1 **Title:** Spatially organized flicker can evoke high-frequency responses above 100Hz in
2 visual cortex

3 **Running Title:** High-frequency SSVEP above 100Hz

4 **Authors:** Julian Keil[1,2,3], Hanni Kiiski[2,3], Liam Doherty[2], Victor Hernandez-Urbina[2], Hamed
5 Bahmani[2,4]

6 **Affiliations:** [1]Department of Psychology, Christian-Albrechts-University Kiel, Germany;
7 [2]Ababax.Health GmbH Berlin, Germany; [3]Department of Cognitive Science, University of
8 Potsdam, Germany; [4]Bernstein Center for Computational Neuroscience, Tuebingen,
9 Germany

10 **Keywords:** Visual stimulation, High-Frequency, EEG, SSVEP, Gamma

19 **Abstract:**

20 Flickering visual stimulation targeting the entire visual field can evoke steady-state visual
21 evoked potentials (SSVEPs), and these SSVEPs can potentially influence ongoing brain
22 activity. Here, we aimed at extending previous findings to evoke high-frequency SSVEPs.
23 We hypothesized that the sequential targeting of neighboring retinal areas allows evoking
24 a high-frequency series of visual evoked potentials which sum to a high-frequency SSVEP
25 across the visual cortex. By selectively and sequentially targeting neighboring retinal areas
26 with high-frequency flickering light, each area was only stimulated every 10ms, but
27 neighboring areas were stimulated at a lag of 8.33ms, 6.06ms, 5.55ms, and 5.26ms (i.e., 120,
28 165, 180 and 190Hz), for 60 trials of 2s, while we recorded 64-channel EEG from 10
29 participants. In line with our hypothesis, we measured SSVEPs for 120Hz and 180Hz
30 stimulation with an occipital topography. For the first time, we show that it is possible to
31 evoke high-frequency SSVEPs as high as 180Hz across the visual cortex by using a
32 spatially organized noninvasive visual brain stimulation. This critically extends previous
33 findings on SSVEPs following full-field visual stimulation. Spatially organized noninvasive
34 visual stimulation could potentially be used as a tool to influence high-frequency
35 oscillations, which opens the possibility of targeted therapeutic interventions.

36 **Introduction:**

37 Brain oscillations synchronize neural activity across brain regions for efficient information
38 processing and learning (Siegel *et al.*, 2012; Fries, 2015). Low-frequency oscillations
39 provide short windows of temporal integration (Busch & VanRullen, 2010; VanRullen, 2016),
40 and these discrete integration windows can be considered as a low-pass filter for visual
41 input. Gamma band oscillations are relevant for stimulus processing where single cycles
42 may represent specific stimulus features (Martinovic & Busch, 2011). Short ripples in
43 frequencies above the gamma band (i.e., sharp-wave ripples, SWR) are especially relevant
44 for the synchronization between neocortex and hippocampus during memory encoding,

45 consolidation, and retrieval (Dickey *et al.*, 2022). Artificially enhancing these oscillations
46 could potentially boost perception and information absorption (Hanslmayr *et al.*, 2019),
47 but research on evoking high frequency oscillations, especially noninvasively, is scarce.

48 Flickering visual stimulation can evoke steady-state visual evoked potentials (SSVEPs) in
49 visual cortical areas (Keil *et al.*, 2009; Norcia *et al.*, 2015). While SSVEPs to high
50 frequencies, up to 165Hz have been reported (Herrmann, 2001; Herbst *et al.*, 2013), most
51 research focuses on lower frequencies (Vialatte *et al.*, 2010). When stimulating the whole
52 visual field with flickering stimuli, the properties of the retina prevent evoking responses
53 above 100Hz: The retinal cones respond with a peak latency of approximately 10ms,
54 thereby creating a 100Hz low-pass filter to visual stimulation (Schneeweis & Schnapf,
55 1995). SSVEP paradigms often employ repeated flickering stimulation of the same location
56 in the visual field, for example to "tag" a specific spatial location with a specific stimulation
57 frequency. Notably, this frequency tagging can be reliably used at high frequencies
58 outside of the perceptual range at multiple locations in the visual field simultaneously
59 (Zhigalov *et al.*, 2019; Seijdel *et al.*, 2023). This indicates that it is possible to selectively
60 target specific areas of the retina at high frequencies.

