ms). Interestingly, this effect reversed for the much later SSVEP amplitude decrease when the respective feature had to be ignored. Besides, feature-based processes started earlier when it comes to color processing compared to rotation. This holds true for both the amplitude increase of the to-be-attended feature (color: Ø 520 ms, rotation: Ø 944 ms) and the amplitude decrease of the to-be-ignored feature (color: Ø 1629 ms, rotation: Ø 1803 ms).

Fig. 6 illustrates the SSVEP amplitude time courses before their normalization, separately for color (5.67 Hz) and for rotation (8.5 Hz), and for both experimental design versions. Time courses for all experimental conditions, i.e., when the respective feature was attended, when it was unattended and when both features were attended, are depicted. In all cases, amplitudes increased after the onset of the cue for all experimental conditions. Bayes statistics, testing differences between the mean SSVEP amplitudes of the “attend rotation” and “attend color” condition, during the first time window, from cue onset until the earliest amplitude increase (i.e., 316 ms after cue onset), revealed substantial evidence in favor of the null hypothesis, i.e., no differences between mean amplitudes when the respective feature was attended or unattended (rotation trial-by-trial $BF10 = 0.2 \pm 0\%$; rotation block $BF10 = 0.2 \pm 0\%$; color trial-by-trial $BF10 = 0.23 \pm 0.01\%$; color block $0.2 \pm 0\%$). After the homogenous increase of all three time courses, several hundred milliseconds later, time courses are drifting apart from each other dependent on which object feature(s) was/were attended.

The *post hoc* power analyses revealed adequate statistical power in both versions of our experiment (trial-by-trial: power = 0.95, block: power = 0.98), based on the effect-sizes of the one-tailed t-tests of the averaged SSVEP amplitudes (trial-by-trial Ø $d = 0.64$, block: Ø $d = 0.72$), as described above.

Table 3
Onset of SSVEP amplitude modulations relative to the condition when subjects attended to the entire object, i.e., both features. Left column onset of SSVEP amplitude increase, right column onset of SSVEP amplitude decrease, relative to cue onset, respectively. All time points refer to running *t*-test data after cluster correction for multiple comparisons. Averages are given in the last lines, respectively.

		onset SSVEP amplitude increase in ms after the cue	onset SSVEP amplitude decrease in ms after the cue
8.5 Hz	trial	938	1375
(rotation)	block	949	2230
5.67 Hz	trial	723	1449
(color)	block	316	1809
average	rotation	944	1803
	color	520	1629
	trial	831	1412
	block	633	2020
	overall	732	1716

Note: trial = trial-by-trial cueing; block = block-wise cueing.

4. Discussion

The present work seeks to investigate temporal neural dynamics of feature-based attention in visual object processing. As outlined in the introduction, a number of studies have reported prioritization of the task-relevant feature in visual object processing, at odds with the integrated competition account that suggests that both the task-relevant and task-irrelevant features of an object will be processed together without specific prioritization (see Duncan, 1984; O'Craven et al., 1999). In our previous study (Brummerloh et al., 2019), we used frequency tagging of two features within one object, allowing us to analyze SSVEPs, elicited by continuous rotation and simultaneous color changes. In line with previous research, we found greater amplification of the to-be-attended feature as opposed to the to-be-ignored feature. We reasoned that one possible explanation for inconsistent results might be the processing time within the respective experiments. Indeed, as detailed in Table 1, studies with very short presentation times were in favor of the integrated competition account, while studies with longer object exposure and/or processing time resulted in task-relevant feature prioritization. Given this trend, we further hypothesized it might be very likely that feature prioritization follows an early feature integration process within objects.

From our previous studies (see Andersen and Müller, 2010; Fuchs et al., 2008; Müller et al., 1998; Müller, 2008), we knew that frequency tagging provides a precise tool to investigate temporal neural dynamics in early visual cortical areas in the human brain. To determine temporal neural dynamics of feature-based attention in visual object processing, we refined our design of a rotating square that simultaneously changed color (Brummerloh et al., 2019) into an attentional shifting experiment. In either a trial-by-trial or a block-wise cueing design, subjects first attended to a central fixation cross and then shifted attention to rotation, to color or to the entire object (i.e., to both rotation and color) and detected target events at the cued feature(s) for a period of 3 s. Our results are suggestive of a biphasic process of early integration of all object constituent features after the cue, followed by feature selection, with facilitation (amplification) of the to-be-attended feature first that was then followed by the suppression of the to-be-ignored feature at a much later latency. As predicted, facilitation of the to-be-attended feature occurred earlier after the cue in the block design than in the trial-by-trial design. Importantly, behavioral data followed the biphasic process with no differences in d’-values during early integration, followed by significantly reduced d’-values when subjects attended to the whole object, i.e., both features, compared to when they needed to attend to only one feature.

