



Developmental experiences alter the temporal processing characteristics of the visual cortex: Evidence from deaf and hearing native signers

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Abstract

To date, the extent to which early experience shapes the functional characteristics of neural circuits is still a matter of debate. In the present study, we tested whether congenital deafness and/or the acquisition of a sign language alter the temporal processing characteristics of the visual system. Moreover, we investigated whether, assuming cross-modal plasticity in deaf individuals, the temporal processing characteristics of possibly reorganised auditory areas resemble those of the visual cortex. Steady-state visual evoked potentials (SSVEPs) were recorded in congenitally deaf native signers, hearing native signers, and hearing nonsigners. The luminance of the visual stimuli was periodically modulated at 12, 21, and 40 Hz. For hearing nonsigners, the optimal driving rate was 12 Hz. By contrast, for the group of hearing signers, the optimal driving rate was 12 and 21 Hz, whereas for the group of deaf signers, the optimal driving rate was 21 Hz. We did not observe evidence for cross-modal recruitment of auditory cortex in the group of deaf signers. These results suggest a higher preferred neural processing rate as a consequence of the acquisition of a sign language.

KEYWORDS

deaf, intramodal plasticity, sign language, steady-state visual evoked potentials, visual processing

Abbreviations: A, amplitude; DGS, Deutsche Gebärdensprache—German Sign Language; DS, deaf signers; EEG, electroencephalogram; FPVS, fast periodic visual stimulation; GLMMs, generalized linear mixed models; HN, hearing nonsigners (all hearing nonsigners who were tested for this study); HNDS, hearing nonsigners (controls for deaf signers); HNHS, hearing nonsigners (controls for hearing signers); HS, hearing signers; ICA, independent component analysis; LMM, linear mixed effects; M, magnocellular; MA, mean amplitude; NA, normalized amplitude; ROI, region of interest; SSVEP, steady-state visual evoked potential.

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1 | INTRODUCTION

Sensory-deprived individuals provide a unique opportunity to study to what extent the structural and functional organisation of the brain is dependent on environmental input (see Merabet & Pascual-Leone, 2010, for a review). Research in deaf individuals has documented extensive evidence for behavioural compensation and neural plasticity in the visual domain. For example, compared with hearing individuals, deaf individuals have been shown to be faster at detecting visual targets (Bottari et al., 2010, 2011; Codina et al., 2017; Hong Loke & Song, 1991), faster at detecting the direction of moving visual stimuli (Neville & Lawson, 1987), and better at reorienting attention in peripheral visual space (Bosworth & Dobkins, 2002a; Parasnis & Samar, 1985). Enhanced visual abilities in deaf individuals have been linked to intramodal plasticity, that is, plasticity within visual brain areas (Bottari et al., 2011; Smittenaar et al., 2016), and cross-modal plasticity, that is, a reorganisation of the deprived auditory cortices to process visual input (Lomber et al., 2010; Scott et al., 2014; see Alencar et al., 2019, and Cardin et al., 2020, for a review).

However, not all aspects of vision are changed following congenital deafness (Bavelier et al., 2006). Overall sensitivity for low-level visual aspects have been shown to be comparable in deaf and hearing individuals, including brightness discrimination (Bosworth et al., 2013; Bross, 1979), different aspects of contrast sensitivity (Finney & Dobkins, 2001), and direction and velocity of motion thresholds (Bosworth & Dobkins, 1999, 2002b; Brozinsky & Bavelier, 2004). Moreover, studies that have compared the visual temporal resolution of deaf and hearing individuals by means of critical flicker fusion (Bross & Sauerwein, 1980; Poizner & Tallal, 1987) or temporal order judgement paradigms (Nava et al., 2008; Poizner & Tallal, 1987) did not find differences between the groups. These findings are surprising in the light of studies showing that in hearing individuals one week of auditory deprivation is sufficient to improve the temporal resolution of the visual system (Bross & Zubek, 1975). However, the studies that reported null effects in deaf individuals used small sample sizes, thus possibly lacking power. In addition, the study by Nava et al. (2008) included deaf subjects with heterogeneous backgrounds in terms of aetiology and the age at onset of deafness. In contrast to congenitally deaf individuals, people with acquired deafness are more likely to have suffered neurological trauma or experienced a comorbid disorder (Dye & Bavelier, 2013). Such confounds might have masked the effects of auditory deprivation on visual functioning. Moreover, decision-criterion effects, which affect processing stages following early sensory encoding, could

have influenced the measurement of the critical flicker fusion thresholds (Clark et al., 1967) in the studies by Bross and Sauerwein (1980) and by Poizner and Tallal (1987). Such response biases may have masked differences between groups which are related to earlier processing stages.

Visual processing changes in deaf individuals not only seem to be the result of different sensory experiences but may additionally be linked to altered language experiences. Deaf individuals rely on visual communication strategies such as speech reading and sign language, and it has been shown that the habitual use of a sign language can lead to changes in the processing of visual information. Indeed, the reaction time advantage for peripheral stimuli previously reported for deaf individuals (Bottari et al., 2010, 2011; Hong Loke & Song, 1991; Neville & Lawson, 1987) seems to extend to hearing sign language interpreters (Codina et al., 2017), thus suggesting that these visual processing advantages might be the result of the habitual use of a sign language rather than of deafness.

Overall, it seems that deafness and the habitual use of a sign language lead to reaction time advantages in visual processing, rather than to enhanced visual sensitivity. What the underlying neural mechanisms for these reaction time advantages are and at which processing stage they emerge remains to be determined. It could be hypothesised that the reaction time advantages observed in deaf and hearing signers are due to changes in the temporal processing characteristics of the brain systems supporting visual processing. To directly assess the temporal processing characteristics for visual information in deaf and hearing adults, the present study recorded the electroencephalogram (EEG) during fast periodic visual stimulation (FPVS). A periodic visual stimulus typically leads to a periodic neural response, also known as the steady-state visual evoked potential (SSVEP; Regan, 1966), expressed in the EEG frequency spectrum as an amplitude increase at the stimulation frequency. This paradigm has the advantage that it does not require an overt response to measure temporal neural processing capacities and thus does not involve decision criteria related processes.

It has been shown that the magnitude of SSVEPs is markedly greater for particular stimulation frequencies than for others and that the optimal stimulation frequency differs between the different sensory systems. While the primary visual cortex shows the highest SSVEPs for presentation rates between 9 and 18 Hz (Kuś et al., 2013; Nakanishi et al., 2014; Pastor et al., 2003; Regan, 1966, 1975), the primary auditory cortex maximally responds to auditory periodic stimulation around 40 Hz (Galambos, 1982; Stapells et al., 1984), and

the somatosensory cortex to tactile periodic stimulation between 20 and 27 Hz (Tobimatsu et al., 1999). It has been suggested that individuals with higher optimal stimulation frequencies have better temporal resolution in perception (Baltus & Herrmann, 2016). Evidence for this notion is provided by findings that individuals with higher optimal stimulation frequencies have lower gap detection thresholds for auditory stimuli than people with lower optimal stimulation frequencies (Baltus & Herrmann, 2015). Thus, the temporal frequency tuning function of the neural system can be interpreted as a temporal filter characteristic and can provide information about its temporal resolution.

The aim of the present study was to assess whether deafness and/or the acquisition of a sign language leads to changes in the temporal processing characteristics of the neural systems supporting visual processing. To this end, we used a fast periodic visual stimulation (FPVS) paradigm to record SSVEPs from congenitally deaf native signers, hearing native signers, and from hearing nonsigners as controls. In different runs, the luminance of the visual stimuli was periodically modulated at 12, 21, and 40 Hz. These frequencies were selected to approximately match the optimal stimulation frequencies of the primary visual, somatosensory, and auditory system, respectively. Thus, the different stimulation frequencies allowed us to assess whether the sensory cortices in question show the highest SSVEPs in response to their typical driving frequencies, in response to frequencies typical for the other input modalities, and/or at an intermediate frequency. By testing deaf and hearing native signers, as well as hearing nonsigners, we were able to assess whether possible group effects were driven by deafness, the acquisition of a sign language or by an interaction of the two.

Therefore, this design allowed us to test for both intramodal and cross-modal mechanisms that could contribute to the visual processing advantages that have previously been observed in deaf individuals. Intramodal plasticity would show up in a change of the optimal stimulation frequency for FPVS in visual areas. We hypothesised that both deafness and the acquisition of a sign language would lead to higher optimal stimulation frequencies for FPVS in early visual areas. In addition, we tested whether, assuming cross-modal plasticity in deaf

individuals, the auditory cortex of deaf individuals develops to have similar temporal processing characteristics as the visual cortex, or if the temporal processing characteristics of the deprived auditory cortex resemble those of hearing individuals. The former outcome would suggest that the temporal processing characteristics of sensory areas are experience-dependent, while the latter outcome would suggest experience-independent temporal processing characteristics of sensory areas. In this latter case, we expected to observe a cross-modal recruitment of auditory cortex by FPVS for the group of deaf signers, but not for either of the hearing groups, with the highest SSVEP amplitudes in response to 40-Hz stimulation.