61 Support for the idea, that spatially targeted high-frequency stimulation could evoke neural
62 activity at higher frequencies comes from a study in which participants could perceive
63 stroboscopic effects up to 300Hz (Bullough *et al.*, 2011). The solution to the apparent
64 contradiction between the low-pass filtering properties of the retina and the perceptual
65 reports of high-frequency stroboscopic effects could lie in the spatial response pattern of
66 the retina (Norcia *et al.*, 2015). While the retinal low-pass filter affects repeated stimulation
67 of the same retinal area, the stroboscopic effect at 300Hz was reported in the context of
68 saccadic eye movements, which shift the stimulated retinal area relative to the light input
69 (Bullough *et al.*, 2011). Thus, we asked whether it is possible to evoke high-frequency
70 SSVEPs using a high-frequency flickering light in combination with a spatial targeting
71 approach, which shifts the retinal target area. We hypothesized that sequentially targeting
72 neighboring retinal areas would evoke a high-frequency series of visual evoked potentials
73 which sum to a high-frequency SSVEP across the visual cortex (figure 1A and B). More
74 specifically, we hypothesized (hypothesis 1) that power of neural activity during our
75 stimulation should be strongest at the stimulation frequencies, and (hypothesis 2) at
76 electrode Oz over the primary visual cortex. We aimed at extending previous findings
77 (Herrmann, 2001; Herbst *et al.*, 2013) with spatially organized flicker stimuli to evoke
78 SSVEPs in the high frequency range above 100Hz.

79 **Material and Methods:**

80 To answer this question, we used a stroboscope (Rheintacho RT STROBE qbLEDs, 40
81 LEDs, 8x10cm) which allowed precise high-frequency flickering stimulation. As mentioned,
82 due to the refractory period of the retinal cones, stimulating the entire retina at the same
83 time is limited by the retinal low-pass filter properties (figure 1A). To achieve spatially
84 selective stimulation of neighboring retinal areas, we placed a 26cm rotating disk
85 comprising opaque and transparent sections in front of the stroboscope to build the
86 stimulation apparatus (figure 1B). We set the rotational speed of the disk so that the
87 opaque section travelled to the former position of a transparent section during the
88 stroboscope off stage. This allowed the synchronous targeting of retinal areas
89 corresponding to the transparent section of the disk, while the opaque sections blocked
90 the previously stimulated retinal areas from further stimulation for the duration of the
91 refractory period. By selectively and sequentially targeting neighboring retinal areas with

high-frequency flickering light, each area was stimulated with a lag of at least 10ms, but neighboring areas were stimulated at a lag of 8.33ms, 6.06ms, 5.55ms, and 5.26ms (i.e., 120, 165, 180 and 190Hz), depending on the rotational speed of the disk. Thus, while the stimulation during one flash only activated a spatially selective area of the retina, a different part of the retina was stimulated in each flash, and the lower visual field was stimulated across the two second stimulation interval.
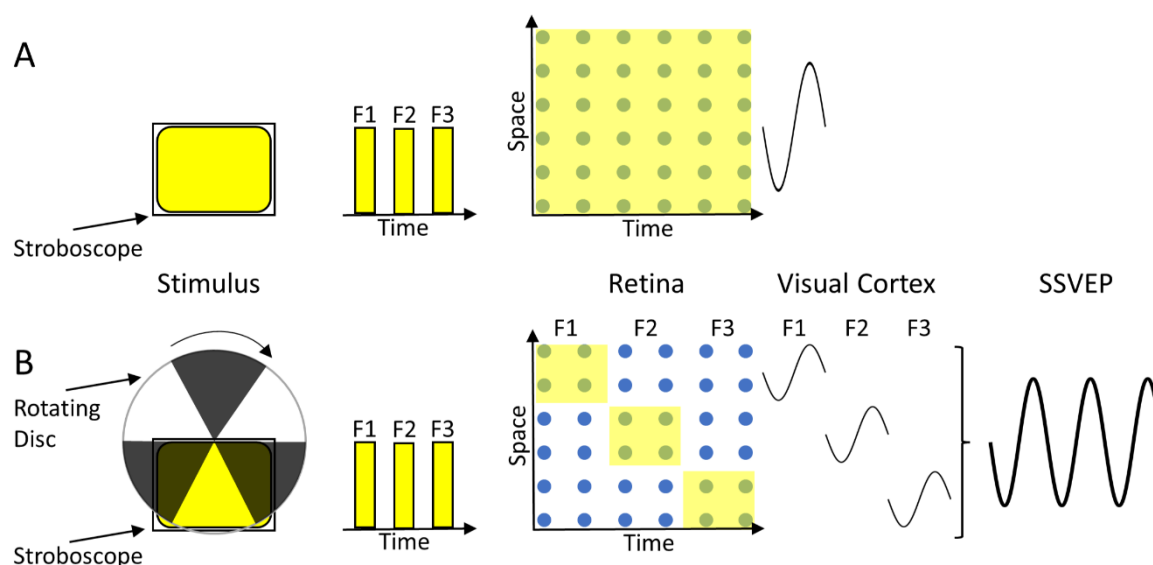