While we have successfully addressed a basic neural principle of visual object processing when a feature of that object becomes task-relevant, it is worth noting a limitation of our study that the absolute latencies as we have found them here may vary depending on several extraneous factors, such as the temporal resolution of our Gabor filters. Another crucial factor might be complexity of the visual object, and thus, the number of its constituent features and their relative saliency. The number of constituent features of an object that become task-relevant may also affect the absolute latencies. Given these considerations, we will not focus on the exact onset and duration of a certain process but will extrapolate the underlying neural mechanism from relativities instead. Besides, given our frequency tagging design, it is worth noting that the neural mechanisms discovered here are located in early visual areas (see e.g. Di Russo et al., 2007). It is unknown to what extent the SSVEP transmits to higher cortical areas such as prefrontal or parietal areas. Therefore, we refrain from speculations regarding the contribution of these areas to our results.

When subjects shifted attention from the central fixation cross to the square, SSVEP amplitudes were modulated by this shift of attention (visible in a homogenous increase of SSVEP amplitudes after cue onset in all experimental conditions – see Fig. 6). The first roughly 500 ms after the cue, however, run the risk that SSVEP amplitude increases are partially influenced by the ERP to the cue, given that the ERP has some spectral power in the frequency bands of the used Gabor filters. Thereby, unnormalized SSVEP amplitudes might be overestimated during this first period. Yet, this ERP is independent from the experimental conditions. Bayes statistics indicate, by supporting the null hypothesis, that there are no differences between amplitudes when the respective object feature was attended or unattended in the first time window after cue onset until the earliest amplitude increase. By subtracting the "attend both features" condition, we were able to eliminate that possible confound as can be seen in Fig. 5. Similar to the Bayes analyses of unnormalized time courses, normalized SSVEP amplitudes did not differ significantly from zero when subjects shifted attention to rotation or color during the first time period after cue onset (on average 831 ms for trial-by-trial and 633 ms for block design – see Table 3). In other words, SSVEP amplitudes were practically identical to the condition when subjects shifted attention to both features, i.e., the entire object, indicating feature integration. Both Duncan's integrated competition model (Duncan, 1984) and Roelfsema's incremental grouping model (Roelfsema, 2006) explain this process in terms of neuronal network activity. Neurons tuned to a certain to-be-attended feature will be activated first, and this activation is then transmitted to other brain areas, which code for the other object constituent feature(s). This spreading of activation is time-consuming and presents as a rapid serial process (roughly 60 ms), previously shown by Schoenfeld et al. (2014). Our temporal resolution is beneath what is necessary to measure such rapid processes. However, from our data, it is obvious that feature integration is transient, as suggested by (Xu, 2010), and is followed by the facilitation of the to-be-attended feature in cases of prolonged presentation times and task relevance of that specific feature. This second process started with the significant increase of SSVEP amplitudes against zero, and continued in a sustained fashion until the end of the epoch. This amplification clearly follows predictions of the feature similarity gain model (Treue, 2001; Treue and Martinez-Trujillo, 1999) with a sensory gain of the to-be-attended feature(s). The significant increase of SSVEP amplitudes for the to-be-attended feature, i.e., feature-specific prioritization, in our previous study most certainly resulted from that amplification process. Interestingly, when we look at the SSVEP amplitude time course of the to-be-ignored feature, it maintains values in the range of zero for a prolonged period, indicating no relative change compared to the condition when both features of the object were to be attended.

In our previous study, a surprising finding was the significant SSVEP amplitude reduction when subjects attended to both features compared to when they attended to a single feature (driven mainly by the SSVEP amplitude for color). We offered an explanation that amplitude reduction was a product of competitive interactions between the two features when they constitute one object and both were regarded as task-relevant (Desimone and Duncan, 1995; Freeman et al., 2014). Another alternative explanation we discussed is the division of attentional weights (Duncan and Humphreys, 1989) between two feature dimensions in the "attend to both features" condition (Müller and O'Grady, 2000), which would also result in a reduction of SSVEP amplitudes, even in the absence of competition. In light of the present findings, the competition hypothesis most convincingly explains our results. If one assumes a single pool of attentional resources, shifting of attentional weights to the to-be-attended and away from the to-be-ignored feature after the integration process would result in an instantaneous reduction of SSVEP amplitudes for the to-be-ignored feature, which was obviously not the case in the present study. Only if one assumes independent attentional weights for each feature dimension can one explain our results about SSVEP amplitude time courses. Competitive interactions during the integration process, however, could cause amplification of the to-be-attended feature, while leaving the SSVEP amplitude for the to-be-ignored feature unaltered since only the to-be-attended feature would be released from competition (Duncan and Humphreys, 1989). To further resolve this competition, at a much later time point, the to-be-ignored feature is further suppressed as indicated by the significant SSVEP amplitude reductions against zero. As emphasized above, we will not speculate on the exact time point of that suppression; however, the observed sustained amplification that is followed by a delayed and also sustained suppression seems to be a general neural mechanism in feature-based attention, when features share the same location or space. In two recent studies, we reported exactly that pattern when subjects were presented with two superimposed red or blue random dot kinematograms (RDKs) and voluntarily shifted attention to one of the two RDKs after a central cue (Andersen and Müller, 2010; Forschack et al., 2017).