2 | MATERIALS AND METHODS

2.1 | Participants

Twenty-seven congenitally deaf native signers, 19 hearing native signers, and 36 hearing nonsigners participated in the experiment. The data from four deaf native signers and three hearing signers had to be excluded due to technical difficulties with the stimulation device. All the deaf signers were congenitally deaf and reported severe hearing loss (>85 dB in the better ear), were born to deaf parents and acquired a sign language as their primary and first language. All but one deaf signer (for this participant this information is missing) indicated their sign language skill to be 7 on a scale of 1–7 (1 = *not very good at all*, 7 = *excellent*), and all deaf signers communicated with the researchers in German Sign Language (Deutsche Gebärdensprache: DGS). All the hearing signers were born to deaf parents and acquired a sign language as their first language. Most of the hearing signers indicated their level of sign language proficiency to be 7 (median, interquartile range [IQR] = 1.25, range = 2–7). From the total set of 36 hearing, nonsigning controls 23 were selected to match the group of deaf signers in age, gender, and handedness, and 16 to match the group of hearing signers (eight hearing nonsigners were included in both groups of hearing controls).

The demographic data of all four groups are shown in Table 1. All the deaf signers and all the hearing controls

TABLE 1 Demographic characteristics of the participants

Group	<i>n</i> total	Age (s.e.m.)	<i>n</i> females	<i>n</i> males
Deaf signers (DS)	23	28.1 (5.9)	14	9
Hearing nonsigners (HNDS—controls for deaf signers)	23	27.5 (5.5)	14	9
Hearing signers (HS)	16	31.7 (9.2)	14	2
Hearing nonsigners (HNHS—controls for hearing signers)	16	30.8 (9.4)	14	2

for the deaf signers were right-handed. In each of the groups of hearing signers and their matched controls, 14 participants were right-handed, one participant was ambidextrous, and one participant was left-handed.

All participants had normal or corrected to normal vision and none reported any history of psychiatric or neurological disorders. They gave written informed consent and received monetary compensation or course credit for taking part in the study. All procedures followed the standards set by the Declaration of Helsinki and were approved by the local ethics committee of the University of Hamburg.

2.2 | Stimuli

The stimuli were generated using the PsychToolbox extensions (Brainard, 1997) running under Matlab 2009 (The MathWorks, USA). The visual stimuli were presented using an Asus LCD VG248 computer monitor (refresh rate: 120 Hz), which was mounted in parallel to the tabletop. A mirror mounted below the screen in a 22.5° angle reflected the display. The stimulus was a white circle (2.2° or 2.8 cm) displayed on a grey background. The circle was presented either at the centre of the screen or in the left or right hemifield at 14.8° (or 19.26 cm) eccentric to fixation (from the centre of the circle). The luminance of the circle was modulated sinusoidally at 12, 21, or 40 Hz and oscillated between intensities of 0.3 (dark grey) and 1 (white). Thus, nine different conditions were presented, each repeated seven times, resulting in a total of 63 trials. The order of the presentation was fully randomised. Each stimulus stream lasted 34 s.

2.3 | Procedure

Participants were seated comfortably in a quiet, darkened room. An adjustable chinrest enabled a fixed effective viewing distance of approximately 74 cm and alignment of the participant's eyes with the central fixation cross. Before the main experiment, a short practice block consisting of six short trials (duration = 5 s) ensured that participants had understood and were comfortable with the task. Experimenters monitored participants' performance during the practice block, answering questions and offering clarification when necessary. The practice trials were not included in the data analysis. The experiment consisted of nine blocks of seven trials each.

During recording, participants were instructed to adapt a relaxed sitting position, to avoid any head or body movements, and to keep their eyes on the fixation cross. Each trial began with 3 seconds of fixation, followed by

the presentation of the visual stimulus. During each trial, participants were asked to detect changes in the colour of the circle from white to red for five frames. These colour changes were inserted at a random position in nine trials. These trials were excluded from the analysis. At the end of each stimulus, a screen appeared with the question of whether a colour change had been detected or not. Participants responded with their eyes by fixating on either 'yes' (German: 'Ja') presented 10.8° (or 14 cm) to the left of fixation or 'no' (German: 'Nein') presented 10.8° (or 14 cm) to the right of fixation. We chose this form of response because all of the participants additionally completed an experiment with tactile stimulation (not reported here) where a manual response was not possible. No performance feedback was given. The change detection task ensured that participants maintained attention on the stimulus during recording. After each block, participants were asked whether they wanted to take a break or continue with the experiment.

To ensure central fixation during stimulus presentation we monitored participants' eye movement with an EyeLink 1000 eye tracker (SR Research, Kanata, Ontario, Canada), which were sampled at 1000 Hz. Trials during which participants failed to maintain central fixation were excluded from the EEG data analysis. This led to the exclusion of 2.8% of the trials for the group of deaf signers and 5.8% of the trials for their matched controls. For the group of hearing signers, 5.8% of the trials were excluded and 4.9% of the trials for their matched controls. The number of excluded trials did not significantly differ between the groups (all $ps > 0.199$).

2.4 | EEG acquisition

EEG data were acquired with 74 sintered Ag-AgCl electrodes mounted into an elastic cap (EASYCAP GmbH, Herrsching, Germany). Electrodes were arranged according to the standard 10–10 system and connected to a BrainAmp DC Amplifier (Brain Products GmbH, Gilching, Germany; <http://www.brainproducts.com>). Electrode impedances were kept below 20 k Ω . EEG data were recorded referenced to the left earlobe at a sampling rate of 1 kHz. A 0.016- to 250-Hz hardware bandpass filter was used during the recording.

2.5 | Analysis

2.5.1 | Behavioural data

We analysed accuracy using generalised linear mixed models (GLMMs) with a binomial link function

(Jaeger, 2008). As fixed effects, we entered group, frequency, visual hemifield, and their interaction terms into the model. As random effects, we included intercepts for subjects. Significance of fixed effects was assessed with likelihood ratio tests comparing the model with the maximal fixed effects structure and a model that excluded the fixed effect of interest. These comparisons were calculated using the afex package (Singmann et al., 2018) and employed Type III sums of squares and sum-to zero contrasts. Fixed effects were considered significant at $p < 0.05$. Post-hoc comparisons of significant interactions were conducted using approximate z -tests on the estimated marginal means (Lenth, 2018). The resulting p -values were corrected for multiple comparisons following the procedure proposed by Holm (1979).

2.5.2 | EEG data

The analyses were performed using Letswave 6, an open-source toolbox (<http://nocions.webnode.com/letswave>) running over MATLAB R2017b (MathWorks, USA). Continuous EEG recordings were filtered using a fourth-order zero-phase Butterworth band-pass filter, with cutoff values of 0.05–120 Hz. Data were downsampled to 250 Hz and then segmented into epochs of 36 s, including 2 s before and after each trial. To remove blink artefacts, independent component analysis (ICA) was applied to data of participants who blinked more than 0.2 times/s on average during the epochs. Channels that were artefact-prone across more than five trials (less than one channel on average per subject) were linearly interpolated using three neighbouring electrodes. All EEG channels were referenced to the common average of scalp electrodes.

Each epoch was re-segmented from +2 to +32 s relative to the onset of the stimulus train to obtain 30-s-long epochs. The first 2 s of each trial were excluded to avoid any contamination by the initial transient responses evoked by the onset of the stimulation. For each subject

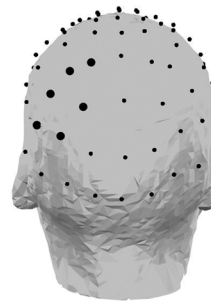
and condition, epochs were averaged across trials in the time domain to cancel out EEG signals that were non-phase locked to the stimulus. The data were then transformed into the frequency domain using a discrete Fourier transform, resulting in a frequency spectrum ranging from 0 to 250 Hz with a resolution of approximately 0.03 Hz (1/30 s). Because noise levels vary across the spectrum of EEG data (usually being higher at lower frequencies and higher in certain frequency bands, such as the alpha band), a local baseline-subtraction was applied. The baseline, as defined by the average amplitude of the 20 frequency bins surrounding each frequency bin (Rossion & Boremanse, 2011; Srinivasan et al., 1999) (excluding the immediately adjacent bins and the local maximum and minimum amplitude bins of the surrounding frequency bins), was subtracted from each frequency bin.

In a first step, a region of interest (ROI) analysis was performed for each viewing condition (central vs. peripheral) on the baseline-subtracted amplitudes of the first harmonic (stimulation frequency) to assess whether the optimal stimulation frequency differed as a function of group. The ROIs were defined separately for each of the three stimulation conditions (left, central, right). For central stimulation, a parieto-occipital ROI was defined that comprised channels Oz, Iz, O1, O2, O9, O10, POz, PO3, PO4, PO7, and PO8 (see Figure 1a, based on the visual ROI defined by Porcu et al., 2013). For peripheral stimulation, a left and a right parieto-occipital ROI were defined. The left parieto-occipital ROI comprised channels O1, PO3, PO7, P1, P3, P5, and P7 (see Figure 1b). The right parieto-occipital ROI comprised channels O2, PO4, PO8, P2, P4, P6, and P8 (see Figure 1c). Baseline-subtracted values at individual channels were averaged within the ROIs for statistical comparisons. Subsequently, we normalised the obtained amplitudes of each participant with the following formula: $NA = (A + 1) / (MA + 1)$, where NA is the normalised amplitude, A is the amplitude for a specific condition (frequency, site of stimulation [peripheral or

(a) parieto-occipital



(b) left parieto-occipital



(c) right parieto-occipital



FIGURE 1 Electrode montage. Electrode clusters used in the analyses are marked in bold

central)), and MA is the mean amplitude over all the stimulation frequencies for a specific site of stimulation (Porcu et al., 2013). This normalisation procedure removed inter-individual variance in absolute amplitude while retaining the effect of frequency. For group-level display, the grand-averaged amplitude spectra were computed for each channel.