Figure 1: Overview of the stimulation. (A) High-frequency visual stimulation with a stroboscope creates a flickering visual stimulus (F1, F2, F3). Stimulating the entire retina simultaneously does not result in an oscillation, but one evoked potential to the stimulus onset due to the low-pass filtering properties of the retina. (B) Combining the high-frequency visual stimulation with a rotating disk allows sequentially targeting neighboring retinal areas, which should result in a temporal sequence of evoked potentials in adjacent parts of the visual cortex. Summed across the visual cortex, this results in an SSVEP.

Participants were seated 45cm in front of the clockwise rotating disk and fixated on a blue LED positioned 4cm above the center of the disk on top of the stroboscope, so that the visual stimulation arrived in the lower visual field. During 60 trials of each of the four frequencies (i.e., 120, 165, 180 and 190Hz) with two seconds of stimulation and an inter-stimulus-interval of two seconds, we recorded 61-channel EEG of 10 adult participants (3 females, 7 males, age range 20-62 years), who provided informed consent to participate in the experiment. In the current experiment, we used the 64-channel ANT eego mylab system (61 scalp electrodes, https://www.ant-neuro.com/products/eego-mylab) with CPz as the online reference electrode and AFz as the ground electrode at a sampling rate of 4000Hz, organized according to the 10–5 system (Oostenveld & Praamstra, 2001). Vertical, unilateral electro-oculogram was recorded by a single Ag/Cl electrode (same reference as EEG) placed approximately 2 cm below the left eye. Two electrodes were placed on the mastoids. Impedance was maintained below 20 kOhm.

Raw data were imported and analyzed in the EEGLab (Delorme & Makeig, 2004) toolbox (v14.1.2, http://sccn.ucsd.edu/eeglab) for MATLAB in conjunction with the FASTER plug-in (http://sourceforge.net/projects/faster). EEG data were high-pass filtered at 1Hz and low-pass filtered at 220Hz, with the notch frequency set to 48-52Hz (FIR filter). FASTER automatically identified and removed artefactual (i.e., non-neural) independent components, removed epochs with large artefacts (e.g., muscle twitch) and interpolated

124 channels with poor signal quality. Visual inspection of the EEG data was then performed
125 using ManualQC EEGLab plug-in (https://github.com/zh1peng/ManualQC). Epochs were
126 extracted around the flicker onset in a window from –2s before flicker onset to 2s after to
127 cover both the baseline interval as well as the flicker stimulation period. The resulting data
128 were then offline re-referenced to the average reference in the FieldTrip (Oostenveld *et
129 al.*, 2011) toolbox (https://www.fieldtriptoolbox.org/) for MATLAB, and an estimate of the
130 scalp current density (SCD) using the second-order derivative of the EEG potential
131 distribution based on spherical spline interpolation was computed (Pernier *et al.*, 1988;
132 Perrin *et al.*, 1989).

133 To analyze SSVEP power, single trial data were first averaged across trials and the
134 resulting event-related potential was then transformed to time-frequency representations
135 with a single-taper convolution-based time-frequency analysis. A Hanning taper was
136 applied to a fixed time window of 400ms for each frequency from 5 to 200Hz with 1Hz
137 spacing, shifted from –2 to 2s, in steps of 5ms. The resulting power spectra were averaged
138 in time across the baseline (–0.7 to –0.2s) and stimulation interval (0.2 to 1.7s), and the
139 relative power change between the stimulation and baseline interval was computed. The
140 time around stimulus onset was excluded from the data to avoid contamination by the
141 stimulus-onset event-related potential (ERP).

