Attentional modulation in early visual cortex: a focused reanalysis of steady-state visual evoked potential studies

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Abstract

Steady-state visual evoked potentials (SSVEPs) are a powerful tool for investigating selective attention. Here, we conducted a combined re-analysis of multiple studies employing this technique in a variety of attentional experiments in order to, first, establish benchmark effect sizes of attention on amplitude and phase of SSVEPs, and second, harness the power of a large dataset to test more specific hypotheses. Data of eight published SSVEP studies were combined, in which human participants (n=135 in total) attended to flickering random dot stimuli based on their defining features (e.g. location, color, luminance, or orientation) or feature-conjunctions. The reanalysis established that in all the studies attention reliably enhanced amplitudes, with color-based attention providing the strongest effect. In addition, the latency of SSVEPs elicited by attended stimuli was reduced by ~4 ms. Next, we investigated the modulation of SSVEP amplitudes in a subset of studies where two different features were attended concurrently. While most models assume that attentional effects of multiple features are combined additively, our results suggest that neuronal enhancement provided by concurrent attention is better described by multiplicative integration. Finally, we used the combined dataset to demonstrate that the increase in trial-averaged SSVEP amplitudes with attention cannot be explained by increased synchronization of single-trial phases. Contrary to the prediction of the phase locking account, the variance across trials of complex Fourier coefficients increases with attention, which is more consistent with boosting of a largely phase-locked signal embedded in non-phase-locked noise.

Introduction

Selective attention is a mechanism which prioritizes stimuli for processing on the basis of their simple features, such as color, orientation, spatial location, or direction of motion. For example, while waiting for a friend outside a busy train station, selective attention allows us to tune our vision to the station exit as well as the color of their hair or clothes, while ignoring other colors and locations. The implementation of selective attention in the brain has been studied using a wide array of neuroscientific techniques – from single-cell recordings (Moran & Desimone, 1985; Treue & Martínez Trujillo, 1999) to fMRI (Saenz et al., 2002) to event-related fields and potentials (Hillyard & Münte, 1984; Hopf et al., 2006).

Steady-state visual evoked potentials (SSVEPs), recorded through electroencephalography (EEG), are a particularly powerful tool for investigating selective attention. The SSVEP is a continuous oscillatory response of the visual cortex that has the same fundamental frequency as the driving stimulus. A considerable number of studies show that the amplitude of this response is substantially increased by spatial as well as feature-based attention (see (Andersen, Müller, et al., 2011; Norcia et al., 2015 for review). When multiple stimuli flickering at different frequencies are presented concurrently, each one of them will drive an SSVEP at its respective frequency, thereby allowing for the assessment of the allocation of attention to each element in a multi-stimulus display. This convenient property of SSVEPs together with a high signal-to-noise ratio sparked a number of research programs where SSVEPs were used to study various aspects of cognition (Morgan et al., 1996; Silberstein et al., 1990, 1995; Wilson & O'Donnell, 1986). Once it was established that task-relevance of the flickering stimulus modulates SSVEP amplitude, the SSVEP technique has been used in numerous studies investigating various aspects of selective attention (reviewed in Andersen et al., 2011).

We here present a re-analysis of eight published studies that investigated attentional selection in the early visual cortex through SSVEPs. The goal of this re-analysis is two-fold. First, we aim to consolidate, analyze, and share the knowledge about applying SSVEPs to study visual attention in the hope that this will encourage other groups to employ this method and help implement their own SSVEP paradigms and analyses. This overview will allow us to explain the chosen analytical approach and share the reasoning behind it, give a bird's eye view of expected effect sizes across multiple types of stimuli and tasks, and overall make implicit knowledge explicit for the benefit of the research community. Consequently, such a reanalysis will highlight the areas of SSVEP research which need further methodological enquiries. Second, we will harness the power of the large, combined dataset to answer the questions which individual studies could not or did not address.

The analyses presented here will tackle six separate issues, starting with the properties of the SSVEP signal itself. We will

1. Describe the magnitude and variability of SSVEPs across participants, stimulation frequencies, and experiments.
2. Examine the relationship between these basic properties and the strength of attentional modulation of SSVEPs as well as the consequences these have for data analysis in SSVEP studies.

3. Present the overview of effect sizes that different feature-dimensions of attention have on SSVEPs.
4. Resolve whether attentional effects of different feature-dimensions are combined additively or multiplicatively.
5. Quantify attentional effects on the latency of the SSVEP.
6. Determine whether SSVEP attention effects in the trial-average are due to changes in phase-locking between trials, changes in magnitude of the SSVEP in individual trials, or a combination of both.

Parts (4) – (6) each tackle an outstanding question on attentional effects on SSVEPs. The first question, discussed in (4), is whether attentional effects of different features are combined additively or multiplicatively. Existing models of attention such as the feature-similarity gain model (Maunsell & Treue, 2006; Treue & Martínez Trujillo, 1999) or the Theory of Visual Attention (TVA;(Bundesen, 1990; Bundesen et al., 2005) assume that attentional selection o(Adamian et al., 2019; Andersen et al., 2013; Andersen, Fuchs, et al., 2011)f different features is additively independent. However, there is evidence for super-additive combination of attention to different features at early visual processing stages both from single-unit recordings (Hayden & Gallant, 2009), SSVEPs (Adamian et al., 2020; Andersen, Fuchs, et al., 2011) and modelling of human behavioral data (Nordfang et al., 2017).

The second question is whether and how attention affects the latency of SSVEP responses. While it is well established that the amplitude of the SSVEP response is modulated by attention, whether or not attention also speeds up neural processing in the early visual cortex is a subject of debate (Di Russo & Spinelli, 1999; Russo et al., 2003a; Silberstein et al., 1996; Sundberg et al., 2012; Zhigalov & Jensen, 2020). To test whether the SSVEP response to attended stimuli is faster, in (5) we will estimate and compare SSVEP latencies in attended and unattended conditions across studies.

Last, in (6) we will examine whether increased SSVEP amplitudes in the trial-average are attributable to an increase of phase synchronization between trials, as proposed by Kim et al. (2007). As we will illustrate in simulated data, phase-locking results not only in increased response amplitude, but also necessarily leads to a reduction of the variance of the complex amplitudes between trials. We will use the aggregated single-trial SSVEPs to test whether this predicted reduction of variance is observed in the experimental data.

General methods

The data for the re-analysis came from eight studies authored by S. K. Andersen and colleagues published between 2008 and 2020 (Adamian et al., 2019, 2020; Andersen et al., 2008, 2009, 2011, 2012, 2013, 2015). These studies investigated sustained attentional selection along one or two dimensions (color, space, orientation, etc.; see Table 1) using of the SSVEP technique. All studies used as stimuli randomly moving dots or bars which flickered at a designated ‘tagging’ frequency (see Table 1). Sets of dots or bars flickering at different frequencies (60 to 150 items per stimulus) were spatially overlapped, allowing for manipulation and measurement of feature-based attention without the confounds of spatial attention. The following section briefly describes the hypotheses and results of each of the experiments.

Brief descriptions of studies

1. “Attention facilitates multiple stimulus features in parallel in human visual cortex” (Andersen et al., 2008). This study tested whether attending to a conjunction of features (color and orientation) involves attentional facilitation of both attended features separately. The results showed that attention to a conjunction (e.g. ‘attend red horizontal’) enhances responses in the early visual cortex to stimuli possessing either feature (‘red vertical’ or ‘blue horizontal’ stimuli) as well as both features (‘red horizontal’ stimulus). Moreover, the attended conjunction enjoys attentional facilitation approximating the sum of attentional enhancements of corresponding single features.
2. “Color-selective attention need not be mediated by spatial attention” (Andersen et al., 2009). This study establishes that feature-based attention acts independently of spatial attention. Participants attended to one of two spatially fully overlapping sets of random dots based on a non-spatial feature (color). Coordinates of all dots were randomly redrawn at each cycle of the flicker, thereby making spatial tracking impossible. The results showed that the to-be-attended feature elicited larger SSVEP amplitudes even though spatial selection was impossible.
3. “Effects of feature-selective and spatial attention at different stages of visual processing” (Andersen et al., 2011). The study explored concurrent attentional selection of color and space. Two pairs of spatially overlapped random dot stimuli were presented in the left and right visual fields, and participants were instructed to attend one type of dots defined by location and color (e.g. ‘attend left red’). The results showed that, similarly to a conjunction of color and orientation, color and location are independently facilitated in the early visual cortex (as measured by SSVEPs). Conversely, later in processing (according to the amplitude of the P3 ERP component) this facilitation is limited to the attended location only.
4. “Bottom-up biases in feature-selective attention” (Andersen et al., 2012). Light and dark dots were presented against a changing luminance background, making one set of dots higher contrast than the other while preserving the luminance difference between the stimuli. This procedure allowed to explore the integration of bottom-up (stimulus induced) and top-down (attentional) biases. SSVEP amplitudes increased with higher contrast of the driving stimulus, and the slope of this increase in the early visual cortex depended on attention, suggesting multiplicative integration of biases.
5. “Global facilitation of attended features is obligatory and restricts divided attention” (Andersen et al., 2013). This study tested the boundaries of the ‘global effect’ of feature-based attention – preferential processing of the attended feature throughout the visual field. In the first experiment participants observed two pairs of red and blue random dot stimuli located in the left and right visual field. Their task was either to attend to the same color on both sides, or to attend to different colors (for example, blue was simultaneously to-be-attended on the left and to-be-ignored on the right). When the same color was attended throughout the display, SSVEP amplitudes to the attended stimuli were enhanced. However, when opposite colors were attended, amplitudes did not differ between attended and unattended stimuli, demonstrating that global feature-based selection cannot be overcome by the task demands. The second experiment used a

similar design to show that it is possible to attend to two different colors in two different locations.

6. “Attentional selection of feature conjunctions is accomplished by parallel and independent selection of single features” (Andersen et al., 2015). Building on the previous study of feature conjunctions (Andersen et al., 2008), this experiment asked whether the magnitude of attentional enhancement of a conjunction is related to the magnitude of the attentional enhancement of its constituent features. For example, if we knew the size of attentional modulation of color and orientation separately (i.e. the difference between the SSVEP amplitudes elicited by the same stimulus when it is attended and unattended), could we predict the effect of attention to both these features together? The results show that SSVEP amplitudes in conditions where single features were selected accurately predict the SSVEP amplitudes during conjunction selection.
7. “Top-down attention is limited within but not between feature dimensions” (Adamian et al., 2019). This experiment tested whether spatial and feature-based attention are independent or whether they rely on a common limiting mechanism. Participants were presented with two pairs or red and blue random dot stimuli located in the left and right visual fields. Color-based attentional enhancement was measured while spatial attention was focused (e.g. ‘attend red on the left’) or divided (‘attend red on the left and right). The magnitude of feature-based enhancement did not change depending on the demands of spatial attention, demonstrating that the two dimensions of attention are indeed independent. This study extends previously established parallel and independent selection (Andersen et al., 2015) to the combination of feature-based and spatial attention.
8. “Parallel attentional facilitation of features and objects in early visual cortex” (Adamian et al., 2020) This study examined whether an attended feature (luminance polarity) can be selected globally across attended and unattended objects (motion-defined surfaces). Participants observed four sets of dots (light and dark, rotating clockwise and counterclockwise) while attending to one of them (e.g. ‘dark clockwise’). Similar to the cases when the attended stimulus was defined as a conjunction of features or a combination of feature and spatial location, attentional enhancement of SSVEP amplitudes was not restricted by object boundaries (e.g. frequencies corresponding to the ‘dark counterclockwise’ and ‘light clockwise’ stimuli were also enhanced when attending to ‘dark clockwise’).

Common materials and methods

Stimuli were presented against a gray background. Where color was used, equiluminance of colors to the background was determined by heterochromatic flicker photometry for each participant (with exception of Adamian et al., 2019 where physical luminance was used). Each dot or bar moved on each frame. In the majority of studies items moved a set step in a random direction, reappearing on the opposite side when reaching the boundary of the field. One study used rigid rotational motion (Adamian et al., 2020) and in one study dots were redrawn in random positions on each flicker onset (Andersen et al., 2009). In all cases, dots were drawn in random order to prevent depth cues from systematic occlusion.

Trials in these studies lasted from 3 to 15 s. A few hundreds of milliseconds after flicker onset were excluded from SSVEP amplitude calculation to allow for SSVEPs to build up and for transient onset-VEPs to end. During each trial, participants observed flickering stimuli while performing a behavioral task – detecting a target event (e.g. coherent motion streak or luminance decrement) in a cued set of stimuli while ignoring the same (distractor) event in the other set(s) of stimuli. Cues specifying the to-be-attended feature (e.g. color, orientation or direction of motion) were presented visually prior to the start of each trial.