Additionally, we analysed the sum across all significant harmonics (Retter et al., 2021) to test whether possible group differences were specific to the first harmonic (i.e., the stimulation frequency) or also present at integer multiples of the stimulation frequency (i.e., higher harmonics). The full details and results of this analysis can be found in the Supporting Information.

Statistical comparisons between groups and conditions were performed separately for central and peripheral stimulation. We used R (R Core Team, 2017) and nlme (Pinheiro et al., 2020) to perform a linear mixed effects analysis of the baseline-subtracted amplitude within the given ROIs. For the analysis of the central data, we entered group (deaf, hearing) and stimulation frequency (12, 21, or 40 Hz), as well as their interaction terms as fixed effects into the model. As random effects, we included intercepts for subjects. For the analysis of the peripheral data, we entered group (deaf, hearing), stimulation frequency (12, 21, or 40 Hz), ROI (left, right), and visual hemifield (left, right), as well as their interaction terms as fixed effects into the model. As random effects, we included intercepts for subjects. Fixed effects were considered significant at $p < 0.05$. Post-hoc comparisons were conducted using approximate t -tests on the estimated marginal means (Lenth, 2018). The resulting p -values were corrected for multiple comparisons following the procedure proposed by Holm (1979).

Assuming cross-modal plasticity in deaf individuals, we expected to find differences in scalp distribution between the groups of deaf signers and hearing nonsigners, that is, relatively higher amplitudes at frontal electrodes. Thus, in a second step, we computed cluster-based permutation tests (Maris & Oostenveld, 2007) to assess whether the topography differed between the groups for the different frequency and site of stimulation combinations. To this end, we conducted two-tailed independent t -tests comparing the amplitudes between the groups in question for each frequency and site of stimulation combination, at each channel. Clusters were defined by grouping together spatially adjacent channels that showed a t -test with $p < 0.05$. Then, a cluster-level statistic was calculated by taking the sum of the t -statistic for each channel within every cluster. The significance probability of the clusters was calculated by comparing each cluster-level statistic to values obtained from 1000 samples of a permutation distribution

constructed from the comparison between two groups that were generated by randomly reassigning the participants. The significance probability of the clusters was computed using the (nonparametric) Monte Carlo method. The Monte Carlo significance probability (p value) was determined by calculating the proportion of clusters from random partitions of the data that resulted in a larger test statistic than the clusters on the observed test statistic. A significance value of $p < 0.025$ was used to threshold the cluster statistic for all analyses. To control for Type 1 errors, a Bonferroni correction was applied for each pairwise comparison ($n = 9$), and the level of significance was adjusted to 0.006 (0.05/9).

3 | RESULTS

3.1 | Behavioural data

3.1.1 | Deaf signers and hearing nonsigners

Deaf signers and their matched controls performed the detection task with a median score of 0.97 proportion correct (deaf signers IQR = 0.048). The GLMM on accuracy did not reveal any interaction or main effects including the factor group.

3.1.2 | Hearing signers and hearing nonsigners

Hearing signers performed the detection task with a median score of 0.96 (IQR = 0.052) proportion correct and their matched controls with a median score of 0.97 (IQR = 0.067) proportion correct. The GLMM on accuracy revealed no interaction or main effects including the factor group.

3.2 | EEG data

3.2.1 | Intramodal plasticity—Region-of-interest analyses

Central stimulation

Deaf signers and hearing nonsigners (matched controls). The LMM on the baseline-subtracted amplitude revealed a two-way interaction between group and frequency of stimulation ($F(2, 88) = 8.42, p < 0.001$), suggesting that the effect of stimulation frequency differed between the two groups (see Figure 2). Indeed, post-hoc tests established that the group of deaf signers showed the

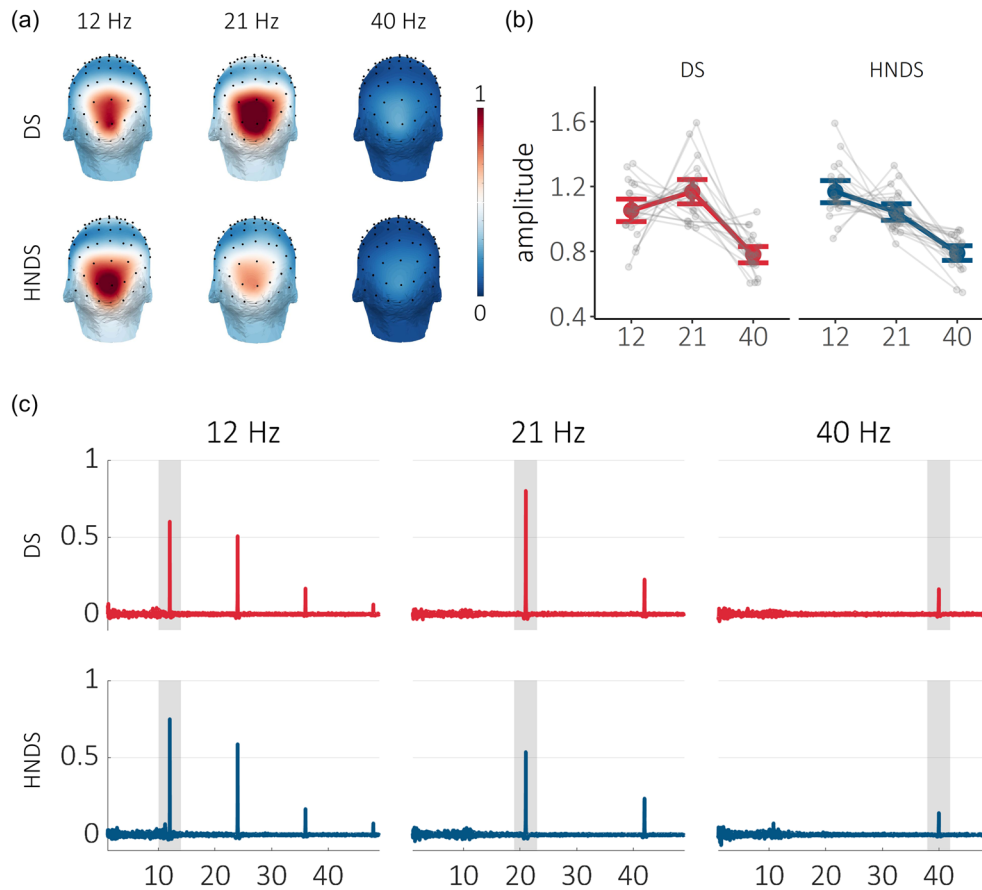


FIGURE 2 Frequency-tuning function of the SSVEPs in response to luminance changes in the central visual field. (a) Topographical distribution of the SSVEPs as a function of stimulation frequency and group. Amplitudes were baseline-subtracted. (b) Frequency-tuning function over the parieto-occipital region of interest as a function of stimulation frequency and group. Amplitudes were baseline-subtracted and normalised. Error bars indicate 95% confidence intervals. (c) EEG spectra as a function of stimulation frequency and group. Spectra were extracted from the parieto-occipital region of interest. Clear responses were observed at the fundamental frequency of stimulation (shaded in grey) and its harmonics. Amplitudes were baseline-subtracted and normalised. DS = deaf native signers, HNDS = hearing nonsigners (controls for DS)

TABLE 2 Results of post hoc tests comparing each of the stimulation frequencies within the groups of deaf signers (DS) and hearing nonsigners (HNDS) for the parieto-occipital ROI

Contrast	Group	Estimate	SE	df	<i>t</i> ratio	<i>p</i> value
12–21	DS	−0.115	0.042	88	−2.764	0.007
12–40	DS	0.274	0.042	88	6.595	<0.001
21–40	DS	0.388	0.042	88	9.359	<0.001
12–21	HNDS	0.126	0.042	88	3.025	0.007
12–40	HNDS	0.379	0.042	88	9.123	<0.001
21–40	HNDS	0.253	0.042	88	6.098	<0.001

largest SSVEP amplitudes in response to stimulation at 21 Hz, whereas the group of hearing nonsigners showed the largest SSVEP amplitudes in response to stimulation at 12 Hz (see Table 2). In addition, we assessed whether the response to the three stimulation frequencies differed between the groups. At 12 Hz, the group of deaf signers

showed weaker responses than the group of hearing nonsigners ($\beta = -0.115$, $se = 0.042$, $t = -2.772$, $p = 0.016$). At 21 Hz, the group of deaf signers showed stronger responses than the group of hearing nonsigners ($\beta = 0.125$, $se = 0.042$, $t = 3.017$, $p = 0.013$). At 40 Hz, the responses did not differ between the two groups

($\beta = -0.010$, $se = 0.042$, $t = -0.244$, $p = 0.808$). (See Table S2 for descriptive statistics of the data and Table S3 for the full results of the LMM.)