142 To identify significant modulation of SSVEP power and to test our two hypotheses, we
143 used two different bootstrapping approaches. We created randomly permuted data as a
144 null distribution under the assumption of no systematic differences between stimulation
145 condition by pooling trials across conditions within each participant. For 100 iterations, we
146 then drew the lowest number of trials across conditions from the pooled data and
147 computed the same time-frequency analysis as in the original data. To test hypothesis 1 in
148 the first approach across participants, for each stimulation condition, we compared
149 baseline-corrected power at the stimulation frequency to the median across the randomly
150 permuted data at all electrodes using a cluster-based nonparametric permutation t-test
151 based on 1024 iterations (Maris & Oostenveld, 2007). To test hypothesis 2 in the second
152 approach within participants, for each stimulation condition, we compared baseline-
153 corrected power spectra to randomly permuted data at all frequencies at electrode Oz.
154 The SSVEP at a given frequency was considered significant if the corresponding peak in
155 the power spectrum was larger than 97.5% (p < 0.025) of the power in the spectra of the
156 randomly permuted data (Herbst *et al.*, 2013). Furthermore, we conducted a Bayesian
157 linear analysis (Bürkner, 2017) based on two chains with 5000 iterations to evaluate the
158 hypothesis that the power modulation at electrode Oz is larger than the median across the
159 randomly permuted data.

160 **Results:**

161 To test the SSVEP power modulation compared to baseline, we conducted nonparametric
162 permutation-based (Maris & Oostenveld, 2007; Herbst *et al.*, 2013) and Bayesian (Bürkner,
163 2017) statistical comparisons of baseline-corrected power at the stimulation versus
164 randomly permuted data.

165 In a first step, across participants, we tested the hypothesis, that the high-frequency
166 visual stimulation evokes larger power than the median across randomly permuted data at
167 the stimulation frequencies using one-sided comparisons at all electrodes with cluster-
168 correction for multiple comparisons. In contrast to our first hypothesis, the cluster-based
169 permutation tests did not reveal significant differences between any of the conditions and
170 the permuted data. However, during 120Hz stimulation, the difference was most

171   pronounced across parieto–occipital electrodes (cluster t–value = 6.427, p = 0.057, figure
172   2A), and during 180Hz stimulation the difference was most pronounced across occipital
173   electrodes (cluster t–value = 7.043, p = 0.073, figure 2B), which indicates that the
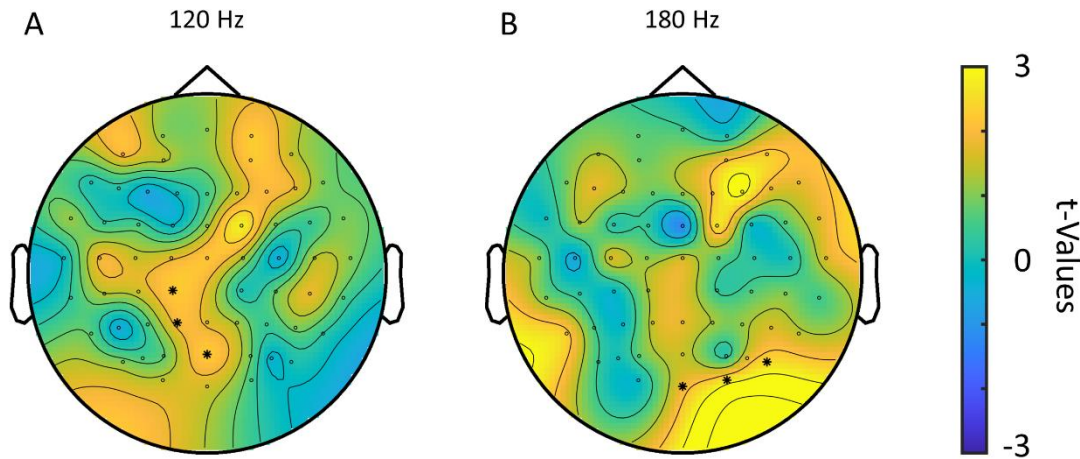174   strongest power modulation at 120Hz and 180Hz occurred over visual areas.