Common EEG recording and analysis methods

Brain electrical activity was recorded from 32 - 128 Ag/AgCl scalp electrodes (see Table 1 for details) by means of ActiveTwo (BioSemi) amplifiers, except two studies (Adamian et al., 2020; Exp. 2 Andersen et al., 2013) where recordings were done via 64 tin electrodes mounted in an elastic cap (Electro-cap International) and SA Instrumentation amplifier. In data collected with BioSemi amplifier, only the in-built antialiasing filter was applied online. Bandpass filtering was applied to the data collected through SA Instrumentation amplifier (0.1 to 80 Hz). Eye movements and blinks were monitored through electrooculographic recordings (vertical EOG was recorded from the outer canthi of the eyes, horizontal EOG – from electrodes above and below one of the eyes).

This set of studies was carried out using a very consistent EEG processing and analysis pipeline performed in MATLAB (The MathWorks) using the EEGLAB toolbox (Delorme & Makeig, 2004) as well as custom-built routines. This consistent approach lends itself well to pooling the results together for the purposes of re-analysis. However, it is important to note that we did not re-preprocess any of the data. While it may be of interest to fully harmonize these datasets (for example, by choosing individual peak electrodes as opposed to pre-defined electrode clusters), such an approach would introduce more analytical degrees of freedom and potentially make the analysis less optimal for each individual dataset. Instead, we follow the published analyses for each study, restricting the analytic choices to those already made based on the purposes and characteristics of each study.

Epochs for SSVEP analyses were extracted using one of two methods. The first method selects trials where no target or distracter events were present (50% – 70% of total trial number). Epochs are then extracted accounting for onset- and offset- related activity changes: epochs start a few hundred milliseconds after flicker onset (400 ms in most cases, 600 ms in Adamian et al., 2020; 500 ms in Andersen, Fuchs, et al., 2011) to account for the visual evoked response and allow time for the SSVEP to build up. Epochs end 50-100 ms before flicker offset (see Table 1). The second method segments each trial into multiple 1-s epochs, subsequently discarding any epoch containing target or distractor related activity as well as the first epoch of each trial. Importantly, the signal resulting from the data acquired via longer or shorter epochs is comparable as long as the total time of recording per condition submitted to the Fourier transform is equal. The second method is more complicated in implementation, but allows more data to be preserved, especially if the experiment requires that frequent target and distractor events embedded in the ongoing stimulation are excluded from the analysis. In all cases, the epoch extraction method was determined at the planning stage of the experiment, prior to any data collection.

Mean and linear trends were removed in all epochs (detrending). No other filters were applied offline to any of the data. Epochs with blinks and eye movements (larger than 20 μV) were excluded, and remaining artifacts were corrected using an automated SCADS algorithm (statistical correction of artifacts in dense array studies: Junghofer et al., 2000), except for Andersen, Fuchs et al., 2011, where artifact rejection was performed manually). The SCADS routine rejected artifact-contaminated epochs based on the statistical properties of the data or replaced individual sensor's data through spherical interpolation. Data were then re-referenced to average reference, and epochs were averaged for each condition. SSVEP amplitudes were calculated for each electrode of interest, condition, and frequency by Fourier analysis (Fast Fourier transform algorithm implemented in MATLAB function fft.m) zero padded to 2^{14} points and quantified as the absolute value of the complex Fourier coefficients.

Electrodes for analysis were selected based on the average voltage maps of SSVEP amplitudes. Their selection was preserved in the re-analysis. In studies where stimulation was presented centrally, averaged SSVEP amplitudes were presented on the maps as a narrow occipitally located peak (Andersen et al., 2008, 2009, 2015). When stimulation was presented peripherally, this peak was extended parietally, leading to selecting a wider cluster of electrodes (Adamian et al., 2019; Andersen et al., 2013; Andersen, Fuchs, et al., 2011) Two of the studies (Adamian et al., 2020; Andersen et al., 2012) were originally analyzed using scalp current density (SCD) transformation (Pernier et al., 1988; Pernier et al,. 1989) which increases spatial resolution and allows better correspondence to cortical generators. In this case, average reference was used in the reanalysis.

Table 1. Properties of SSVEP stimulation, data acquisition and experimental manipulations in re-analysed experiments

Study	n	Number of trials	Epoch duration (ms)	Seconds of data per condition	Stimulus positions	Stimulation frequencies (Hz)	Sampling rate (Hz)	Total number of scalp electrodes	Electrodes selected for analysis	Dimension(s) of attention manipulated	Targets and Distractors	Number of attention conditions for which SSVEPs were measured (+ attended, - unattended)
Andersen, Hillyard & Müller, 2008	15	600	2400	360	Central	10, 12, 15, 17.14	256	128	POz, Oz, Iz, SIz	Color (C), Orientation (O)	Coherent motion	4 (C+O+, C+O-, C-O+, C-O-)
Andersen, Müller & Hillyard, 2009	15	432	2500	360	Central	10, 12	256	64	Oz, O1, O2, Iz	Color	Luminance decrement	3 (valid, neutral, invalid cue)
Andersen, Fuchs & Müller, 2011	19	600	3300	495	Peripheral	8.46, 11.85, 14.81, 19.75	512	32	TO1, TO2, P3, P4, PO1, POz, PO2, O1, O2, INz, IPz**	Color (C), Space (S)	Coherent motion	4 (C+S+, C+S-, C-S+, C-S-)
Andersen, Müller & Martinovic, 2012	16	300	1000 (8 epochs per trial)	240	Central	10, 12	256	64	O1, O2, Oz, Iz, POz*	Luminance Polarity	Coherent motion	10 (attended/unattended x five contrast ratios) ***
Andersen, Hillyard & Müller, 2013; Experiment 1	13	560	2500	350	Peripheral	7.5, 8.57, 10, 12	256	64	PO7, PO3, POz, PO4, PO8, O1, Oz, O2, I1, Iz, I2	Color	Luminance decrement	4 (attended/unattended x same/different cues for two locations)
Andersen, Hillyard & Müller, 2013; Experiment 2	11	560	2500	350	Peripheral	7.5, 8.57, 10, 12	250	61	PO7, PO3, POz, PO4, PO8, O1, Oz, O2, I1, Iz, I2	Color	Luminance decrement	4 (attended/unattended x two color pairs)
Andersen, Müller &	15	192	1000 (15	360	Central	8, 10, 12, 15	256	64	Oz, Iz, POz, O1, O2	Color (C), Orientation (O)	Coherent motion	8 (C+O+, C+O-, C-O+, C-O-, C+, C-,

Hillyard, 2015			epochs per trial)									O+, O-)
Adamian, Slaustaite & Andersen, 2019	16	672	2500	280	Peripheral	7.5, 8.57, 10, 12	256	64	PO3, PO4, PO7, PO8, O1, O2, I1, I2, Oz, Iz, POz	Color(C), Space (S)	Luminance decrement	6 (C+S+, C+S-, C-S+, C-S-, C+Sdivided, C-Sdivided)
Adamian, Andersen & Hillyard, 2020	15	560	2500	350	Central	12, 15, 17.14, 20	250	61	Oz, Iz, SIz *	Luminance Polarity (L), Surface (S)	Radial motion	4 (L+S+, L+S-, L-S+, L-S-)

*These studies were analyzed using scalp current density (SCD) transformation (Pernier et al., 1988; Pernier et al,. 1989) which led to a different topography and electrode selection
** Due to considerable variations in topography between individual participants, one electrode out of this cluster with the greatest SSVEP amplitude was selected for each frequency and participant
*** Different contrast conditions were averaged for the re-analysis

1. Variability of the magnitude of SSVEPs across participants and frequencies

SSVEP experiments are typically interested in measuring the modulation of SSVEPs by cognitive factors or physical stimulus properties. To this end, the first step in setting up a new SSVEP experiment is to ascertain that the stimulation elicits strong and reliable SSVEPs. In this first part, we will describe the variability of the SSVEP across participants and stimulation frequencies. This will provide researchers with general context and help to interpret their own pilot data or evaluate data of other studies for which raw data is available. Additionally, in part 2 we will derive some consequences of the variability of SSVEPs combined with the proportional nature of attention effects for their statistical analysis.

For the purposes of these analyses SSVEP amplitudes were calculated as described above for each condition, frequency, and participant in each of the studies, totaling 679 observations across 136 participants. Amplitudes at each frequency were averaged across experimental conditions. Since multiple datapoints from each experiment were entered into an aggregated correlation analysis and these observations are not independent, we calculated repeated measures correlations using the *rmcorr* package for R (Bakdash & Marusich, 2017) denoted as r_{rm}. This technique estimates the common regression slope shared among clusters of non-independent data points and adjusts for inter-individual (or, in our case, inter-study) variability.

An important property of SSVEP amplitudes is that they are measured on a true ratio scale, i.e. the point zero of the scale is non-arbitrary and corresponds to a total absence of oscillatory power at a given frequency. Although transient ERP components may, at least theoretically, also be on a ratio scale, this is not the case in practice, where the magnitude of ERP components is measured against an (arbitrary) baseline, as opposed to a true zero. As a consequence, positive ERP deflections (e.g. the visual P1) can have a negative amplitude for individual participants and/or conditions due to noise or drifts (and vice versa for negative deflections), making it impractical to describe any differences or effects as relative (e.g. twice or half as big) and instead differences are typically described and statistically analysed in absolute terms (e.g. 0.5 microvolt larger or smaller), in accordance with these measures being merely on an interval scale. This is not the case for SSVEP amplitudes, whether quantified as the absolute of Fourier coefficients or of time-varying oscillations (e.g., via Wavelets or Gabor-filters), which will in a strict mathematical sense always be non-negative. Therefore, SSVEP effects can readily be quantified in relative terms, and as we will see in part 2, SSVEP attention effects are indeed largely proportional to SSVEP magnitude. As a further consequence of SSVEP-amplitudes having a fixed lower bound of zero, the distribution of SSVEP amplitudes, e.g. across participants, will often not be symmetric, but instead exhibit a skewed distribution with outliers in the positive direction straying much further from the mean or median (see Fig. 1), similar to theoretical distributions with a fixed lower bound of zero, such as the discrete Binomial and Poisson distributions or continuous log-normal distributions.

SSVEP amplitudes (averaged across attentional conditions) in our 9 studies varied strongly between participants: the interquartile ratio (i.e. the ratio between the 75^{th} and 25^{th} percentiles of the data) across participants, calculated for each frequency (stimulus) in each experiment separately, was on average 1.83 (±0.28). Thus, even in fairly small samples (e.g. 13-19 participants in the datasets analyzed here), one can easily expect the magnitude of

SSVEP amplitudes to differ by a factor of two or more, with much higher ratios between the lowest and highest amplitudes in a larger sample. Variability and magnitude of SSVEP amplitudes scale together (correlation between the amplitude mean and standard deviation of each experiment x frequency sample: $r_{rm(19)} = 0.92$, $p < 10^{-8}$, 95%CI = [0.81 0.97], Figure 1C). In addition to the variability between participants, SSVEP amplitudes also vary substantially between frequencies (stimuli), with larger amplitudes tending to be elicited at lower frequencies (correlation between the mean amplitude and stimulation frequency: $r_{rm(22)} = -0.8$, $p < 10^{-5}$, 95%CI = [-0.91 -0.57], Figure 1C, 1D). In the literature SSVEP amplitudes are often expressed as signal-to-noise ratio (SNR) -- ratio of the amplitude at the flicker frequency to the average of adjacent (noise) frequencies (Norcia et al., 2015). SNR also tends to be higher at lower stimulation frequencies ($r_{rm(22)} = -0.72$, $p < 10^{-4}$, 95%CI = [-0.87 -0.43], Figure 1E).