The additional analysis of the summed harmonics revealed that the frequency tuning function was indistinguishable for the groups of deaf signers and hearing nonsigners, that is, both groups showed the largest responses at 12 Hz and the weakest responses at 40-Hz stimulation (see Supporting Information for the full results of the analysis). Thus, the group difference seems to be specific to the first harmonic.

Hearing signers and hearing nonsigners (matched controls). The LMM on the baseline-subtracted amplitude revealed a main effect of frequency ($F(2, 60) = 59.19$, $p < 0.001$). The two-way interaction between group and frequency was not significant ($F(2, 60) = 1.99$, $p = 0.145$). However, given that we had a priori hypothesis about the effect of sign language use on the temporal processing characteristics of the visual system, we conducted post-hoc tests that assessed the effect of frequency within each group. These tests showed that for the group of hearing signers the SSVEP amplitudes for stimulation at 12 and 21 Hz were larger than for stimulation at 40 Hz (see Table 3 and Figure 3). The SSVEP amplitudes for 12- and 21-Hz stimulation did not significantly differ in the group of hearing signers. By contrast, the group of hearing nonsigners showed a clear maximum at 12-Hz stimulation, that is, in hearing nonsigners the SSVEP amplitudes for 12-Hz stimulation were significantly larger than for 21- or 40-Hz stimulation. In addition, we assessed whether the response to the stimulation frequencies differed between the groups. None of the comparisons were significant. (See Table S7 for descriptive statistics of the data and Table S8 for the full results of the LMM.) To explore whether the lack of a significant group by frequency interaction might be due to the relatively lower power due to smaller group sizes, we compared the group of hearing signers ($n = 16$) to all the hearing nonsigners ($n = 31$) who participated in this study. Here, the two-

way interaction between group and frequency turned out to be significant ($F(2, 90) = 3.40$, $p = 0.038$) and post-hoc tests assessing the effect of frequency within each group confirmed the results from the previous analysis (see Supporting Information for the full results of this analysis).

The additional analysis of the summed harmonics revealed, irrespectively of whether a subgroup of or all matched hearing nonsigners were included, that the frequency tuning function was indistinguishable for the groups of hearing signers and hearing nonsigners, that is, both groups showed the largest responses at 12 Hz and the weakest responses at 40-Hz stimulation (see Supporting Information for the full results of the analysis). Thus, the effect of group seems to be specific to the first harmonic.

Deaf and hearing signers. The results from the previous analyses suggested that the temporal frequency function seems to be shifted towards higher frequencies in both deaf and hearing signers. However, whereas deaf signers showed a clear maximum for stimulation at 21 Hz, the SSVEP amplitudes in hearing signers seemed to be indistinguishable for stimulation at 12 and 21 Hz. These findings suggest that deafness may additionally cause the visual system to be shifted towards higher optimal frequencies. To test this hypothesis, we compared the groups of deaf and hearing signers. The LMM on the baseline-subtracted amplitude revealed a main effect of frequency ($F(2, 74) = 62.60$, $p < 0.001$). The interaction between group and frequency was not significant ($F(2, 74) = 0.828$, $p = 0.441$). Post-hoc test showed that for the group of signers the SSVEP amplitudes for stimulation at 12 and 21 Hz were larger than for stimulation at 40 Hz. Additionally, the SSVEP amplitudes for 21 Hz were larger than for 12 Hz, although this was only a trend (see Table 4). (See Table S20 for descriptive statistics of the data and Table S21 for the full results of the LMM.) These results suggest that the effects observed between the groups of deaf and hearing signers and the

TABLE 3 Results of post hoc tests comparing each of the stimulation frequencies within the groups of hearing signers (HS) and hearing nonsigners (HNHS) for the parieto-occipital ROI

Contrast	Group	Estimate	SE	df	t ratio	p value
12-21	HS	-0.023	0.050	60	-0.464	0.644
12-40	HS	0.325	0.050	60	6.524	<0.001
21-40	HS	0.348	0.050	60	6.988	<0.001
12-21	HNHS	0.117	0.050	60	2.339	0.045
12-40	HNHS	0.381	0.050	60	7.640	<0.001
21-40	HNHS	0.264	0.050	60	5.301	<0.001

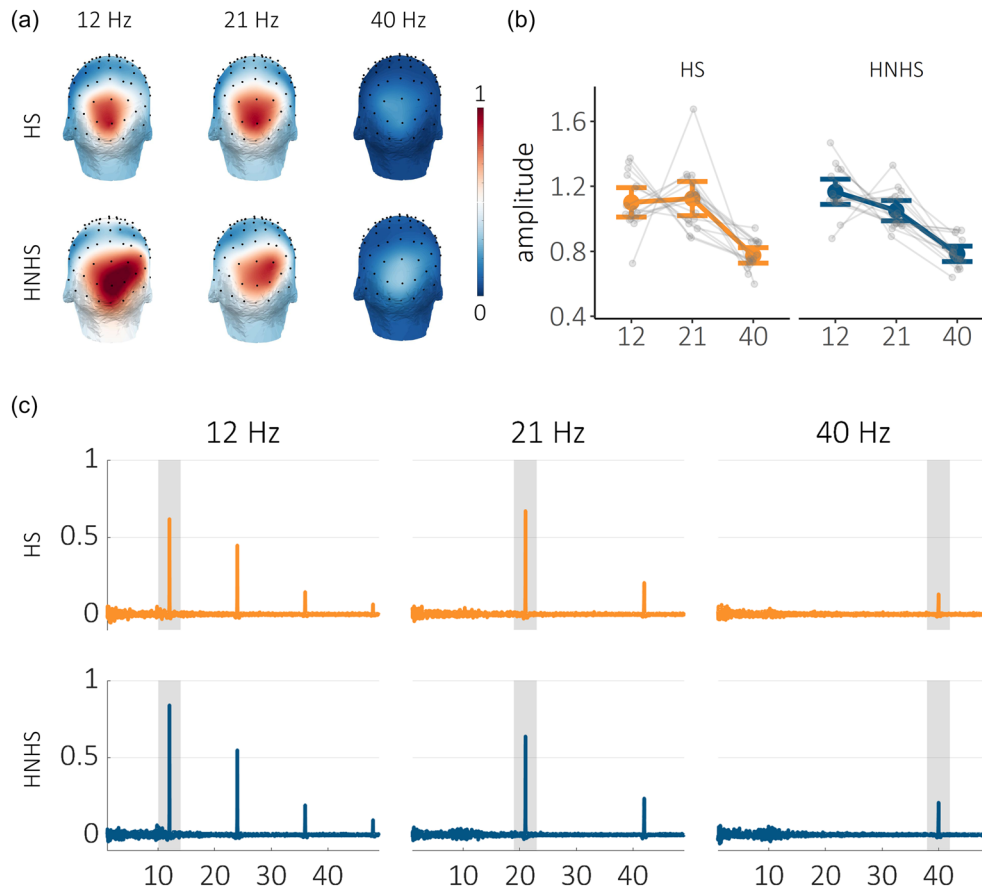


FIGURE 3 Frequency-tuning function of the SSVEPs in response to luminance changes in the central visual field. (a) Topographical distribution of the SSVEPs as a function of stimulation frequency and group. Amplitudes were baseline-subtracted. (b) Frequency-tuning function over the parieto-occipital region of interest as a function of stimulation frequency and group. Amplitudes were baseline-subtracted and normalised. Error bars indicate 95% confidence intervals. (c) EEG spectra as a function of stimulation frequency and group. Spectra were extracted from the parieto-occipital region of interest. Clear responses were observed at the fundamental frequency of stimulation (shaded in grey) and its harmonics. Amplitudes were baseline-subtracted and normalised. HS = hearing native signers, HNHS = hearing nonsigners (controls for HS)

TABLE 4 Results of post hoc tests assessing the effect of frequency within the parieto-occipital ROI

Contrast	Estimate	SE	df	<i>t</i> ratio	<i>p</i> value
12–21	−0.069	0.036	74	−1.932	0.057
12–40	0.299	0.036	74	8.395	<0.001
21–40	0.368	0.036	74	10.328	<0.001

groups of hearing nonsigners were predominantly driven by the acquisition of a sign language.

The additional analysis of the summed harmonics revealed that the frequency tuning function was indistinguishable for the groups of deaf and hearing signers, that is, both groups showed the largest responses at 12 Hz and the weakest responses at 40-Hz stimulation (see Supporting Information for the full results of the analysis).