175

176   *Figure 2: Results of the statistical analyses with cluster-based permutation tests across participants. (A)*
177   *During stimulation at 120Hz, the most pronounced difference in SSVEP power occurred across parieto-*
178   *occipital electrodes (p = 0.057, cluster highlighted in bold). (B) During stimulation at 180Hz, the most*
179   *pronounced difference in SSVEP power occurred across occipital electrodes (p = 0.073, cluster highlighted in*
180   *bold).*

181   In a second step, within participants, we tested the hypothesis, that the high–frequency
182   visual stimulation evokes larger power than 97.5% of the power of randomly permuted
183   data at electrode Oz. In line with our hypothesis, we found significant power increase at
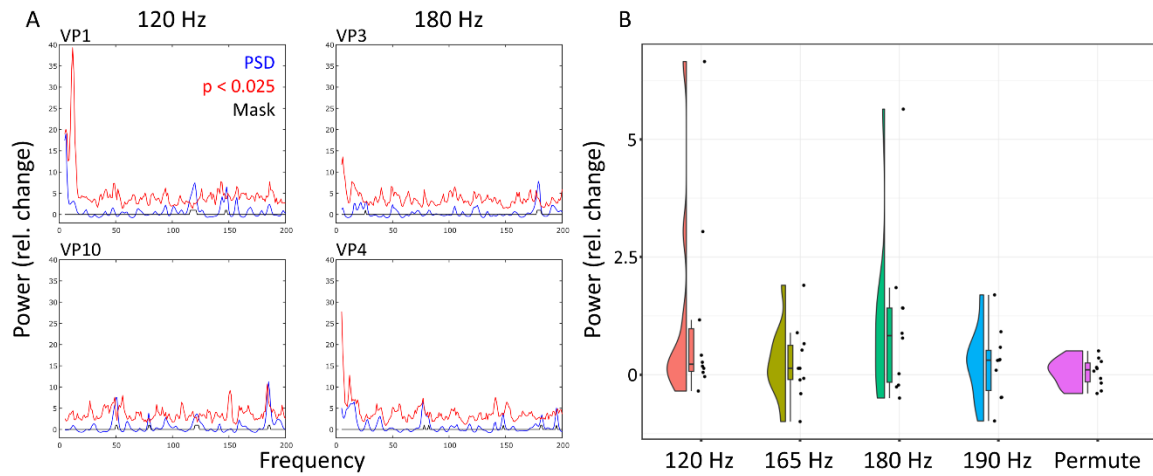184   120Hz and 180 Hz in 4 out of 10 participants (figure 3).

Figure 3: Results of the statistical analyses at electrode Oz. (A) During stimulation at 120Hz and 180Hz, four participants responded with significant (p < 0.025) power increase relative to randomly permuted data. The blue line illustrates the power spectrum at electrode Oz, the red line illustrates the 97.5% significance threshold based on 100 random permutations of data across conditions, and the black line marks frequencies in which the power spectrum is above the significance threshold. (B) Participants responded differently to the different stimulation conditions, with the largest tendency towards a consistent power increase at 120Hz and 180Hz.

Bayesian analyses provided small to moderate evidence for the hypothesis that the high–frequency visual stimulation evokes larger power than the power of randomly permuted data at electrode Oz (table 1), with the strongest evidence for a power increase at 180Hz.

Fre-quency	Mean Diff.	t-Value (df = 9)	p-Value	Cohens' d	BRMS Esti-mate	CI L	CI U	Evi-dence Ratio	Post-erior Prob.
120	1.087	1.642	0.067	0.519	0.18	−0.04	0.53	11.03	0.92
165	0.202	0.752	0.236	0.238	0.22	−0.1	0.55	6.77	0.87
180	**1.038**	**1.837**	**0.049**	**0.581**	**0.7**	**0.12**	**1.26**	**40.67**	**0.98**
190	0.177	0.815	0.218	0.258	0.21	−0.11	0.53	6.53	0.87

Table 1: Results of the one–sided statistical analysis of power increase relative to randomly permuted data at electrode Oz based on a parametric t–test and a Bayesian linear analysis.

Discussion:

In the current experiment, we asked whether it is possible to evoke high–frequency SSVEPs using a high–frequency flickering light in combination with a spatial targeting approach. We hypothesized that sequentially targeting selected neighboring retinal areas could evoke synchronized higher frequency responses summed across the primary visual cortex. In line with this hypothesis, we show that it is possible to evoke SSVEPs above 100Hz across occipital electrodes by using a spatially selective noninvasive visual brain stimulation. Importantly, this critically extends previous findings of high–frequency SSVEPs using full–field stimulation (Herrmann, 2001; Herbst *et al.*, 2013), or repeated stimulation of specific locations (Zhigalov *et al.*, 2019; Seijdel *et al.*, 2023). Statistical tests indicated the most pronounced power change from baseline at 120Hz and 180Hz in occipital electrodes. The current results could provide an answer for the question how perceiving stroboscopic

210   effects at 300Hz is possible: The sequential activation of neighboring retinal areas evokes
211   a series of ERPs in the visual cortex. We interpret our results to potentially indicate a
212   similar effect, in which sequentially targeting neighboring retinal areas likely evokes a
213   series of ERPs, which then sum up to an SSVEP across the visual cortex. The nature of the
214   cortical response to our stimulation however needs to be examined in closer detail using,
215   for example, intracranial recordings from visual areas in animals or epilepsy patients with
216   implanted electrodes.