As mentioned above, our behavioral data mimic our electrophysiological findings. However, the experiment was not designed to determine an exact time course of behavioral performance. This is because the amount of additional trials with target and distractor events needed to receive a finer temporal structure would have been unbearable to our subjects due to the duration of the experiment. Yet, we were able to group all events into three consecutive time windows of 1 s each without temporal overlap of events. In the first time window, we found no differences in d'-values regardless of the task. This was true for both trial-by-trial and block-wise cueing. While the similar behavioral performance for "attend rotation" and "attend color" was expected, given our difficulty adjustment procedure during training, the finding that performance was similar when we compared "attend to one feature" with "attend to both features" is supportive for our prediction of an early feature integration process. In the second time window, the comparisons between conditions became significant with just one exception (i.e., when color was attended to in the block design). At the present time, we cannot explain this outlier in this second time window. Certainly, this was not due to a bias in the difficulties of the respective tasks between trial-by-trial and block design. As can be seen in Table 2 for the adjusted difficulty, as well as for reaction times and for d'-values, Bayesian statistics were in favor of the null hypothesis, i.e., no differences between the two experimental design types. Likewise, the conducted ANOVA revealed no significant interactions with the between-subject factor "design version". However, during this time window neural facilitation of the to-be-attended feature occurred. In the third window, all comparisons between "attend to one feature" and "attend to both features" were significant. During this time window the attended feature received an additional sensory gain by a suppression of the to-be-ignored feature. Inspection of performance over time does also reveal that d' values are much smaller during the last two time windows, compared to the first one (see Table 2 - apparent also in a main effect of the within-subject factor "time window" in the conducted ANOVA). We assume this is most likely an effect of fatigue, which we often observe in our experiments. However, participants were able to fulfill the respective tasks far above chance level during all three time windows. The high d' values during the first time window do, furthermore, provide evidence that participants were already able to attend to the object features instead of still being busy with the shift of attention. The latter could otherwise have been an alternative explication for identical SSVEP amplitudes across conditions during this initial phase. However, it should be considered that d'-values were such high during this first time window that ceiling effects cannot be fully excluded as an alternative explication for the pattern of identical performance across experimental conditions. Though, d'-values were in a similar range in our previous study (Brummerloh et al., 2019) in which, by contrast, we found costs in the dual feature condition. Importantly, it can be excluded that ceiling level performance has determined similar SSVEP amplitudes during the first time window as a previous study demonstrated that SSVEP amplitudes are independent of task difficulty (Attar and Müller, 2012).

In our previous study (Brummerloh et al., 2019), we did not analyze the time course of behavioral performance, given the pre-trial cueing design, and reported only the behavioral costs of subjects attending to two features at once, which is the same finding as in the last two time windows in the present study. In this previous study, we discussed that the loss of accuracy in the dual feature condition might partly reflect the different decision factors between single feature and dual feature tasks, and/or the need to monitor two kinds of targets simultaneously, which makes the dual feature condition more difficult. However, during the first time window in the present study we did not find any differences between the three experimental conditions, i.e., performance was similar when subjects attended to two compared to one feature. This finding contradicts the alternative explication and strengthens our interpretation that behavioral data mirror neural processes in the early visual cortex when subjects are required to attend to specific feature(s) within an object. This interpretation is also in line with a previous study demonstrating a direct correlation between behavioral data and SSVEP amplitudes (Andersen and Müller, 2010). Future studies are needed to obtain a more refined time course of behavioral data to check whether a change in behavioral performance is temporally linked to the observed SSVEP amplitude changes.

5. Conclusions

Herein we report a time-dependent perceptual process within object-based attention when subjects were cued to one feature of an object. Contrasting with other studies, we used one coherent object with two constituent features (rotation and color changes) to mimic everyday selection better compared to overlapping moving dot arrays (cf. eg. Schoenfeld et al., 2014). We have discovered a biphasic neural process commencing with a transient period of several hundreds of milliseconds of neural feature integration as predicted by the integrated competition model (see O'Craven et al., 1999; Schoenfeld et al., 2014), which was followed by feature-based neural mechanisms (Treue and Martinez-Trujillo, 1999) with sustained amplification of the to-be-attended feature. As reported in our previous studies (Andersen and Müller, 2010; Forschack et al., 2017), amplification of the to-be-attended feature was followed by sustained suppression of the to-be-ignored feature. Behavioral data followed this biphasic pattern of integration and feature prioritization. Therefore, our results offer an appealing solution to apparent inconclusive results within the field of visual object-based attention. It would appear from this work that time matters; short stimulus presentations in the range of a few hundred milliseconds will result in feature integration, but longer exposure to the task and/or processing time of the stimulus allows feature-based attentional mechanisms to predominate, resulting in feature-specific prioritization of the to-be-attended feature within an object.

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