Peripheral stimulation

Deaf signers and hearing nonsigners. The LMM on the baseline-subtracted amplitude revealed an interaction between frequency and group ($F(2, 484) = 3.68$, $p = 0.026$). Post-hoc tests showed that for the group of deaf signers the SSVEP amplitude for stimulation at 12 Hz was larger than for stimulation at 21 and 40 Hz (see Table 5 and Figure 4). Moreover, the SSVEP amplitude in response to 21-Hz stimulation was larger than for stimulation at 40 Hz; however, this was only a trend. Similarly, in hearing nonsigners, the SSVEP amplitudes for 12-Hz stimulation were significantly larger than for 21- or 40-Hz stimulation. Moreover, for hearing nonsigners, the SSVEP amplitude for 21 Hz was significantly larger than the SSVEP amplitude for 40-Hz stimulation. Thus, the two groups showed similar frequency tuning functions for peripheral stimulation. In addition, we assessed whether the response to the stimulation

TABLE 5 Results of post hoc tests comparing each of the frequencies within the groups of deaf signers (DS) and hearing nonsigners (HNDS) for the parieto-occipital ROI

Contrast	Group	Estimate	SE	df	t ratio	p value
12–21	DS	0.107	0.011	484	9.820	<0.001
12–40	DS	0.125	0.011	484	11.529	<0.001
21–40	DS	0.019	0.011	484	1.709	0.088
12–21	HNDS	0.067	0.011	484	6.146	<0.001
12–40	HNDS	0.095	0.011	484	8.738	<0.001
21–40	HNDS	0.028	0.011	484	2.592	0.020

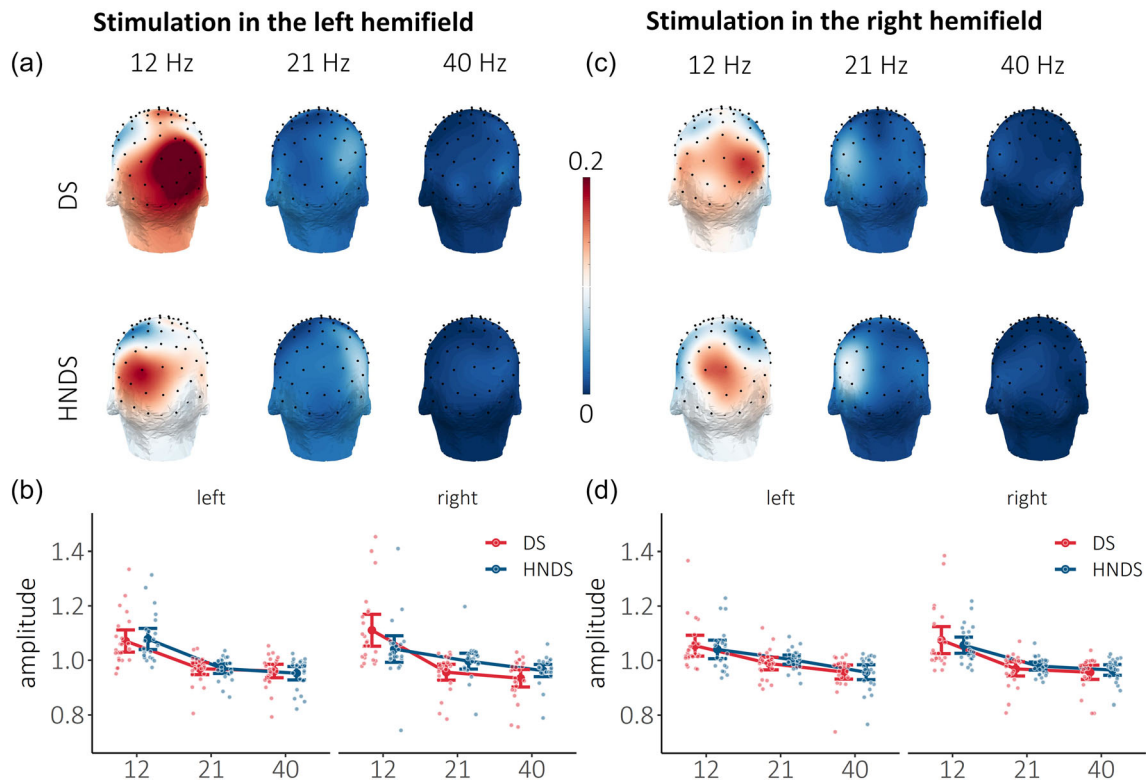


FIGURE 4 Frequency-tuning function of the visual cortex for processing luminance changes in the periphery. (a,c) Topographical distribution of visual SSEPs as a function of frequency and group. Amplitudes are baseline-subtracted. (b,d) Frequency-tuning function as a function of frequency and group. Amplitudes are baseline-subtracted and normalised. Error bars indicate 95% confidence intervals. DS = deaf native signers, HNDS = hearing nonsigners (controls for DS)

frequencies differed between the groups. None of the comparisons were significant (all $ps > 0.110$). Thus, the response profiles of the two groups were indistinguishable. (See Table S26 for descriptive statistics of the data and Table S27 for the full results of the LMM.) Moreover, we did not observe any evidence of cross-modal recruitment for this condition (see below for the results of the cluster-based permutation test and Figure S5). Thus, we did not observe effects of deafness and/or sign language use for peripheral stimulation. We therefore refrained from contrasting hearing signers and hearing nonsigners,

as hearing signers were included only to be able to dissociate possible effects of deafness and the acquisition of a sign language in case we observed differences between deaf signers and hearing nonsigners.

The additional analysis of the summed harmonics revealed that the frequency tuning function was indistinguishable between the two groups the largest responses at 12 Hz and the weakest responses at 40-Hz stimulation (see Supporting Information for the full results of the analysis). Thus, the effect of group seems to be specific to the first harmonic.

3.2.2 | Cross-modal plasticity—Cluster-based permutation tests

Deaf signers and hearing nonsigners (matched controls)

Auditory steady-state evoked potentials at 40 Hz have been suggested to reflect neural activation of the thalamus and the auditory cortices in response to auditory stimulation (Giraud et al., 2000; Herdman et al., 2003; Luke et al., 2017; Reyes et al., 2004) and typically show a maximum over frontal electrodes (Porcu et al., 2014; Zhang et al., 2013). Thus, assuming cross-modal recruitment in deaf individuals, we expected to find differences between deaf and hearing individuals at frontal electrodes. However, the comparison between the groups of deaf signers and hearing nonsigners did not reveal any clusters that significantly differed between the two groups (see Figure S5). Because we did not observe any evidence of cross-modal recruitment for this condition, we refrained from contrasting hearing signers and hearing nonsigners, as hearing signers were included as a control group to be able to dissociate possible effects of deafness and the acquisition of a sign language.

4 | DISCUSSION

The goal of the present study was to find out whether deafness and/or the acquisition of a sign language lead to changes in the temporal processing characteristics of the neural systems supporting visual processing. In addition, we wanted to test whether, assuming cross-modal plasticity in deaf individuals, the temporal processing characteristics of auditory areas resemble those of typical visual areas. To this end, we compared the optimal driving frequencies for luminance modulations as measured by SSVEPs between deaf native signers, hearing native signers, and hearing nonsigners. The comparison of the first harmonic response revealed that the groups of signers (including both deaf and hearing signers) and hearing nonsigners differed in their optimal driving frequencies in response to central visual stimulation: For the group of hearing nonsigners, the optimal driving rate was 12 Hz, which concurs with previous studies (Kuś et al., 2013; Pastor et al., 2003; Regan, 1966, 1975). By contrast, for the group of deaf signers, the optimal driving rate was 21 Hz, whereas for the group of hearing signers the optimal driving rates were 12 and 21 Hz. These results suggest that the acquisition of a sign language can alter the temporal processing characteristics of the early visual cortex. We did not find any evidence for cross-modal recruitment of auditory areas in the group of deaf signers.

The shift in optimal driving frequency in both deaf and hearing signers raises the question about the underlying neural mechanisms for this group difference in the visual temporal processing characteristics and at which stage in the processing stream it emerges. Previous studies have provided evidence that SSVEPs elicited by rapid luminance flicker originate in primary visual areas (Kamp et al., 1960; Pastor et al., 2003, 2007; Wittevrongel et al., 2018). Thus, our findings suggest that deafness and the acquisition of a sign language alter bottom-up visual processing at the earliest cortical stages.

It has been proposed that individuals with higher preferred frequencies have the possibility for faster sequencing of neural processes and therefore exhibit better temporal resolution in perception (Baltus & Herrmann, 2016). Indeed, individuals with higher optimal driving frequencies seem to have lower gap detection thresholds for auditory stimuli than people with lower optimal stimulation frequencies (Baltus & Herrmann, 2015). Thus, our findings might suggest that deafness and the acquisition of a sign language enhance the temporal resolution of the visual system. In fact, there is evidence that perceptual experience can substantially alter the temporal resolution of the visual system. For example, Seitz et al. (2005, 2006) have shown that the temporal resolution of the visual system increases after perceptual learning. In these studies, participants performed a letter-identification task, whereby a sequence of eight letters was presented in the centre of the screen. The sequence contained two target letters, which were presented with another luminance than the distractors, and the participants' task was to report the targets. At the same time, coherent motion stimuli in a peripheral annulus were presented. One motion direction temporally overlapped the target letters, so the targets were always paired with the same direction of the motion stimulus. Other, nonpaired directions temporally overlapped the distractors. After a training phase, the critical flicker fusion thresholds increased on average by 30% (Seitz et al., 2005). It could be argued that sign language processing constitutes a similar exposure to motion. During signed discourse, signers typically fixate on the eyes of the person signing to them (Emmorey et al., 2009; Muir & Richardson, 2005; Siple, 1978). However, signing space extends from the navel to above the head and most signs are typically produced below the eyelevel. Thus, a large amount of information about the handshape and hand movement needs to be processed in the peripheral visual field. So just like in the studies by Seitz et al. (2005, 2006), information from motion signals in the periphery needs to be extracted and is typically paired with information in the central visual field (e.g., facial expressions). Thus, the higher optimal stimulation frequencies

observed in the groups of signers may be due to perceptual training of motion during sign language processing.