217   Previous research on high-frequency SSVEPs showed that endogenous gamma
218   oscillations and exogenously driven SSVEPs coexist in the visual cortex (Duecker *et al.*,
219   2021), and might not propagate beyond visual cortex (Schneider *et al.*, 2023; Soula *et al.*,
220   2023). Our results show that it is possible to exogenously drive SSVEPs in visual areas at
221   high frequencies, and it needs to be examined, whether high-frequency visual stimulation
222   can entrain and thus directly influence ongoing brain activity. However, entrainment might
223   not strictly be necessary to influence brain activity, as different routes to this end can be
224   conceived: On the one hand, directly influencing or hijacking endogenous, ongoing neural
225   rhythms using electrical or cross-modal stimulation can influence perception (Thut *et al.*,
226   2011; Bauer *et al.*, 2021). On the other hand, exogenous stimulation can evoke brain activity
227   across a wide range of frequencies (Vialatte *et al.*, 2010), and these exogenously evoked
228   oscillations could give rise to functionally relevant brain activity in downstream brain
229   areas, albeit not necessarily in the stimulation frequency. Furthermore, previous SSVEP
230   studies used either full-field visual stimulation or repeated stimulation of the same retinal
231   area, and the low-frequency properties of the retina could be the reason for the limited
232   signal propagation. Thus, the range of signal propagation of spatially organized high-
233   frequency stimulation beyond sensory cortex, and the nature of the downstream effects
234   needs to be carefully investigated.

235   Whereas we identified cortical responses to our spatially organized high-frequency
236   stimulation in line with our hypothesis, there are still open questions to be addressed in
237   future follow-up studies. First, EEG records the summed dendritic postsynaptic potentials
238   across large neural populations (Cohen, 2017). Therefore, it is not clear whether the SSVEP
239   response we recorded in electrodes over the visual cortex represents the summation of
240   spatially adjacent local ERPs or the synchronous activity across the neural population
241   (Keitel *et al.*, 2022). To answer the question, whether entrainment of neural oscillations is
242   possible at high frequencies, it would be necessary to examine the sustained neural
243   activity in the stimulation frequency after stimulation offset with longer inter-stimulus
244   intervals. Moreover, a random spatial sequence instead of targeting neighboring areas of
245   the visual field, or recordings with a higher spatial resolution using intracranial recordings
246   could be useful to identify the extent of the neural network involved in the high-frequency
247   response. Second, whereas we found the strongest effects at 120Hz and 180Hz, the
248   absence of effects at the other frequencies as well as the large interindividual variability
249   need to be examined in closer detail. It is possible that different participants have
250   different preferred stimulation frequencies, and a replication in a larger sample could help
251   clarify this discrepancy.

252   **Conclusions:**

253   Our novel findings introduce a new, important avenue of research as spatially organized
254   noninvasive visual stimulation could potentially be used as a tool to artificially induce
255   naturally occurring high-frequency oscillations during stimulus processing, attentional

256 information selection, and memory (Abadchi *et al.*, 2020). This opens the possibility of
257 targeted therapeutic interventions based on high-frequency visual stimulation.

258

259 **Abbreviations**

260 SSVEP: Steady-State Visual Evoked Potential
261 ERP: Event-Related Potential
262 EEG: Electroencephalography
263 Hz: Hertz
264 LED: Light-emitting diode
265 SCD: Scalp Current Density
266 BRMS: Bayesian Regression Models using 'Stan'
267
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345

346 **Graphical Abstract:** Flickering visual stimulation targeting the entire visual field can evoke
347 steady-state visual evoked potentials. Sequentially targeting selected neighboring retinal
348 areas could allow evoking high-frequency responses in the synchronized summed activity
349 across the visual cortex. We show that it is possible to evoke steady-state visual evoked
350 potentials as high as 180Hz across the visual cortex by using a spatially selective
351 noninvasive visual brain stimulation.

Rotating Disc

Stroboscope

F1 F2 F3

Space

Time

180Hz

352