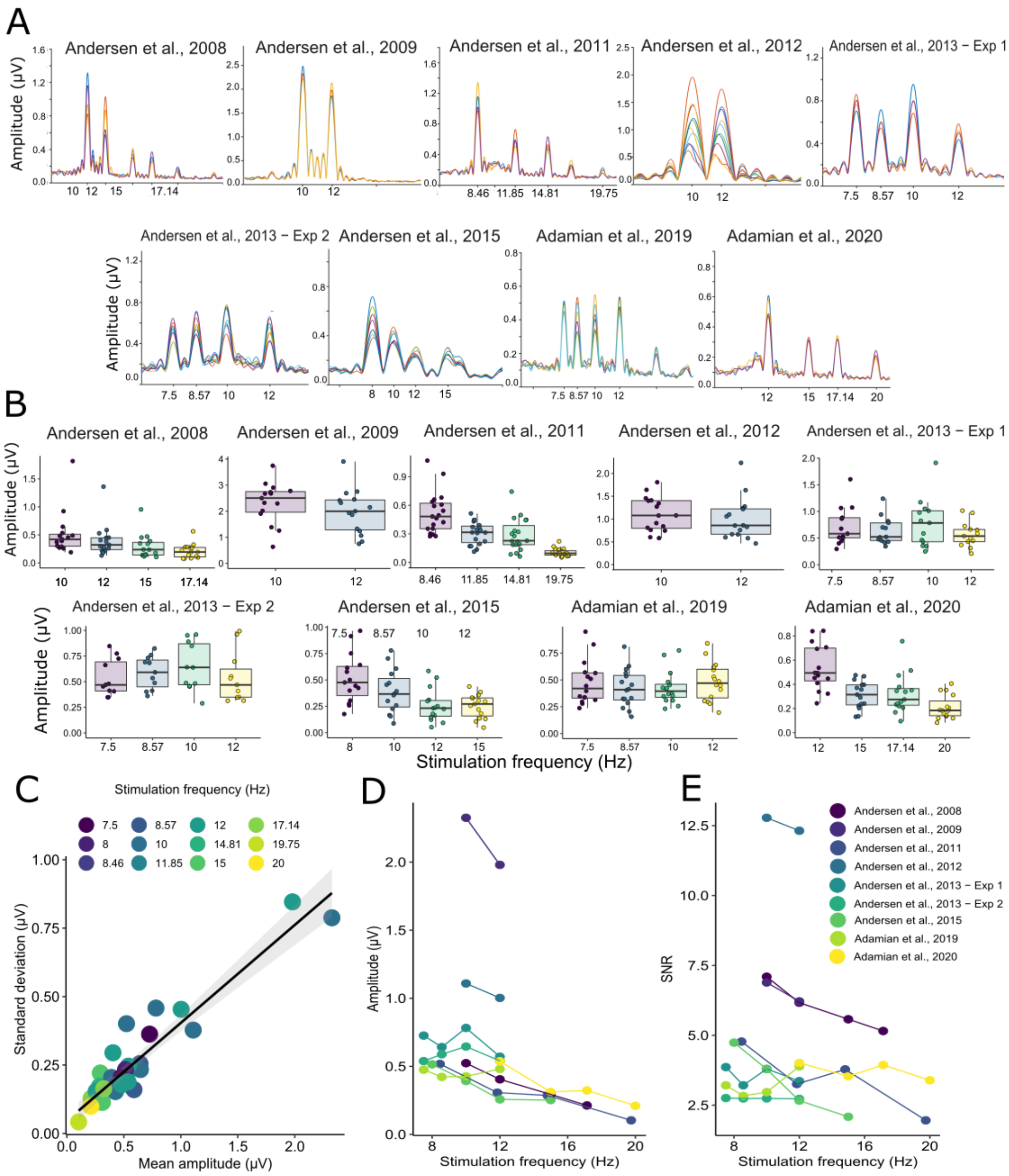

Figure 1. Summary of SSVEP amplitudes at different frequencies. A: Grand-average amplitude spectra obtained by Fourier transformation zero padded to 2^{14} (=16384) points B: SSVEP amplitudes vary between participants and stimulation frequencies. Dots represent SSVEP amplitudes of individual participants averaged across conditions, box plots show median, first and third quartiles of the between-participant distribution. C: Variability of SSVEP

amplitudes scales with their magnitude. D: Lower stimulation frequencies elicit stronger SSVEP amplitudes. Note that in two studies with noticeably higher amplitudes (Andersen et al., 2009, 2012), only two stimuli were presented foveally (see Walter et al. (2012) for a comparison between foveally and peripherally attended stimuli). Furthermore, in Andersen et al., 2009 position changes in the RDK were fully synchronized with the flicker. In the other studies, either more stimuli were superimposed, or stimuli were presented outside the fovea. E: SSVEP amplitudes at lower frequencies have higher signal-to-noise ratio (SNR)

In many published SSVEP studies, including all the current datasets, SSVEP amplitudes were measured at multiple frequencies (four in the majority of cases, two in Andersen et al., 2009 and 2012) for each participant. Given the high variability of SSVEP amplitudes across participants and frequencies it is of interest to consider the extent to which this variability between participants is shared across frequencies (stimuli). This is especially the case as some studies have included frequency as a factor in between-subjects statistical analyses, thus implicitly assuming that SSVEP amplitudes at different frequencies are consistently correlated across participants. To evaluate this claim, we correlated SSVEP amplitudes of all pairs of frequencies in our selection of studies (Figure 2) across participants. SSVEP amplitudes were positively correlated across participants for all pairs of frequencies, with only one exception where the correlation was not significantly different from zero (between 12 Hz and 17.14 Hz in Adamian et al., 2020). Aggregated data shows the strongest relationship between the two lowest frequencies selected for each experiment ($r_{rm(125)} = 0.79$, $p < 10^{-29}$, 95%CI = [0.72 0.85]), and the weakest – between the two highest frequencies ($r_{rm(96)} = 0.46$, $p < 10^{-5}$, 95%CI = [0.28 0.60]). Thus, one can expect somewhere between roughly one quarter to two thirds of the variance in signal magnitude between participants to be shared across frequencies. In summary, there is a consistent but modest correlation of SSVEP magnitude at different frequencies across participants. As a consequence, it is to be expected that when driving SSVEPs at multiple frequencies, some participants may exhibit strong SSVEPs at some frequencies but less so at others. Additionally, using standard within-subjects statistical analyses may not be an ideal way of controlling this variability in signal magnitude (see also subsequent section) as correlations across different frequencies can be modest in size.

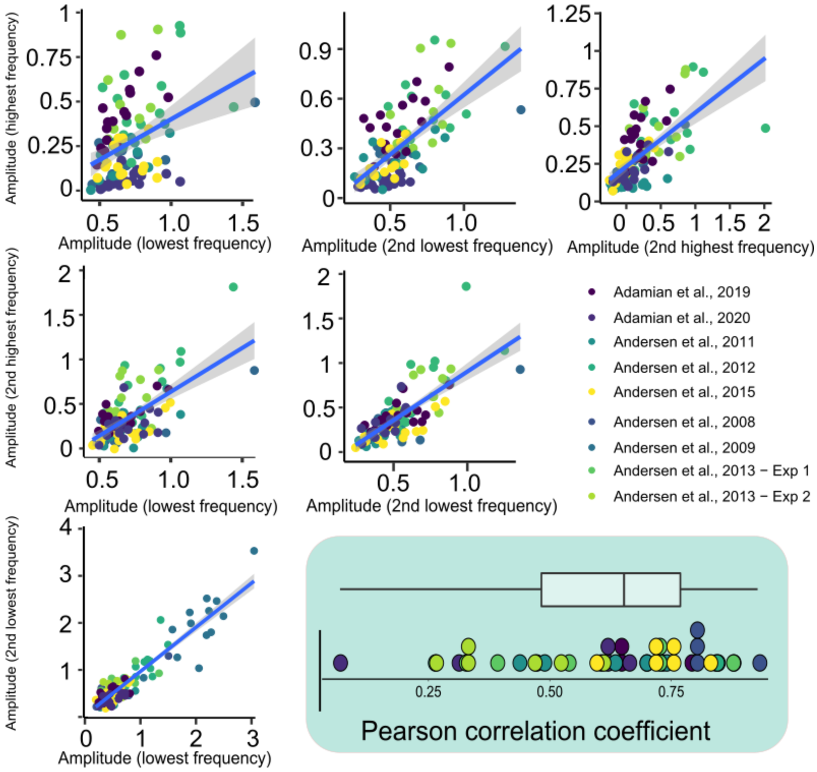

Figure 2. SSVEP amplitudes elicited at different frequencies are moderately correlated across participants. Panels: Scatterplots of SSVEP amplitudes by pairs of stimulation frequencies. Inset: Distribution of correlation coefficients across all studies and frequencies. This reveals that the correlation between SSVEP magnitudes at different frequencies is consistent albeit modest.

2. Attentional modulation is proportional to signal magnitude

The assumption of standard within-subjects parametric statistical tests (e.g. paired t-test, repeated-measures ANOVA) is that within-subjects variability in the magnitude of the dependent variable is of an additive nature, i.e. the size of effects is independent of the overall magnitude. This assumption is clearly violated for SSVEPs in our studies (Figure 3). The magnitude of attention effects (attended minus unattended) was positively correlated with and largely proportional to the overall signal magnitude (average of SSVEP amplitudes across all conditions) in all but one of our studies (Andersen et al., 2013 Experiment 2). Aggregated across studies, there was a highly significant positive correlation between individual SSVEP

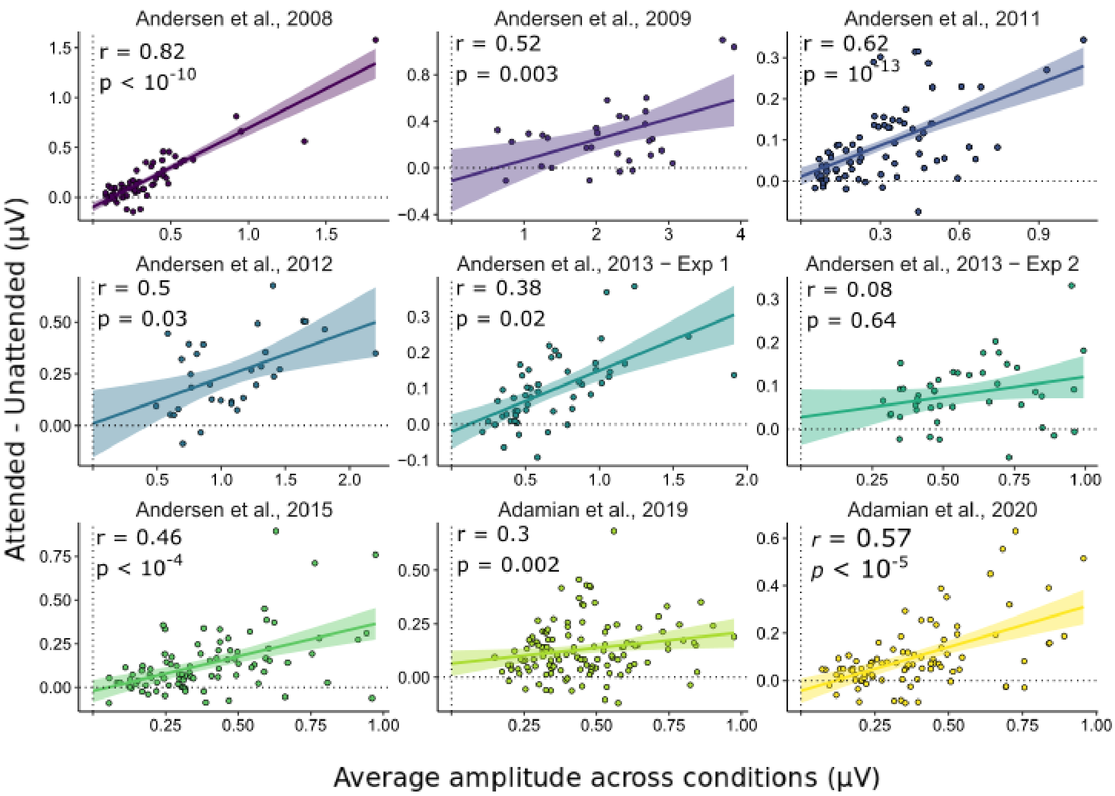

Figure 3. Attentional modulation of SSVEPs scales with SSVEP amplitude. Each dot represents one frequency-participant combination.

magnitude and attentional modulation ($r_{rm(668)}$ = 0.51, $p < 10^{-45}$, 95%CI = [0.45 0.56]).

To explore the relationship between stimulation frequency, SSVEP amplitude, and attentional modulation, we used a linear mixed-effect model with SSVEP amplitudes as a dependent factor and participants as a random factor. Stimulation frequency and average amplitude across conditions was included as fixed effects. The results showed that the magnitude of attentional enhancement decreases with increasing frequency (β = -0.006, *SE* = 0.003, p = 0.02) and increases with increasing amplitude (β = 0.17, *SE* = 0.07, p = 0.01) while the interaction of frequency and amplitude has no effect (β = -0.001, *SE* = 0.006, p = 0.78).

Together the analyses in (1) and (2) reveal three important characteristics of SSVEPs: (1) SSVEP amplitudes vary substantially between participants and frequencies, (2) SSVEP amplitudes depend on the stimulation frequency – the higher the frequency, the lower the amplitude, and (3) the effect of attention on SSVEP amplitudes is roughly proportional to the overall SSVEP amplitude, i.e. attentional modulation of SSVEPs is a relative boost, not an absolute one. These observations were consistent across the studies presented here.

Combined, these properties imply that it is not ideal to enter raw SSVEP amplitudes into a statistical analysis that assumes additivity. To give a simple example: if we measured three participants with unattended amplitudes of 1.0 μV, 2.0 μV, and 3.0 μV and attended amplitudes of 1.2 μV, 2.4 μV, and 3.6 μV, respectively, then the attentional effect, in relative terms, would be an entirely consistent boost of 20%. However, entering these values into a paired samples t-test would yield seemingly highly variable attention effects of 0.2 μV, 0.4 μV, and 0.6 μV, and thus systematic variance would be incorrectly identified as unsystematic variance, resulting in a loss of statistical power. To make things even worse, because attentional effects are proportional to the amplitude of the signal, any averaging of 'raw' or unscaled SSVEP amplitudes overweighs attentional effects contributed by datapoints with higher amplitudes (e.g. lower frequencies or individual participants).