Perceptual learning has often been found to be restricted to the visual features that have been trained, such as the location and/or the orientation of stimuli (Crist et al., 1997; Karni & Sagi, 1991). Electrophysiological studies in nonhuman primates have suggested that visual perceptual learning results in an increase in neuronal sensitivity in primary visual cortex that is specific to the relevant stimulus features (Schoups et al., 2001). Correspondingly, perceptual learning results in increased responsiveness of primary visual cortex representing the trained part of the visual field (Schwartz et al., 2002). These findings suggest that perceptual learning relies on changes in early cortical stages of visual processing (Schwartz et al., 2002) and lend further support for the notion that the acquisition of a sign language alter bottom-up visual processing at the earliest cortical stages.

Possibly, the visual system of signers is tuned to higher frequencies because the neurons involved in the perception of motion are the same that underlie the perception of higher temporal frequencies and vice versa (Seitz et al., 2006). This would be consistent with the processing characteristics of the magnocellular (M) pathway, which responds optimally to higher temporal frequencies and is particularly important for the processing of motion. Thus, it could be hypothesized that the visual system of signers is tuned to higher frequencies because the neurons involved in the perception of motion are the same that underlie the perception of higher temporal frequencies and vice versa (Seitz et al., 2006). Indeed, previous studies have postulated selective enhancements of the M-pathway in deaf individuals (Armstrong et al., 2002; Stevens & Neville, 2006). However, these studies compared deaf signers to hearing nonsigners and did not include a control group of hearing signers. Thus, it is difficult to assess whether the observed effects in these studies were due to deafness, the acquisition of a sign language, or an interaction of the two.

In the present study, tuning to higher temporal frequencies in the visual system was observed in the groups of signers when stimuli were presented in the fovea, but not when they were presented in the periphery. These findings stand in contrast to the widespread assumption that deafness and the acquisition of a sign language lead to selective enhancements of processing of the peripheral visual field (Armstrong et al., 2002; Neville & Lawson, 1987). However, enhanced processing speed as indicated by shorter reaction times in deaf individuals have been observed in both the central and the peripheral visual field (Bottari et al., 2010, 2011). In hearing signers, reaction time advantages have so far only been observed in the peripheral visual field (Codina et al., 2017).

We observed larger SSVEP amplitudes for stimuli presented in the fovea than for stimuli presented in the periphery, indicating that stimuli of constant size result in less cortical activity when presented at more eccentric areas of the visual field. This finding concurs with the well-known cortical magnification in the primary visual cortex (Harvey & Dumoulin, 2011). Moreover, previous studies using the critical flicker fusion paradigm have shown that the temporal resolution of the visual system for stimuli of constant size and luminance varies with visual field location (Granit & von Ammon, 1930; Hartmann et al., 1979; Poggel et al., 2006; Raninen & Rovamo, 1987; Rovamo & Raninen, 1984; Tyler, 1987). Studies in monkeys have found that the number of M-cells increases with eccentricity (Azzopardi et al., 1999), which has led to the prediction that the processing of visual information should be faster at more eccentric locations (Carrasco et al., 2003). However, for stimuli of constant size and luminance, the temporal resolution seems to decrease with increasing eccentricity (Poggel et al., 2006; Raninen & Rovamo, 1987). Thus, we possibly did not cover the appropriate frequencies to probe the temporal tuning functions in the periphery. The null result regarding differences in the temporal processing characteristics between the groups of deaf signers and hearing nonsigners for stimuli presented in the periphery may thus reflect a floor effect that masked any between-group differences.

In deaf humans, greater activation of auditory areas than in hearing individuals has been reported for face processing (Benetti et al., 2017), moving dot arrays (Fine et al., 2005; Finney et al., 2001), visual change detection (Bottari et al., 2014), and most pertinent to our study, visual-rhythm discrimination (Bola et al., 2017). While these studies have provided evidence for the view that the specific functions of the auditory cortices are preserved in cross-modal plasticity (Lomber et al., 2010), it is less known whether basic processing characteristics, such as the optimal driving frequency, are also preserved. Here, we wanted to assess whether the deprived auditory cortices of deaf individuals develop to have a similar optimal driving frequency like the nondeprived cortices (i.e., visual) or whether the optimal driving frequency of the deprived auditory cortices resemble those of nondeprived individuals and are independent of experience. The scalp topographies of auditory steady-state evoked potentials have been reported to show a maximum over frontal electrodes (Porcu et al., 2014; Zhang et al., 2013) and auditory steady-state evoked potentials are thought to reflect neural activation of the thalamus and the auditory cortices in response to auditory stimulation (Giraud et al., 2000; Herdman et al., 2003; Luke et al., 2017; Reyes et al., 2004). Thus, assuming cross-modal recruitment in

deaf individuals, we expected to find differences between deaf and hearing individuals over frontal electrodes. However, we did not observe evidence for cross-modal recruitment of the auditory cortex in the group of deaf signers. We hypothesise that this null result is due to the clear bottom-up driven character of the present paradigm.

For example, Bola et al. (2017) observed that deaf—but not hearing participants—showed increased activation in auditory regions when they were processing visual rhythms. In this study, participants had to compare the rhythms of two sequentially presented sequences. While the stimulation protocols in our experiment and in the experiment by Bola et al. (2017) involved visual rhythms, they were task relevant in the study by Bola et al. (2017), whereas in our study, they were not. Previous studies that failed to observe cross-modal recruitment in deaf individuals either used passive stimulation (Hauthal et al., 2014) or tasks that, according to the authors, were possibly not difficult enough to elicit recruitment of auditory areas in deaf individuals (Vachon et al., 2013). This concurs with findings from studies in blind individuals where mere stimulation of the hand did not lead to activation of the visual cortex (Gizewski et al., 2003; Sadato et al., 1996).

5 | CONCLUSION

The acquisition of a sign language seems to alter the temporal processing characteristics of the visual system at the earliest cortical stages. Thus, our results provide evidence for the notion that the optimal driving frequency of neural circuits is not a genetically defined property of neural circuits but is shaped by experience.

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CONFLICT OF INTEREST

The authors declare no competing financial interests.

AUTHOR CONTRIBUTIONS

Anna-Lena Stroh: Conceptualization, Methodology, Software, Formal analysis, Investigation, Participant recruitment, Resources, Data curation, Writing, Editing & Approving, Visualization, Project administration,

Funding acquisition. **Konstantin Grin:** Investigation, Participant recruitment, Editing & Approving, Project administration. **Frank Rösler:** Conceptualization, Methodology, Writing, Editing & Approving, Supervision. **Davide Bottari:** Conceptualization, Editing & Approving. **José Ossandón:** Software, Formal analysis, Editing & Approving. **Bruno Rossion:** Methodology, Formal analysis, Editing & Approving. **Brigitte Röder:** Conceptualization, Methodology, Writing, Editing & Approving, Supervision, Resources, Funding acquisition.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The period of recruitment, data collection, and data analysis was 2017–2021. Anonymized data and materials will be made available to external investigators upon reasonable request to the corresponding author through data transfer agreements approved by the stakeholders, under stipulations of applicable law including but not limited to the General Data Protection Regulation (EU 2016/679).

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REFERENCES

- Alencar, C. D. C., Butler, B. E., & Lomber, S. G. (2019). What and how the deaf brain sees. *Journal of Cognitive Neuroscience*, 31(8), 1091–1109. https://doi.org/10.1162/jocn_a_01425
- Armstrong, B. A., Neville, H. J., Hillyard, S. A., & Mitchell, T. V. (2002). Auditory deprivation affects processing of motion, but not color. *Brain Research. Cognitive Brain Research*, 14(3), 422–434. [https://doi.org/10.1016/s0926-6410\(02\)00211-2](https://doi.org/10.1016/s0926-6410(02)00211-2)
- Azzopardi, P., Jones, K. E., & Cowey, A. (1999). Uneven mapping of magnocellular and parvocellular projections from the lateral geniculate nucleus to the striate cortex in the macaque monkey. *Vision Research*, 39(13), 2179–2189. [https://doi.org/10.1016/s0042-6989\(98\)00319-8](https://doi.org/10.1016/s0042-6989(98)00319-8)
- Baltus, A., & Herrmann, C. S. (2015). Oscillatory activity in the auditory cortex determines auditory temporal resolution. *Frontiers in Human Neuroscience*, 9, 12. <https://doi.org/10.3389/conf.fnhum.2015.217.00012>
- Baltus, A., & Herrmann, C. S. (2016). The importance of individual frequencies of endogenous brain oscillations for auditory cognition—A short review. *Brain Research*, 1640(Pt B), 243–250. <https://doi.org/10.1016/j.brainres.2015.09.030>
- Bavelier, D., Dye, M. W. G., & Hauser, P. C. (2006). Do deaf individuals see better? *Trends in Cognitive Sciences*, 10(11), 512–518. <https://doi.org/10.1016/j.tics.2006.09.006>
- Benetti, S., van Ackeren, M. J., Rabini, G., Zonca, J., Foa, V., Baruffaldi, F., Rezk, M., Pavani, F., Rossion, B., & Collignon, O. (2017). Functional selectivity for face processing

- in the temporal voice area of early deaf individuals. *Proceedings of the National Academy of Sciences of the United States of America*, 114(31), E6437–E6446. <https://doi.org/10.1073/pnas.1618287114>
- Bola, L., Zimmermann, M., Mostowski, P., Jednoróg, K., Marchewka, A., Rutkowski, P., & Szwed, M. (2017). Task-specific reorganization of the auditory cortex in deaf humans. *Proceedings of the National Academy of Sciences of the United States of America*, 114(4), E600–E609. <https://doi.org/10.1073/pnas.1609000114>
- Bosworth, R. G., & Dobkins, K. R. (1999). Left-hemisphere dominance for motion processing in deaf signers. *Psychological Science*, 10(3), 256–262. <https://doi.org/10.1111/1467-9280.00146>
- Bosworth, R. G., & Dobkins, K. R. (2002a). The effects of spatial attention on motion processing in deaf signers, hearing signers, and hearing nonsigners. *Brain and Cognition*, 49(1), 152–169. <https://doi.org/10.1006/brcg.2001.1497>
- Bosworth, R. G., & Dobkins, K. R. (2002b). Visual field asymmetries for motion processing in deaf and hearing signers. *Brain and Cognition*, 49(1), 170–181. <https://doi.org/10.1006/brcg.2001.1498>
- Bosworth, R. G., Petrich, J. A. F., & Dobkins, K. R. (2013). Effects of attention and laterality on motion and orientation discrimination in deaf signers. *Brain and Cognition*, 82(1), 117–126. <https://doi.org/10.1016/j.bandc.2013.01.006>
- Bottari, D., Caclin, A., Giard, M.-H., & Pavani, F. (2011). Changes in early cortical visual processing predict enhanced reactivity in deaf individuals. *PLoS ONE*, 6(9), e25607. <https://doi.org/10.1371/journal.pone.0025607>
- Bottari, D., Heimler, B., Caclin, A., Dalmolin, A., Giard, M.-H., & Pavani, F. (2014). Visual change detection recruits auditory cortices in early deafness. *NeuroImage*, 94, 172–184. <https://doi.org/10.1016/j.neuroimage.2014.02.031>
- Bottari, D., Nava, E., Ley, P., & Pavani, F. (2010). Enhanced reactivity to visual stimuli in deaf individuals. *Restorative Neurology and Neuroscience*, 28(2), 167–179. <https://doi.org/10.3233/RNN-2010-0502>
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, 10(4), 433–436. <https://doi.org/10.1163/156856897X00357>
- Bross, M. (1979). Residual sensory capacities of the deaf: A signal detection analysis of a visual discrimination task. *Perceptual and Motor Skills*, 48(1), 187–194. <https://doi.org/10.2466/pms.1979.48.1.187>
- Bross, M., & Sauerwein, H. (1980). Signal detection analysis of visual flicker in deaf and hearing individuals. *Perceptual and Motor Skills*, 51(3 Pt 1), 839–843. <https://doi.org/10.2466/pms.1980.51.3.839>
- Bross, M., & Zubek, J. P. (1975). Effect of auditory deprivation of visual resolving power. *Canadian Journal of Psychology*, 29(4), 340–347. <https://doi.org/10.1037/h0082036>
- Brozinsky, C. J., & Bavelier, D. (2004). Motion velocity thresholds in deaf signers: Changes in lateralization but not in overall sensitivity. *Brain Research. Cognitive Brain Research*, 21(1), 1–10. <https://doi.org/10.1016/j.cogbrainres.2004.05.002>
- Cardin, V., Grin, K., Vinogradova, V., & Manini, B. (2020). Crossmodal reorganisation in deafness: Mechanisms for functional preservation and functional change. *Neuroscience & Biobehavioral Reviews*, 113, 227–237. <https://doi.org/10.1016/j.neubiorev.2020.03.019>
- Carrasco, M., McElree, B., Denisova, K., & Giordano, A. M. (2003). Speed of visual processing increases with eccentricity. *Nature Neuroscience*, 6(7), 699–700. <https://doi.org/10.1038/nn1079>
- Clark, W. C., Brown, J. C., & Rutschmann, J. (1967). Flicker sensitivity and response bias in psychiatric patients and normal subjects. *Journal of Abnormal Psychology*, 72(1), 35–42. <https://doi.org/10.1037/h0024080>
- Codina, C. J., Pascalis, O., Baseler, H. A., Levine, A. T., & Buckley, D. (2017). Peripheral visual reaction time is faster in deaf adults and British sign language interpreters than in hearing adults. *Frontiers in Psychology*, 8, 50. <https://doi.org/10.3389/fpsyg.2017.00050>
- Crist, R. E., Kapadia, M. K., Westheimer, G., & Gilbert, C. D. (1997). Perceptual learning of spatial localization: Specificity for orientation, position, and context. *Journal of Neurophysiology*, 78(6), 2889–2894. <https://doi.org/10.1152/jn.1997.78.6.2889>
- Dye, M. W. G., & Bavelier, D. (2013). Visual attention in deaf humans: A neuroplasticity perspective. In A. Kral, A. N. Popper, & R. R. Fay (Eds.), *Deafness* (Vol. 47) (pp. 237–263). Springer. https://doi.org/10.1007/2506_2013_9
- Emmorey, K., Thompson, R., & Colvin, R. (2009). Eye gaze during comprehension of American sign language by native and beginning signers. *Journal of Deaf Studies and Deaf Education*, 14(2), 237–243. <https://doi.org/10.1093/deafed/enn037>
- Fine, I., Finney, E. M., Boynton, G. M., & Dobkins, K. R. (2005). Comparing the effects of auditory deprivation and sign language within the auditory and visual cortex. *Journal of Cognitive Neuroscience*, 17(10), 1621–1637. <https://doi.org/10.1162/089892905774597173>
- Finney, E. M., & Dobkins, K. R. (2001). Visual contrast sensitivity in deaf versus hearing populations: Exploring the perceptual consequences of auditory deprivation and experience with a visual language. *Brain Research. Cognitive Brain Research*, 11(1), 171–183. [https://doi.org/10.1016/S0926-6410\(00\)00082-3](https://doi.org/10.1016/S0926-6410(00)00082-3)
- Finney, E. M., Fine, I., & Dobkins, K. R. (2001). Visual stimuli activate auditory cortex in the deaf. *Nature Neuroscience*, 4(12), 1171–1173. <https://doi.org/10.1038/nn763>
- Galambos, R. (1982). Tactile and auditory stimuli repeated at high rates (30–50 per sec) produce similar event related potentials. *Annals of the New York Academy of Sciences*, 388, 722–728. <https://doi.org/10.1111/j.1749-6632.1982.tb50841.x>
- Giraud, A. L., Lorenzi, C., Ashburner, J., Wable, J., Johnsrude, I., Frackowiak, R., & Kleinschmidt, A. (2000). Representation of the temporal envelope of sounds in the human brain. *Journal of Neurophysiology*, 84(3), 1588–1598. <https://doi.org/10.1152/jn.2000.84.3.1588>
- Gizewski, E., Gasser, T., de Greiff, A., Boehm, A., & Forsting, M. (2003). Cross-modal plasticity for sensory and motor activation patterns in blind subjects. *NeuroImage*, 19(3), 968–975. [https://doi.org/10.1016/S1053-8119\(03\)00114-9](https://doi.org/10.1016/S1053-8119(03)00114-9)
- Granit, R., & von Ammon, W. (1930). Comparative studies on the peripheral and central retina. *American Journal of Physiology-Legacy Content*, 95(1), 229–241. <https://doi.org/10.1152/ajplegacy.1930.95.1.229>
- Hartmann, E., Lachenmayr, B., & Brettel, H. (1979). The peripheral critical flicker frequency. *Vision Research*, 19(9), 1019–1023. [https://doi.org/10.1016/0042-6989\(79\)90227-X](https://doi.org/10.1016/0042-6989(79)90227-X)