To circumvent the issue of relative effects, all studies presented here use a rescaling[1] step prior to statistical analyses. In this step, each individual amplitude (A_{ijk}) is divided by the mean of all *n* attentional conditions *k* for each participant *i* and frequency *j* separately (see Equation 1).

$$N_{ijk} = \frac{A_{ijk}}{\frac{1}{n}\sum_{k=1}^{n} A_{ijk}} \tag{1}$$

After such rescaling, amplitudes can be safely averaged across frequencies to yield a standardized value for each condition. Note that in the case of only two conditions (attended (A) and unattended (U), such rescaling yields attention effects $A - U$ that are identical to the frequently used AMI (attention modulation index $\frac{A-U}{A+U}$ (Kastner et al., 1999; Roelfsema et al., 1998), bar a factor of 2.0. Importantly, this transformation is performed on the level of individual frequency and participant, circumventing the issue of unequal weighting of lower frequencies, and taking account for the modest correlation of SSVEP amplitudes between frequencies. Since the denominator includes the average amplitude at a single frequency across conditions, each measurement is rescaled to the mean of 1, and subsequent averaging across frequencies is scale-free, making any amplitude changes uniquely attributable to the experimental manipulation and not the stimulation frequency.

Similarly to the other EEG-based techniques such as the analysis of event-related potentials, there is considerable variability in the methods of preprocessing and analysis of SSVEPs (Clayson et al., 2019; Keil et al., 2014). While multiple approaches may be equally applicable to a given dataset and statistical model, we highlight in this part of the re-analysis the benefits of rescaling SSVEP amplitudes prior to averaging and statistical analysis as compared to 'raw' or unscaled amplitudes. Rescaled amplitudes better conform to

[1] In the texts of the published studies this procedure was sometimes referred to as 'normalisation'

assumptions of common parametric tests (in particular additivity) and allow for a more straightforward interpretation of attentional modulation of SSVEP amplitudes.

One popular method of scaling SSVEP amplitudes is via signal-to-noise ratio (SNR), where SSVEP is expressed as a ratio of the amplitude at the flicker frequency to the average of adjacent (noise) frequencies (Norcia et al., 2015). SNR is particularly useful when seeking to determine whether a particular stimulus elicits a detectable response (e.g., Norcia & Tyler, 1985) or which analytical technique yields the highest SNR (e.g. Cohen & Gulbinaite, 2017). However, the fact that some research questions are most directly addressed by computing SNR does not mean that this is an ideal way of quantifying SSVEPs in other cases. At least two arguments can be made against generally quantifying SSVEPs in terms of SNR: First, the SNR itself may have a poor reliability. After divisive rescaling, the resultant measure (SNR) is affected by the measurement error of both the numerator (signal) and the denominator (noise). In the case of a strong SSVEP amplitude and low noise, the signal itself can be quantified with high precision, but the high SNR itself can only be quantified less precisely due to the variability of the noise measurement (in the hypothetical ideal case of a noise-free measurement the SNR becomes infinite and thus useless). By comparison, our approach of rescaling by dividing by the average of all conditions combines all the available data to compute a denominator with low variability. Second, unless the magnitudes of noise and the SSVEP are highly correlated, rescaling to SNR does not solve the previously identified issues of unequal scaling between participants and stimuli.

To demonstrate the differences between SSVEPs measured as raw values or expressed as SNR, we examined attentional effects (Attended – Unattended) as a factor of stimulation frequency in all studies (Figure 4). You may recall from the previous section that both stimulation frequency and average amplitude predicted attention effects in raw microvolt values. If SSVEPs are expressed as SNR, frequency has no effect on attentional modulation (β = -0.008, *SE* = 0.01, *p* = 0.54), however, attentional effects increase with average SNR (β = 0.34, *SE* = 0.09, *p* = 0.0003). Hence, using SNR to analyze SSVEP amplitudes does not fully protect from the issues highlighted in the previous section. In contrast, when attention effects are calculated based on rescaled SSVEP amplitudes, neither frequency (β = -0.05, *SE* = 0.08, *p* = 0.49) nor pre-rescaling amplitude (β = 0.12, *SE* = 0.87, *p* = 0.88) were significant predictors of attentional modulation. Rescaling SSVEP amplitudes is an effective way of mitigating effects of different signal magnitude between frequencies and participants in studies where multiple frequency tags are used simultaneously.

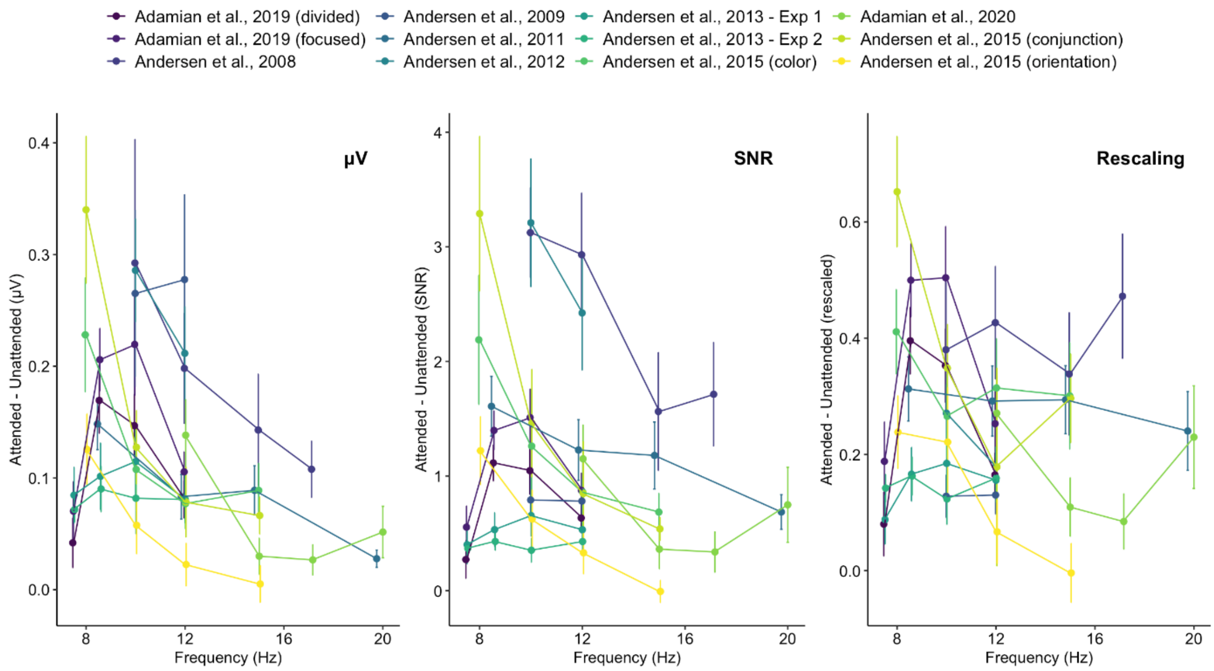

Figure 4. Attentional modulation of SSVEPs as a function of stimulation frequency measured in raw values (left), SNR (middle) or rescaled values (right).

We provide arguments for rescaling SSVEP amplitudes prior to statistical analysis and explain the approach taken in the studies analyzed here. Many other approaches to rescaling or transforming raw data are conceivable, and which one is ideal may depend on the study. For example, in some cases a log-transformation (e.g., dB scale) may be preferable, as it retains overall differences in signal magnitude while transforming relative effects into additive effects and thereby making the data conform better to the assumptions of linear additive models such as ANOVA (see Andersen & Müller, 2015 for an example). Thus, the key point of this section to encourage other researchers to consider the issue and make an informed decision on what is best suited in their studies.

We would like to end this section with two qualifying remarks. First, some participants may exhibit very weak and extremely noisy SSVEP amplitudes. By rescaling or log-transforming such data, small noise fluctuations become magnified and may produce artificial outliers that need to be excluded from statistical analysis. Second, despite the utility of rescaling or transforming raw amplitudes for statistical purposes, we believe that there is a distinct benefit to also reporting raw amplitudes prior to such procedures (e.g. as topographies or spectra), as these facilitate comparison of signals across different studies.

3. Attentional enhancement of SSVEP amplitudes: effect sizes

Having described basic properties of SSVEP amplitudes and caution required to their analysis, we will now turn to describing how attention influences SSVEP amplitudes. The utility of the SSVEP technique in attention-related research lies in the ability to obtain a high-SNR measure of neural activity unambiguously associated with a specific part of the visual input. It allows presenting multiple streams of visual stimuli simultaneously, both in spatially separated and spatially overlapping manner (see Norcia et al., 2015; Andersen et al., 2011 for reviews). Therefore, the SSVEP technique allows to isolate the effects of attentional selection of different spatial and non-spatial dimensions. Studies used in this re-analysis manipulated selection of color, orientation, luminance polarity, and space, sometimes in isolation (Andersen et al, 2009, 2012, 2013) and sometimes in combination (Andersen et al., 2008, 2011, 2019; Adamian et al., 2020). Here we used a meta-analytical approach to estimate and compare the effects of different dimensions of attention. These estimates can be useful as a benchmark for designing new SSVEP paradigms and for planning sample sizes for future experiments.

In all presented studies, attended stimuli produced enhanced SSVEP amplitudes compared to unattended stimuli. Most of the studies included a manipulation of color-based selection, which is partly explained by the fact that color-selective attention produced the largest modulation of SSVEP amplitudes (Figure 5), about a 20% change. Consequently, we were able to estimate this effect size more precisely than others. Spatial and orientation selection increased SSVEP amplitudes by just over 10%. The effect of luminance polarity is similar in magnitude to the effect of color, however, with only two studies with luminance polarity manipulation this estimate is less precise.

It should be noted that while all the presented experiments featured an attentional manipulation, these manipulations were not identical. For instance, Andersen et al. (2009) used Posner-style cueing where attention was cued probabilistically, while in the other studies the uncued color was fully behaviorally irrelevant. Unsurprisingly, probabilistic cueing produced a smaller effect on SSVEP amplitudes. Similarly, in Andersen et al. (2013) – Experiment 2 – two colors were attended at the same time, resulting in smaller attentional modulation. These differences between experiments illustrate that, on one hand, color-based selection has a strong enough effect that it can be demonstrated in a variety of experimental paradigms, and on the other hand, that the meta-analytic effect size based on the present set of studies is more likely to be under- than overestimated.

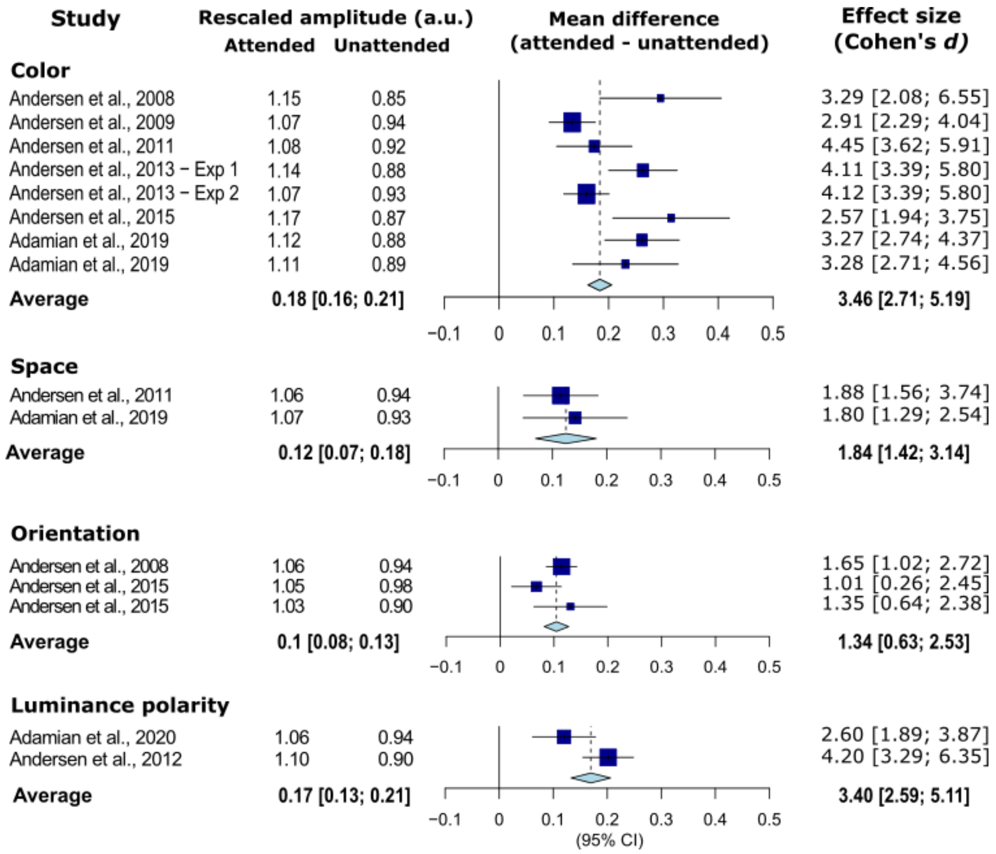

Figure 5. Forest plot of raw effect sizes (attended minus unattended) of different attentional manipulations on rescaled SSVEP amplitudes. The summary polygon in light blue shows the summary estimate of the effect size and its 95% confidence interval.

Comparisons between studies using within-participant measurements are complicated by the fact that there are multiple ways to calculate standardized mean difference for these studies . Figure 5 reports effect sizes based on the pooled standard deviation (s = $\sqrt{\frac{(n\text{-}1)S_A^2 + (n\text{-}1)S_U^2}{2\times n\text{-}2}}$ where S_A and S_U are standard deviations of attended and unattended measurements and n is sample size. J. Cohen, 1988; Goulet-Pelletier & Cousineau, 2018), however, data provided here can be used in all types of calculations in future meta-analyses or power analyses.

To facilitate the use of the present results in planning future studies, in Table 2 we provide the results of power calculations for two potential use cases. The first case is when SSVEPs are measured in two conditions (Attended and Unattended) to establish whether attention can amplify sensory information in a given experimental situation. In this case it is prudent to use a conservative estimate of the effect size (e.g. 50%) and carry out a paired t-test to potentially detect a statistically significant difference between the SSVEP amplitudes in the two conditions. The second case is when the goal of the study is to establish whether an experimental manipulation modulates the effect of attention. In this case a more optimal solution is to implement a 2 x 2 design where the first factor is Attention (Attended / Unattended) and the second factor possibly modulates attentional enhancement (e.g. presence of a secondary task). Table 2 lists minimal sample sizes required for detecting an interaction between the two factors if the modulating factor attenuates or increases the effect of attention by 50%. Of course, these are only two out of many possible experimental scenarios, and the effect sizes provided here can help plan for the effect size of interest more precisely.

Table 2. Standardized effect sizes and minimum sample size recommendations

Selection type	Average standardized effect size (Cohen's *d*)	Sample size required to detect attentional modulation in a paired t-test	Sample size required to detect attentional modulation in a paired t-test (based on 50% of reported effect size)		Sample size required to detect an effect modulating attention by 50% in a 2 x 2 repeated measures ANOVA	
		95% power	80% power	95% power	80% power	95% power
Color	3.46	4	5	7	10	15
Space	1.84	6	12	18	27	42
Orientation	1.34	10	20	31	40	64
Luminance polarity	3.40	4	5	7	18	28

4. Attention to a combination of features and its effect on SSVEPs

Five of the available studies were implemented using a full factorial design simultaneously manipulating attention to two distinct features from different dimensions such as color and space (Andersen et al., 2008; 2015), color and orientation (Andersen et al., 2011; Adamian et al., 2019) and color and luminance polarity (Adamian et al., 2020). This subset of studies allows us to not only measure the individual contribution of each attentional dimension to overall amplitude change, but also to examine the consequences of concurrent selection of two separate features. To preview, the results showed that when two features are selected at the same time, their attentional effects are combined multiplicatively.

Conceptually, the question of how the effects of concurrent attentional selection of different features are combined determines how far attention spreads to stimuli sharing some, but not all, of the attended features. Statistically, this is captured in the interaction of these two independent attentional factors. We can conceptualize the different possible interactions as lying on the continuum between the basic logic operations AND and OR at the extreme end of the spectrum. On the OR end of the spectrum, attentional benefits are evenly distributed among all items possessing at least one attended feature. As demonstrated in Figure 6, in a busy visual environment, this would lead to a wide distribution of attention among many items. Conversely, at the 'AND' end of the spectrum, selection is restricted to visual input combining all individually attended features simultaneously. This would focus cognitive resources very narrowly. Additive combination of attentional effects is towards the center of this spectrum and allows a more nuanced pattern of selection where visual input receives some attentional facilitation for partially sharing attended features and a 'double dose' of attention if both attended features are present. Such distribution of attentional resources can support highly adaptive behaviors such as visual search or foraging (Kristjánsson et al., 2020) where one or multiple targets must be selected from an array of distracting stimuli.

The additively independent combination is featured in several theoretical models of attention including TVA (Bundesen, 1990; Bundesen et al., 2005) and the feature-similarity gain model (Treue & Martinez-Trujillo, 1999). However, some empirical evidence suggests a deviation from a purely additive model in the direction of superadditivity (i.e. in the "and" direction; a stimulus combining multiple attended features receives a stronger attentional boost than the sum of the individual effects for each feature). For example, Hayden and Gallant (2009) examined how the combination of feature-based and spatial attention modulates responses of single V4 neurons and found that while each attentional dimension individually contributed to overall modulation, there was also a small synergistic, super-additive effect enhancing the target of both attentional systems. Similarly, among the five SSVEP studies described here one (Adamian et al., 2020) detected a statistically significant super-additive interaction, while four others reported non-significant effects in the same direction (p-values of 0.09, 0.07, 0.06 and 0.15). Furthermore, two of the studies also analyzed log-transformed SSVEP amplitudes to conclude that the data is better described by a multiplicative combination of independent factors (Andersen et al., 2011; Adamian et al., 2020, also see Nordfang, Staugaard & Bundesen, 2017). On the other side, the pure "AND" combination is unlikely given the number of studies demonstrating that feature-based attention is spatially global, that is, the attended color receives attentional enhancement throughout the visual field (e.g. Treue and Martínez Trujillo, 1999; Saenz et al., 2002, 2003). Thus, the real interaction term is likely to lie between additive and AND cases.

In absolute terms, the difference between the results of the additive and multiplicative combination is a small one. For example, two 20% attentional enhancements could be additively combined to 40%, or multiplicatively – to 44% (1+0.2+0.2 vs. 1.2x1.2, see equations (2) and (3)). The magnitude of the interaction suggests that individual studies may not have had enough statistical power to reliably detect deviations from additivity. Therefore, here we will test this hypothesis using a combined dataset.

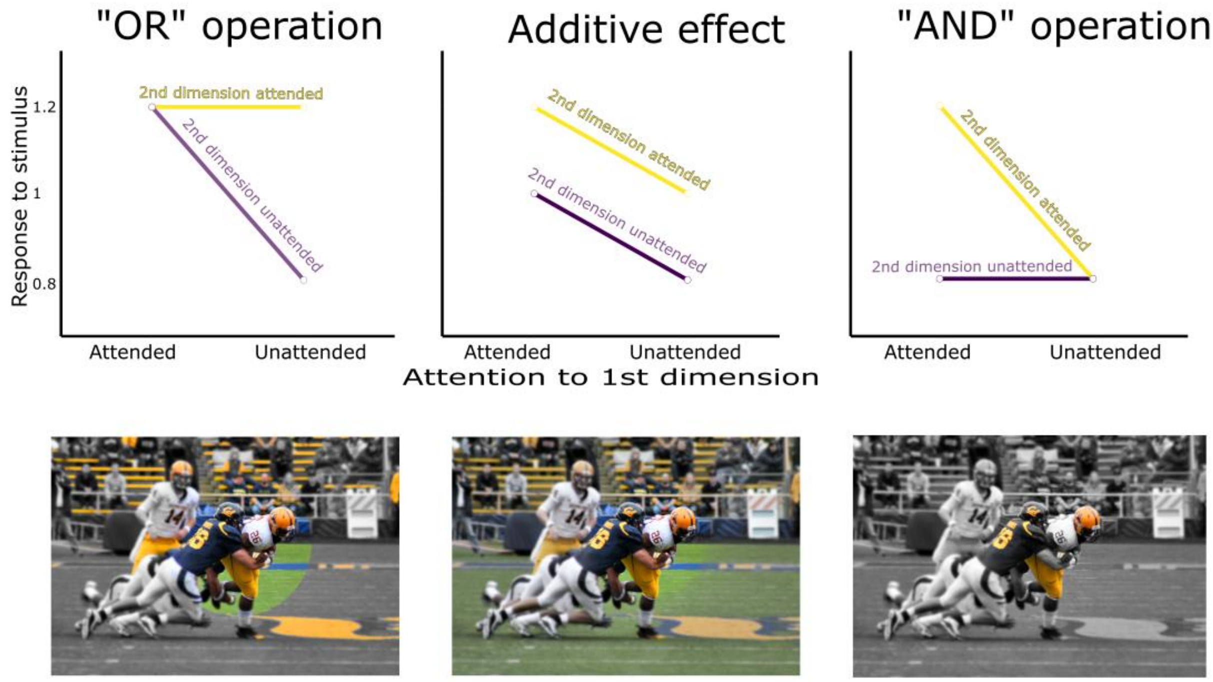

Figure 6. Illustration of the effects of possible combinations of attention to two dimensions. Top row: schematic demonstration of the differences between attended and unattended input in three scenarios. Bottom row: simulation of the three scenarios when to-be-attended features are yellow color and the spatial location of the ball. In the 'OR" scenario, attended objects include the area around the ball as well as all the yellow objects. Yellow parts of the image falling inside the spatially selected area do not receive any additional attentional boost. Under the additive combination of effects, both yellow color and the ball area undergo some attentional enhancement, but the yellow within attentional focus enjoys a double effect. Finally, the 'AND' operation results in the most restrictive selection where the only attended input is the to-be-attended color in the to-be-attended location ("IMG_6593" by John Martinez Pavliga is licensed under CC BY 2.0).

In each experiment (Andersen et al., 2008, 2011, 2015; Adamian et al., 2019, 2020) SSVEP amplitudes were calculated for each participant, condition, and frequency and rescaled as described in Equation (1). The resulting amplitudes were collapsed across frequencies to produce average amplitudes for each of the four attentional conditions (both features attended: A1+A2+, one feature attended: A1+A2-, A1-A2+, both features unattended: A1-A2-). For consistency, the first attentional dimension was, depending on the study, either color or luminance polarity selection and the second attentional factor was selection of orientation, space, or motion direction. Data were submitted to a 2x2 repeated measures ANOVA with both attentional dimensions as factors. If factors are super-additive, the interaction term in this ANOVA is expected to reach statistical significance. A simulation-based sensitivity power analysis (using the package Superpower in R: Lakens & Caldwell, 2021) indicated that with this sample size we will have 94% chance of detecting a deviation from additivity of 4%.

Figure 7 shows the summary of rescaled and averaged SSVEP amplitudes for each of the conditions across the five studies as well as their average. Only in one of these studies the interaction between the two attentional dimensions was originally reported as significant (Adamian et al., 2020). However, in the combined dataset the interaction is highly statistically significant ($F_{(1,79)} = 18.33$, $p < 10^{-5}$, $\eta^2 = 0.03$). This effect persists even if the study with the originally significant interaction is omitted ($F_{(1,63)} = 15.93$, $p < 10^{-4}$, $\eta^2 = 0.03$). This confirms that when two attentional factors are manipulated together, their effects are combined super-additively.

Both main effects of the attentional manipulations also significantly modulate SSVEP amplitudes (color/luminance polarity: $F_{(1,79)} = 249.62$, $p < 10^{-25}$, $\eta^2 = 0.63$; orientation/space/motion: $F_{(1,79)} = 81.92$, $p < 10^{-13}$, $\eta^2 = 0.24$). To test for the dependence of the magnitude of these effects across participants we subjected the main effects for both attentional factors for each participant (n=80) to a repeated measures correlation (Bakdash & Marusich, 2017). Participants with stronger attentional effects in one dimension also tended to exhibit stronger attentional effects in the other dimension ($r_{rm(74)} = 0.3$, $p = 0.008$, 95%CI = [0.08 0.49]), suggesting that attentional modulation of different features has a common influence, perhaps in form of alertness or vigilance, although this is of a very modest magnitude and accounts for less than 10% of variability. Thus, the magnitude of attentional modulation for different feature dimensions is largely independent across participants, which seems consistent with our previous findings of independence of attentional selection of different feature dimensions (Andersen et al., 2015; Adamian and Andersen, 2019).

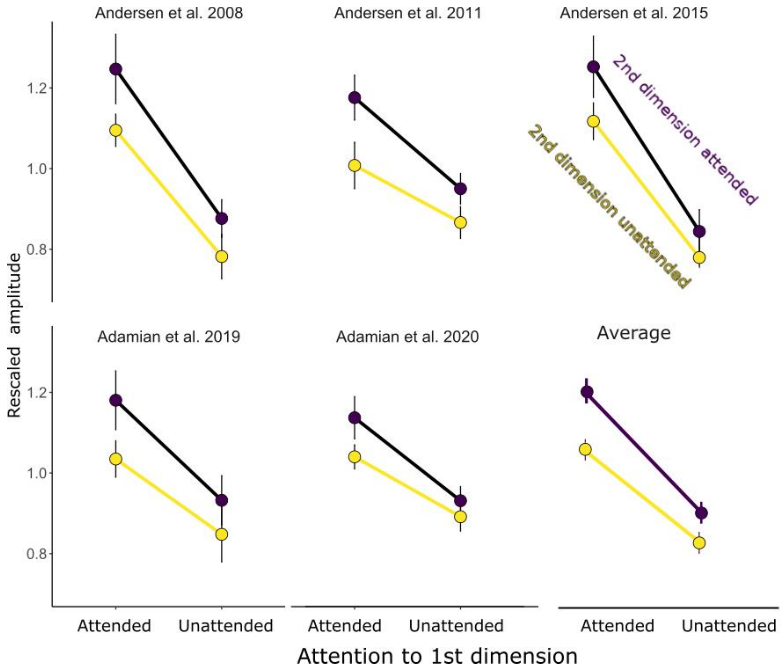

Figure 7. Effects of independent attentional dimensions are combined multiplicatively. Error bars are within-subject 95% confidence intervals (Morey, 2008).

The results of ANOVA allow us to conclude that attentional effects are combined super-additively. To further quantify the strength of this super-additivity we directly compared the fit of additive and multiplicative models to the data. The models took the form (2) and (3) respectively, where SSVEP amplitude (additive μ_a and multiplicative μ_m) is elicited by a combination of attentional coefficients related to two features. $\alpha_1$and α_2 take values of 1 or -1 depending on whether a feature is attended or unattended. The same resulting SSVEP amplitude (the left hand of the equation) could be produced by different β_1 and β_2 coefficients depending on the additive or multiplicative mechanism.

$$\mu_a = 1 + \alpha_1 \times \beta_1 + \alpha_2 \times \beta_2 \qquad (2)$$

$$\mu_m = \left(1 + \alpha_1 \times \beta_1\right) \times (1 + \alpha_2 \times \beta_2) \qquad (3)$$

For each participant regression coefficients β_1 and β_2 in two models were estimated using a non-linear curve-fitting procedure implemented by the MATLAB *fminsearch* function. The residuals of both additive and multiplicative models were entered into one-way ANOVA to determine whether the models explained the systematic variations of the data and which one provides a better fit.

Both additive and multiplicative models explain the data exceptionally well with R^2 of the additive model being 94.3% and R^2 of the multiplicative model being 95.7%. On the other hand, the test of the residuals of both models suggests a small amount of unexplained systematic variation (Additive: $F_{(3,77)} = 18.33$, $p < 10^{-10}$, $\eta^2 = 0.18$; Multiplicative*:* $F_{(3,77)} = 5.8$, $p = 0.0007$, $\eta^2 = 0.06$). The absolute residuals of the multiplicative model are substantially smaller than those of the additive model ($t_{(316)} = 7.16$, $p < 10^{-11}$), suggesting that the multiplicative model provides a better fit to the aggregated experimental data. Importantly, the unexplained variance points in the direction away from additivity, solidifying a multiplicative model as the better descriptor of the integration between attentional factors.

5. Attentional effects on SSVEP latency

The original analyses of the data presented here, as well as the previous sections of the re-analysis, were focused on the attentional effects on SSVEP amplitudes. The next section will turn to the other feature of the SSVEP – its phase. Phase measurements can be used to estimate the delay of SSVEP response from its generating flicker (Norcia et al, 2015; Di Russo et al., 2003). Of interest for the studies of attention is whether attentional enhancement also results in acceleration of stimulus processing. For example, Di Russo and Spinelli (1999) estimated the latency of SSVEPs from the phase and found shorter latencies (a reduction of ~15 ms) at a spatially attended location. Some electrophysiological studies in monkeys also showed that attention speeds up neuronal responses in areas V4 and MT, although the estimated acceleration was much smaller, 1-2 ms (Galashan et al., 2013; Sundberg et al., 2012). Several other studies did not find any influence of attention on neuronal latencies (Lee et al., 2007; Reynolds et al., 2000; Zhigalov & Jensen, 2020). Here we will use a combined SSVEP dataset with a variety of attentional manipulations to test whether attention changes the speed of processing in early visual cortex.

To estimate the latency of SSVEP response we first computed phases of complex amplitudes in radians for each participant, frequency, and electrode. The electrode selection was identical to the analyses of amplitudes. When more than one Attended and Unattended condition was present (Adamian et al., 2019; Andersen et al., 2013, 2015) response latency was estimated for each pair of conditions separately.

Phases φ in each frequency f were converted to latencies t in ms using the following equation:

$$t = -\frac{\varphi - \frac{\pi}{2}}{2\pi f} \tag{4}$$

Note that all phases are rotated by $\frac{\pi}{2}$ to account for the alignment between the phase of the stimulation and phase of the response.

Conversion of SSVEP phases to absolute latencies is ambiguous due to the circularity of the phase parameter. Since 0° phase angle is indistinguishable from 360° phase angle, SSVEP response phase can ‘wrap around’. For instance, for 10 Hz flicker, phase angles repeat every 100 ms. This means that a phase angle of $\frac{\pi}{2}$ occurs at the 25 ms mark, but also at 125 ms, 225 ms and so on. This becomes even more ambiguous at higher frequencies. Previous studies circumvented this ambiguity by recording response phases at multiple frequencies and estimating the slope of the phase-frequency function (Di Russo & Spinelli, 1999; Russo et al., 2003b). Using these previous estimates, we restricted the values that latencies can take from 50 to 200 ms for the purposes of this analysis. In addition, to reduce uncertainty at higher frequencies we ensured that the difference between response latencies at different frequencies within one participant did not exceed 50 ms. Starting with the latency values estimated by equation (4) for each participant and frequency we added or removed full latency cycles (e.g. 100 ms for 10 Hz) until these two conditions (range of values and range of differences) were satisfied.

The estimation procedure based on the restricted absolute and relative values successfully returned unambiguous latencies in all experiments. Average SSVEP latencies across experiments ranged from 88 (±4) to 114 (±7) ms (Figure 8). In the combined dataset, latencies in Unattended conditions were on average 4.8 ms longer than in Attended conditions ($t_{(180)} = 8.02$, $p < 10^{-13}$). On the level of individual studies, four out of 12 comparisons did not reach statistical significance. Note that the resulting meta-analytic effect size (Figure 8: Right) is slightly lower than the simple aggregated mean difference, at 3.4 ms. Based on the standardized effect size of d = 0.32 the minimum sample size required to detect an effect of this size with 80% power is 64 participants.

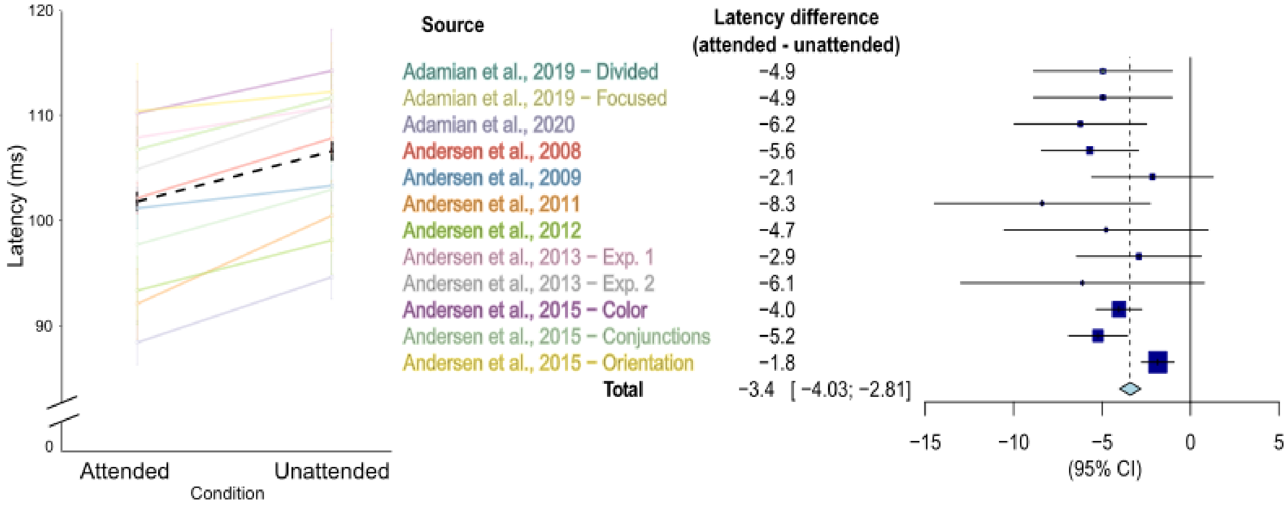

Figure 8. Attention shortens latency of SSVEP response. Left: Average SSVEP response latency in Attended and Unattended conditions. Error bars represent within-subject 95% confidence intervals. Right: Forest plot of effect sizes of attention on SSVEP latencies. The summary polygon in light blue shows the summary estimate of the effect sizes according to the fixed-effect model (Borenstein et al., 2011) and its confidence interval (in ms).

Thus, we identified a small (~4 ms) latency difference in the SSVEP response between attended and unattended conditions, which supports the claim that attention speeds up processing in early visual cortex. The magnitude of this latency change is comparable with previous results in monkey V4 (Sundberg et al., 2012: 1-2 ms). This effect is vastly smaller compared to attentional modulation of SSVEP amplitudes. Interestingly, the smallest attentional modulations of SSVEP latency (Andersen et al., 2009; Andersen et al., 2015 – Orientation) were also associated with relatively small amplitude differences (Figure 5). Low statistical power combined with the ambiguities in estimating absolute latencies from circular phase makes the use of phase delays in studies of attention less practical.

However, these results are of theoretical importance. The effects of attention on neural response are often compared to those of contrast enhancement. One of the similarities is that both attention and contrast increase the magnitude of neural responses (Lee & Maunsell, 2009; Martínez-Trujillo & Treue, 2002; Reynolds & Heeger, 2009), while the effect of attention on response latency has been less clear (McAdams & Reid, 2005; Zhigalov & Jensen, 2020). Our results confirm that similarly to contrast, attention modulates both amplitude and latency of neural responses in the early visual cortex.

While the main goal of the analysis was the estimation of relative latencies between conditions, the absolute latencies of SSVEP response are also of interest, as these are rarely reported in the literature. In our results, the range of obtained latencies was constrained by the latencies reported in the prior literature to avoid ambiguity due to the circularity of phases. Still, the differences between studies are notable. For example, two studies with the smallest SSVEP latencies overall (95 ms: Andersen et al., 2012; 91 ms: Adamian et al., 2020) are the only ones using luminance-defined flicker. This is consistent with a previous study using similar methodology which estimated that the response delay difference between isoluminant and luminance flickering stimuli is ~25 ms (Martinovic et al., 2018). In addition, studies where stimulation was presented peripherally have longer latencies (111 ms: Andersen et al., 2013; 109 ms: Adamian et al., 2019).

6. Attentional modulation of single-trial SSVEPs

As detailed in sections 3-5, attention consistently affects SSVEP amplitudes and latencies (phases) in the trial-averaged signal. Increased SSVEP amplitudes in the trial-average can mathematically result from increased amplitudes, stronger alignment of phases of single trials, or a combination of both. Here, we investigate which of these possibilities best explains the observed attention effects in our data. This question is of relevance for two main reasons: first it contributes to our conceptual understanding of attentional mechanisms and how changes in stimulus processing may be linked with behavioral effects. Whereas single-trial amplitude increases may reflect a sensory gain mechanism (Hillyard et al., 1998; Treue & Martínez Trujillo, 1999) that increases the signal-to-noise ratio of attended stimuli, a stronger alignment of single-trial phases reflects more consistent timing of stimulus processing across trials and therefore increased synchronization of neural populations responding to the stimulus when it is attended (Kim et al., 2007). Second, the analysis of single-trial SSVEP amplitudes has been successfully used to test for alternative accounts of observed effects in multiple studies (Gulbinaite et al., 2017; Soh & Wessel, 2021). For example, this has been used to test whether trial-averaged amplitudes result from a mix of trials with different attentional states (Andersen et al., 2008; Toffanin et al., 2009) or to establish whether single-trial relationships exist between subsequent components in order to narrow down possible causal interpretations (Andersen & Muller, 2010; Steinhauser & Andersen, 2019). A thorough understanding of attentional effects on the SSVEP on the single-trial level supports the optimal implementation of such approaches in future studies.

The idea of phase synchronization (Kim et al., 2007; Rager & Singer, 1998; Srinivasan et al., 1999) as a mechanism for attentional modulation of SSVEPs is based on the observation of increased intertrial phase coherence or ITPC of attended stimuli (Gulbinaite et al., 2019; Kashiwase et al., 2012; Kim et al., 2007). Inter-trial phase coherence (ITPC) is a measure of phase consistency across trials (Tallon-Baudry et al., 1996) which ranges from 0 (uniformly distributed phase) to 1 (perfect phase alignment). ITPC is defined as

$$ITPC(f) = \frac{1}{n}\left|\sum_{i=1}^{n} \frac{a_i(f)}{|a_i(f)|}\right| \qquad (5)$$

with $a_i(f)$ being the complex amplitude of frequency f in trial *i*, and the total number of trials n. ITPC captures the variability of phases -- If SSVEPs become more synchronized to the stimulation frequency, variability of phases decreases and phases become more consistent, increasing the ITPC (M. X. Cohen, 2014). However, when increased ITPC is accompanied by an increase in response amplitude of single trials, interpretation becomes difficult as the increase in synchrony could come about either because of the true synchronization of neural activity or because of the higher signal-to-noise ratio (SNR). With increased SNR, background noise (which has variable phase) contributes less to the overall response, also increasing ITPC (van Diepen & Mazaheri, 2018). Observing an increased ITPC in attended conditions is therefore not sufficient evidence for a pure synchronization account of attention effects, as the increased ITPC might just as well be due to the enhancement of a phase-locked response embedded in random noise. Distinguishing between these possibilities requires consideration.

Figure 9 illustrates three possible transformations of complex single-trial amplitudes (colored arrows) in an “unattended” condition. All three transformations lead to an identical trial-averaged response with ~40% increase of the phase-locked amplitude (black arrow), i.e. despite reflecting very different neural mechanisms, the three transformations are indistinguishable when only observing the trial-averaged response. The three mechanisms lie on a continuum with *pure amplitude increase* and *pure phase synchronization* at the extreme ends and *increased signal in noise* in-between. In the first transformation, pure amplitude increase, each single-trial amplitude receives an attentional boost (here: increase by 40%) without any changes in phase distribution. In the second transformation, pure phase synchronization leaves the magnitude (length of arrows) of all single-trials unchanged but instead rotates the phases to make them more aligned. Even though single-trial amplitudes remain the same, this boosts the phase-locked amplitude. One important consequence of this process is that it decreases variance of the complex amplitudes as trials move closer to each other in the complex plane (i.e. they become more similar). Finally, the *increased signal in noise* transformation assumes that the amplitude in each single trial is the sum of a phase locked signal which is equal to the trial average and noise of random phase and magnitude. In this case, attention only affects the signal part by adding a proportion of the trial averaged amplitude (here: 40%) to each trial. Thus, amplitudes of single trials are uniformly shifted in the complex plane, and the variance between them does not change. However, ITPC still increases as the proportion of the phase-locked signal relative to the random phase noise has been increased.

Overall, this demonstration shows that if phase-locking is the main driver of attentional effects on SSVEPs, single-trial SSVEPs will unavoidably be less variable in the experimental data. This prediction was tested in the aggregated dataset.

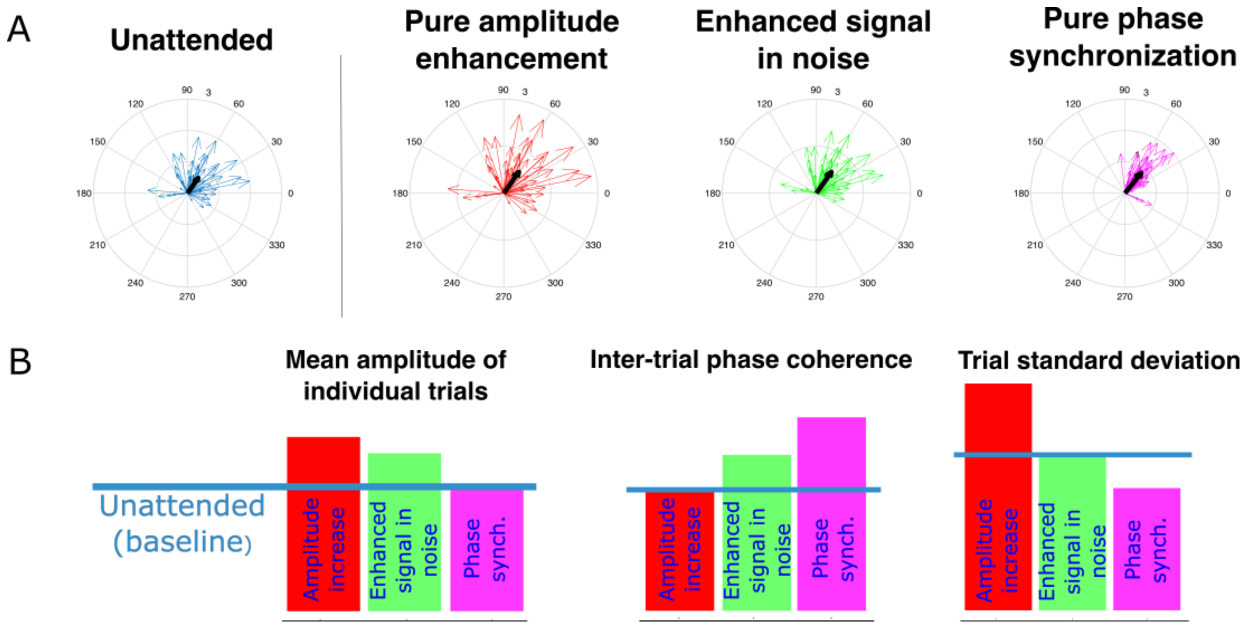

Figure 9. illustration of attentional effects on SSVEPs through three idealized mechanisms. A: example distributions of 50 trials in unattended (blue) and three different theoretical alternatives of attended conditions that yield the same trial-averaged SSVEP amplitude and phase. On these polar plots the length of each vector represents single-trial SSVEP amplitude and the angle is SSVEP phase. The black arrow represents the average phase-locked SSVEP, which is identical in all three theoretically derived attended conditions. Each of the attended polar plots shows a direct transformation of the unattended data. Single-trial SSVEP values (n=50) were generated by sampling real and imaginary components from a normal distribution based on the estimates of the mean and standard deviation of unattended trials across all datasets (m=0.2, sd = 0.5 for real and m=0.5, sd = 0.5 for the imaginary part). The generated 'unattended' values were used as a baseline for three transformations illustrating three paths leading to a ~40% increase of SSVEP amplitude. Pure amplitude increase was achieved by multiplying individual amplitudes (absolute values of the complex numbers) by a constant attentional coefficient of 1.4. Pure phase synchronisation was simulated by rotating the phases of single-trial SSVEPs such that each trial became closer to the average phase. Finally, to simulate the amplification of signal in noise, a proportion of the complex average was added to each single-trial value.
B: mean amplitude of single trials, inter-trial phase coherence and standard deviation of trials for each of the three transformations. Each bar in red (pure amplitude increase), pink (pure phase synchronization) and green (increased signal in noise) should be compared to blue (Unattended) to infer the direction of change.

In order to test which point on the continuum of transformations from pure amplitude enhancement to pure phase synchronization best accounts for observed attention effects in our nine datasets, we computed the average magnitude and standard deviation[2] of complex single trial amplitudes as well as the ITPC for attended and unattended conditions separately. SSVEP amplitudes were quantified as the complex Fourier coefficients at each of the stimulation frequencies in attended and unattended conditions (leaving out conditions where attention was partially directed to the stimulus). In contrast to the analyses described earlier, trials were not averaged prior to transformation into frequency domain but instead performed on each trial separately. Single-trial SSVEPs were then rescaled as described in equation (1), and their mean amplitudes and standard deviations were calculated.

[2] In case of complex numbers standard deviation refers to variability of distances to the complex origin and was calculated through MATLAB function *std*.

All three metrics -- ITPC, mean magnitude and standard deviation of single trials -- were modulated by attention (Figure 10). ITPC was higher in the attended compared to the unattended condition ($t_{(134)}$ = 13.12, $p < 10^{-16}$, d = 1.13) as were magnitudes of single-trial amplitudes ($t_{(134)}$ = 12.77, $p < 10^{-15}$, d = 1.10). Contrary to the prediction of the phase-locking account, standard deviation across trials also increased with attention ($t_{(134)}$ = 4.91, $p < 10^{-4}$, d = 0.42).

Our analysis confirmed the previously reported increased ITPC in attended trials compared to unattended trials. However, the increase in SSVEP magnitude in single trials is not predicted by a pure phase synchronization account and the increased standard deviation across trials directly conflicts with this account. A pure amplitude enhancement predicts increased magnitude and standard deviation, but not the observed change in ITPC. The enhanced signal in noise account is consistent with the increased ITPC and magnitude, but it does not predict a change in standard deviation between trials.

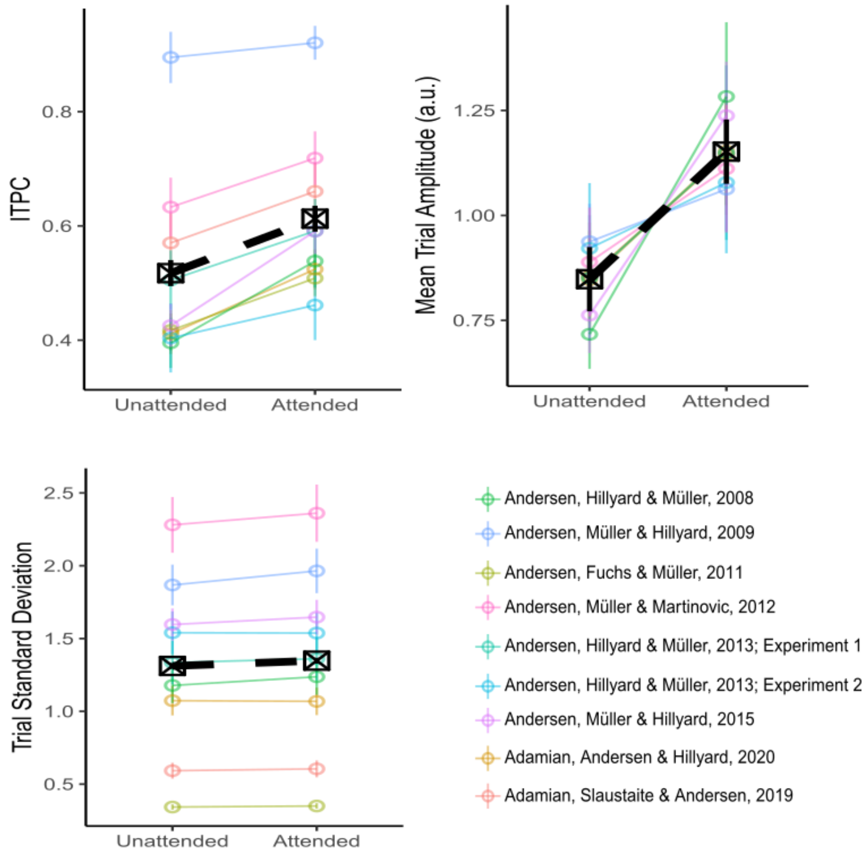

Figure 10. Results of single-trial SSVEP analysis demonstrating that ITPC as well as the magnitude and standard deviation of SSVEP amplitudes on individual trials are modulated by attention. Error bars denote 95% confidence intervals. Note that the unusually high ITPC in Andersen et al. (2009) might be a consequence of the stimulation where each position change in the RDK was synchronized with the flicker.

In summary, none of the three theoretically derived mechanisms (transformations) fully accounts for the observed data. Interestingly, pure phase synchronization (Kim et al., 2007) fares worst, as it is the only account that predicts a change in the opposite direction of what was actually observed. The data seems most consistent with a mechanism lying somewhere between *pure amplitude increase* and *increased signal in noise*. We thus propose that SSVEP attention effects can be accounted for by a boosting of a largely phase-locked signal embedded in non-phase-locked noise. This is similar to the *increased signal in noise* account but assumes that phase locking of the signal across trials is not perfect, thus leading to an increase in the standard deviation across trials with attention. Importantly, this account does not contradict previous findings of increased ITPC of SSVEPs with attention (Gulbinaite et al., 2019; Kim et al., 2007). Instead, it offers an alternative mechanism which explains both the increase in ITPC and the increase in single-trial amplitudes. One possibility for why signal phases are not perfectly aligned could be due to drifts in perceptual sensitivity over the time of a recording (which is typically in the order of one hour in the datasets investigated here). As the phase of the SSVEP systematically depends on stimulus contrast (Di Russo et al., 2001; Martinovic et al., 2018), such changes could affect the signal phase over the course of a recording session.

To conclude, the findings of our re-analysis rule out a phase synchronization account as a mechanism for attentional modulation of SSVEPs, as proposed by Kim et al. (2007). We propose that attention works through multiplicative (sensory gain) amplification of a largely phase-locked signal embedded in non-phase-locked noise.

Discussion

This paper presented the results of a combined reanalysis of nine experiments published in eight papers carried out in over the past 15 years. All of these studies used SSVEPs to probe visual attention and have individually contributed to our understanding of both attention and SSVEPs. Still, their combined reanalysis allowed us to uncover new knowledge without collecting more and bigger datasets.

The reanalysis demonstrated the following:

1) SSVEP amplitudes are highly variable between participants and stimulation frequencies.
2) Attentional modulation of SSVEP amplitudes is proportional to their magnitude. To account for (1) and (2), we recommend rescaling SSVEPs prior to statistical analysis rather than analyzing raw amplitudes.
3) The effect size of selective attention on SSVEP amplitudes is large and consistent across studies, with color-based selection demonstrating the strongest modulation.
4) When multiple features are attended together, attentional effects are combined multiplicatively rather than additively.
5) Attention reduces the latency of SSVEP responses by ~4 ms.
6) Sensory gain enhancement of a phase-locked signal in noise, rather than increased phase-locking across trials, explains the increase of trial-average SSVEP amplitude with attention.

The first part of the reanalysis (sections 1 and 2) focused on SSVEP amplitudes themselves, rather than on their attentional amplification. Perhaps the most important take-home message from this birds-eye view of thousands of SSVEP trials is that raw amplitudes shouldn't be used in parametric statistical analyses that assume additivity of effects, such as ANOVAs. The reason, as we have demonstrated, is that the magnitude of SSVEP amplitudes varies very substantially between participants and frequencies and that attention effects are relative to the overall magnitude of the SSVEP rather than additive. The difference between participants can easily become as big as the difference between measuring lengths in cm and inch (a factor of 2.54), and therefore using raw SSVEP amplitudes for statistical comparison is akin to measuring growth with a mix of measurements in cm and inches. Doing so would make highly consistent effects seem to vary substantially and thus reduce observed effect sizes. As we briefly discussed in section 2, there are multiple ways of transforming the data to make it conform better to the assumptions of additive parametric statistical tests.

In sections 3-6 we used the datasets to explore how SSVEPs are modulated by attention. The combined dataset featuring experiments similar in design provided an ideal ground for the comparison of effect sizes. We demonstrated that colour-based selection provides the strongest amplification of SSVEP amplitudes. This is consistent with the advantage of colour cues found using the visual search paradigm (Anderson et al., 2010; Sobel et al., 2009). However, it is important to remark that in visual search features and locations are not independent from each other, therefore attentional effects in our studies may not directly map onto the mechanisms of visual search. Still, our finding that colour provides the strongest attentional cue amongst simple features at the level of early visual cortex may explain cueing advantages found in visual search and preview paradigms.

We have also demonstrated that when two attentional dimensions are combined, the effects of individual attentional cues are applied multiplicatively, meaning that the combined effect is greater than the sum of individual attentional enhancements. This suggests that different types of attention (e.g. color selection, orientation selection, spatial) are served by separate neural subsystems and can be flexibly allocated to support behavioural goals (Doherty, 2005; Hayden & Gallant, 2009). An interesting extension of this conclusion concerns spatial attention. While some theories of attention posit that spatial location is itself a feature which participates in attentional selection on an equal basis with features such as color (Bundesen, 1990; Bundesen et al., 2005; Martinez-Trujillo & Treue, 2004), others suggest that location is prioritised for selection and that feature-based enhancement operates later (Liu et al., 2007) and is more pronounced at attended locations (Hillyard & Anllo-Vento, 1998). If spatial location dominated selection at the early stages of visual processing, we would have observed a stronger interaction between attentional factors when spatial selection was one of them, and weak or absent interaction between features of other dimensions. Instead, experiments manipulating spatial attention (Adamian et al., 2019; Andersen, Fuchs, et al., 2011) showed a very similar interaction effect size to those combining colour and orientation (Andersen et al., 2008, 2015), or luminance and direction of motion (Adamian et al., 2020), leading to the conclusion that spatial selection is treated equally to selection of other features in early visual processing. In our previous work we contrasted the SSVEP results to the ERP evidence (Adamian et al., 2019; Andersen, Fuchs, et al., 2011) demonstrating that spatial selection can become more dominant in at the later stages of processing of transient events. Based on the combinations of features represented in the current set of studies, we can conclude that in early visual processing selection of features combines multiplicatively, assigning weighted priority to all the potentially behaviourally relevant sensory input.

All the analyses above used participant-level SSVEP amplitudes, asking new questions using the data already reported in published papers. Next (sections 5 and 6), we turned to SSVEP phases, which have generally been analysed less in the SSVEP literature. The phase analysis showed a small but consistent acceleration of SSVEPs with attention which confirmed that attention modulates the latency of neural responses in early visual cortex. Finally, we performed a single-trial analysis of SSVEP amplitudes and phases to test whether the amplification of SSVEP amplitudes can be accounted for by phase-locking and concluded that this is not a plausible mechanism.

Many of the analyses presented here were only possible because we had access to participant-level and trial-level data. By combining multiple datasets to obtain much larger samples than those used in individual studies, we were able to answer our questions with much greater certainty and disambiguate small effects which were beyond the scope of the original studies. Since all the datasets were collected using a consistent set of functions and procedures, we were able to combine the datasets without much difficulty. This highlights the importance of developing interoperable and well documented EEG datasets which would allow reuse of data not only within a research group but also across different labs and platforms (Pernet et al., 2019). While the tools allowing seamless reuse of EEG data are still being developed, we would like encourage others to re-analyse their own work over the years. Many areas of cognitive science use comparable experimental designs across multiple experiments and studies, and as we have showed here, a large dataset combining these studies can yield more knowledge than was intended in the constituent individual papers.

Limitations of the re-analysis

This re-analysis included a cohesive set of studies, which, on one hand, allowed us to combine their results in meaningful ways, but on the other hand, necessarily restricted the variability of data. All the studies presented here were a part of one research program, where the stimulation and analysis code, the types of stimuli used, the questions asked, and the design of the experiments were similar in nature and shared between studies. Despite the fact that the data were collected across three different sites, the experiments were similar in design and execution, which may limit the generalisability of the findings.

The most obvious commonality of these studies is the type of stimulation and behavioural tasks. All the studies used a version of random dot stimuli presented against grey background, which is far from being the only way to elicit SSVEPs. However, this type of stimulation allows to control or manipulate spatial and feature-based attention together while keeping the physical properties of the stimuli identical, which is crucial for the studies of this type. The behavioural tasks in all the studies entailed detecting brief changes in the appearance or in the motion direction of a random subset of items. The advantage of these tasks is that they require attending to the whole set of items together rather than tracking an individual one, and that it is easy to manipulate task difficulty. On the other hand, they all focus on the same type of attention – sustained – and the results may not map directly only other contexts such as when attention is used to prepare for an upcoming stimulus (Battistoni et al., 2017) or to search for an item in an array (Forschack et al., 2022).

Given the high consistency of the results presented here, it is important to note that not all SSVEP studies find attentional effects, and effect sizes are less consistent when compared across a more diverse set of paradigms (Adam et al., 2020). This is not surprising, not only due to statistically expected null results (Ioannidis & Trikalinos, 2007) but also because of large variation in stimuli and analysis choices between studies. We hope that in the future the combination of focused methodological investigations and higher probability of publishing null results (Scheel et al., 2021) will allow to systematically investigate the effect of stimulation and analytical decisions on effect sizes in SSVEP studies.

Tips for successful SSVEP attention experiments

Frequency tagging of SSVEPs is not simply an experimental paradigm or an analysis technique, but the tightly interleaved combination of both with specific requirements for experimental design, stimulus timing, and signal processing. We would like to finish the Discussion of our findings with some advice for those deciding to carry out an SSVEP study of attention. These tips are a combination of take-home messages from our reanalysis and the general knowledge accumulated in the lab over the years.

1) Make sure stimuli elicit a robust SSVEP. If your goal is to detect attentional modulation of the SSVEP, the SSVEP itself should be readily observable, e.g., as peaks at the stimulated frequencies in the spectrum of a few pilot participants. As the SSVEP is highly sensitive to physical stimulus parameters (size, eccentricity, contrast, frequency, etc.), optimising these to produce a strong SSVEP should be a consideration in every study.
2) Pick stimulation frequencies according to your goals (see Andersen & Müller, 2015 for more on this). SSVEPs can be generated across a wide range of frequencies up to around 100 Hz (Hermann, 2001). In practice, most studies have focussed on the lower frequencies, although the use of higher frequencies has been advocated recently facilitated by the availability of high frequency display devices (this is often referred to as “rapid invisible frequency tagging” or RIFT, e.g., Sejjdel et al., 2023). In general, we have observed equivalent patterns of attentional modulation of SSVEPs across a range of frequencies, including those within the alpha band.
   Other considerations:
   - Lower frequencies often yield better SNRs
   - Range of usable frequencies depends on the mechanisms being driven (e.g., SSVEPs elicited by chromatic (isoluminant) flicker rapidly decline as one approaches flicker fusion around 20 Hz).
   - Choose nearby frequencies if keeping stimuli perceptually similar is important.
   - Pick frequencies that are further apart to avoid crosstalk when studying time-courses.
   - Ensure that employed frequencies are not harmonics of each other.
   - Avoid SSVEP frequencies within frequency bands of ongoing oscillations (alpha, beta, etc.) if these are to be quantified independently.
3) The SSVEP is a phase-locked response – analyse it accordingly. Whereas ongoing oscillations are commonly analysed in a non-phase locked manner, doing so for SSVEPs degrades the SNR as non-phase-locked noise is not averaged out.
4) Avoid physical confounds. SSVEPs are highly sensitive to changes in physical parameters, the effects of which can easily exceed those of attentional manipulations (see Andersen et al., 2012 for an example). Most importantly, change in retinal position can have a very big effect, and thus control of eye-movements is essential, especially when investigating spatial attention.
5) Verify stimulus timing. Timing issues like dropped frames may affect phase (and sometimes frequency) of the SSVEP, undermining its accurate quantification. Externally test stimulus timing by means of a photodiode and/or save a log of timestamps for each frame onset of an experiment so that any timing issues can be investigated after the recording session.

6) Tag task-relevant information with SSVEPs. Flickering a co-located stimulus (e.g., a patch of the background) as a proxy is indirect and may not fully reflect the relevant attentional mechanisms.
7) Make experimental paradigm and analysis go hand in glove. Even more than with other approaches, in SSVEP studies the experimental design defines what is measured and how it can be analysed. Test the analysis pipeline with pilot data before collecting the full dataset.
8) Verify the analysis pipeline and data using prior results and data. Do raw SSVEP amplitudes (in microvolt) and their topography match expectations from similar prior studies? Does the analysis pipeline reproduce known effects (e.g., if applied to publicly available datasets)? Are attentional effect sizes within the range of comparable studies? The current paper and the associated online resources provide a range of options for such comparisons.
9) Resist the temptation of overly ambitious studies. It pays off to break down the 'ideal study' into manageable experiments, allowing to verify different aspects of design and analysis step by step. For example, studying the time-course of attention using SSVEPs poses various additional challenges such as SSVEP time-courses being more sensitive to noise than the SSVEP amplitude quantified over a long time-window. Thus, an initial sustained-attention experiment is worthwhile to provide the asymptotic result of the subsequent time-course study, which can then be used as a benchmark.

Conclusion

SSVEP studies are a valuable tool in attention research. If measured and treated correctly, SSVEP amplitudes produce large and consistent attentional effects, which makes studies aimed at quantifying even subtle attentional modulation feasible. In this re-analysis, the first goal was to look at the basics of SSVEPs and demonstrate how intertwined signal properties, experimental design, and statistical analyses are. To summarise these basic properties, we provided practical recommendations on setting up SSVEP studies and analysing their data. The second goal of combining multiple datasets was to push the limits of SSVEP studies beyond testing the hypotheses they were originally designed to test. As a result, we demonstrated that attentional effects are combined multiplicatively when multiple features are attended together, and that SSVEP latency is reduced by attention. We have also showed that the increase of trial-average SSVEP amplitude is explained by a sensory gain mechanism rather than increase in phase-locking across trials. As cognitive neuroscience embraces the age of large-scale collaborative projects, we hope that such "zooming in" on the data to refine measurements and "zooming out" to harness the power of large samples will go hand in hand.

Data availability statement

Preprocessed anonymized data (averaged epochs for each condition) in EEGLAB format for each of the re-analysed studies as well as raw EEG data described in Adamian et al., 2019 are openly available at https://osf.io/rwqz2/.

Author contribution

NA: Conceptualization, Methodology, Software, Data curation, Visualization, Formal Analysis, Writing – Original Draft; SKA: Conceptualization, Methodology, Software, Resources, Funding Acquisition, Supervision, Writing – Review & Editing.

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Citation Diversity Statement

Proportions of citations by gender category are as follows: M/M = .66, W/M = .22, M/W = .05, and W/W = .007.

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