- Harvey, B. M., & Dumoulin, S. O. (2011). The relationship between cortical magnification factor and population receptive field size in human visual cortex: Constancies in cortical architecture. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 31(38), 13604–13612. <https://doi.org/10.1523/JNEUROSCI.2572-11.2011>
- Hauthal, N., Debener, S., Rach, S., Sandmann, P., & Thorne, J. D. (2014). Visuo-tactile interactions in the congenitally deaf: A behavioral and event-related potential study. *Frontiers in Integrative Neuroscience*, 8, 98. <https://doi.org/10.3389/fnint.2014.00098>
- Herdman, A. T., Wollbrink, A., Chau, W., Ishii, R., Ross, B., & Pantev, C. (2003). Determination of activation areas in the human auditory cortex by means of synthetic aperture magnetometry. *NeuroImage*, 20(2), 995–1005. [https://doi.org/10.1016/S1053-8119\(03\)00403-8](https://doi.org/10.1016/S1053-8119(03)00403-8)
- Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, 6(6), 65–70.
- Hong Loke, W., & Song, S. (1991). Central and peripheral visual processing in hearing and nonhearing individuals. *Bulletin of the Psychonomic Society*, 29(5), 437–440. <https://doi.org/10.3758/BF03333964>
- Jaeger, T. F. (2008). Categorical data analysis: Away from ANOVAs (transformation or not) and towards logit mixed models. *Journal of Memory and Language*, 59(4), 434–446. <https://doi.org/10.1016/j.jml.2007.11.007>
- Kamp, A., Sem-Jacobsen, C. W., van Leeuwen, W. S., & van der T-Weel, L. H. (1960). Cortical responses to modulated light in the human subject. *Acta Physiologica Scandinavica*, 48(1), 1–12. <https://doi.org/10.1111/j.1748-1716.1960.tb01840.x>
- Karni, A., & Sagi, D. (1991). Where practice makes perfect in texture discrimination: Evidence for primary visual cortex plasticity. *Proceedings of the National Academy of Sciences of the United States of America*, 88(11), 4966–4970. <https://doi.org/10.1073/pnas.88.11.4966>
- Kuś, R., Duszyk, A., Milanowski, P., Łabęcki, M., Bierzyńska, M., Radzikowska, Z., Michalska, M., Zygierewicz, J., Suffczyński, P., & Durka, P. J. (2013). On the quantification of SSVEP frequency responses in human EEG in realistic BCI conditions. *PLoS ONE*, 8(10), e77536. <https://doi.org/10.1371/journal.pone.0077536>
- Lenth, R. (2018). emmeans: Estimated marginal means, aka least-squares means. R. packages version 1.2.3.: <https://CRAN.R-project.org/package=emmeans>
- Lomber, S. G., Meredith, M. A., & Kral, A. (2010). Cross-modal plasticity in specific auditory cortices underlies visual compensations in the deaf. *Nature Neuroscience*, 13(11), 1421–1427. <https://doi.org/10.1038/nn.2653>
- Luke, R., de Vos, A., & Wouters, J. (2017). Source analysis of auditory steady-state responses in acoustic and electric hearing. *NeuroImage*, 147, 568–576. <https://doi.org/10.1016/j.neuroimage.2016.11.023>
- Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods*, 164(1), 177–190. <https://doi.org/10.1016/j.jneumeth.2007.03.024>
- Merabet, L. B., & Pascual-Leone, A. (2010). Neural reorganization following sensory loss: The opportunity of change. *Nature Reviews. Neuroscience*, 11(1), 44–52. <https://doi.org/10.1038/nrn2758>
- Muir, L. J., & Richardson, I. E. G. (2005). Perception of sign language and its application to visual communications for deaf people. *Journal of Deaf Studies and Deaf Education*, 10(4), 390–401. <https://doi.org/10.1093/deafed/eni037>
- Nakanishi, M., Wang, Y., Wang, Y.-T., Mitsukura, Y., & Jung, T.-P. (2014). Generating visual flickers for eliciting robust steady-state visual evoked potentials at flexible frequencies using monitor refresh rate. *PLoS ONE*, 9(6), e99235. <https://doi.org/10.1371/journal.pone.0099235>
- Nava, E., Bottari, D., Zampini, M., & Pavani, F. (2008). Visual temporal order judgment in profoundly deaf individuals. *Experimental Brain Research*, 190(2), 179–188. <https://doi.org/10.1007/s00221-008-1459-9>
- Neville, H. J., & Lawson, D. (1987). Attention to central and peripheral visual space in a movement detection task: An event-related potential and behavioral study. II. Congenitally deaf adults. *Brain Research*, 405(2), 268–283. [https://doi.org/10.1016/0006-8993\(87\)90296-4](https://doi.org/10.1016/0006-8993(87)90296-4)
- Parasnis, I., & Samar, V. J. (1985). Parafoveal attention in congenitally deaf and hearing young adults. *Brain and Cognition*, 4(3), 313–327. [https://doi.org/10.1016/0278-2626\(85\)90024-7](https://doi.org/10.1016/0278-2626(85)90024-7)
- Pastor, M. A., Artieda, J., Arbizu, J., Valencia, M., & Masdeu, J. C. (2003). Human cerebral activation during steady-state visual-evoked responses. *The Journal of Neuroscience*, 23(37), 11621–11627. <https://doi.org/10.1523/JNEUROSCI.23-37-11621.2003>
- Pastor, M. A., Valencia, M., Artieda, J., Alegre, M., & Masdeu, J. C. (2007). Topography of cortical activation differs for fundamental and harmonic frequencies of the steady-state visual-evoked responses. An EEG and PET H215O study. *Cerebral Cortex (New York, N.Y.: 1991)*, 17(8), 1899–1905. <https://doi.org/10.1093/cercor/bhl098>
- Pinheiro, J., Bates, D., DebRoy, S., Sakar, D., & R Core Team. (2020). `nlme: Linear and Nonlinear Mixed Effects Models`. R package version 3.1-148. <https://CRAN.R-project.org/package=nlme>
- Poggel, D. A., Treutwein, B., Calmanti, C., & Strasburger, H. (2006). Increasing the temporal g(r)rain: Double-pulse resolution is affected by the size of the attention focus. *Vision Research*, 46(18), 2998–3008. <https://doi.org/10.1016/j.visres.2006.03.018>
- Poizner, H., & Tallal, P. (1987). Temporal processing in deaf signers. *Brain and Language*, 30(1), 52–62. [https://doi.org/10.1016/0093-934x\(87\)90027-7](https://doi.org/10.1016/0093-934x(87)90027-7)
- Porcu, E., Keitel, C., & Müller, M. M. (2013). Concurrent visual and tactile steady-state evoked potentials index allocation of inter-modal attention: A frequency-tagging study. *Neuroscience Letters*, 556, 113–117. <https://doi.org/10.1016/j.neulet.2013.09.068>
- Porcu, E., Keitel, C., & Müller, M. M. (2014). Visual, auditory and tactile stimuli compete for early sensory processing capacities within but not between senses. *NeuroImage*, 97, 224–235. <https://doi.org/10.1016/j.neuroimage.2014.04.024>
- R Core Team. (2017). R: A language and environment for statistical computing. R Foundation for statistical computing: <https://www.R-project.org/>
- Raninen, A., & Rovamo, J. (1987). Retinal ganglion-cell density and receptive-field size as determinants of photopic flicker sensitivity across the human visual field. *Journal of the Optical Society*

- of America. *A, Optics and Image Science*, 4(8), 1620–1626. <https://doi.org/10.1364/JOSAA.4.001620>
- Regan, D. (1966). Some characteristics of average steady-state and transient responses evoked by modulated light. *Electroencephalography and Clinical Neurophysiology*, 20(3), 238–248. [https://doi.org/10.1016/0013-4694\(66\)90088-5](https://doi.org/10.1016/0013-4694(66)90088-5)
- Regan, D. (1975). Recent advances in electrical recording from the human brain. *Nature*, 253(5491), 401–407. <https://doi.org/10.1038/253401a0>
- Retter, T. L., Rossion, B., & Schiltz, C. (2021). Harmonic amplitude summation for frequency-tagging analysis. *Journal of Cognitive Neuroscience*, 1–22, 2372–2393. https://doi.org/10.1162/jocn_a_01763
- Reyes, S. A., Salvi, R. J., Burkard, R. F., Coad, M. L., Wack, D. S., Galantowicz, P. J., & Lockwood, A. H. (2004). Pet imaging of the 40 Hz auditory steady state response. *Hearing Research*, 194(1–2), 73–80. <https://doi.org/10.1016/j.heares.2004.04.001>
- Rossion, B., & Boremanse, A. (2011). Robust sensitivity to facial identity in the right human occipito-temporal cortex as revealed by steady-state visual-evoked potentials. *Journal of Vision*, 11(2), 16–16. <https://doi.org/10.1167/11.2.16>
- Rovamo, J., & Raninen, A. (1984). Critical flicker frequency and M-scaling of stimulus size and retinal illuminance. *Vision Research*, 24(10), 1127–1131. [https://doi.org/10.1016/0042-6989\(84\)90166-4](https://doi.org/10.1016/0042-6989(84)90166-4)
- Sadato, N., Pascual-Leone, A., Grafman, J., Ibañez, V., Deiber, M. P., Dold, G., & Hallett, M. (1996). Activation of the primary visual cortex by Braille reading in blind subjects. *Nature*, 380(6574), 526–528. <https://doi.org/10.1038/380526a0>
- Schoups, A., Vogels, R., Qian, N., & Orban, G. (2001). Practising orientation identification improves orientation coding in V1 neurons. *Nature*, 412(6846), 549–553. <https://doi.org/10.1038/35087601>
- Schwartz, S., Maquet, P., & Frith, C. (2002). Neural correlates of perceptual learning: A functional MRI study of visual texture discrimination. *Proceedings of the National Academy of Sciences of the United States of America*, 99(26), 17137–17142. <https://doi.org/10.1073/pnas.242414599>
- Scott, G. D., Karns, C. M., Dow, M. W., Stevens, C., & Neville, H. J. (2014). Enhanced peripheral visual processing in congenitally deaf humans is supported by multiple brain regions, including primary auditory cortex. *Frontiers in Human Neuroscience*, 8, 177. <https://doi.org/10.3389/fnhum.2014.00177>
- Seitz, A. R., Nanez, J. E., Holloway, S. R., & Watanabe, T. (2005). Visual experience can substantially alter critical flicker fusion thresholds. *Human Psychopharmacology*, 20(1), 55–60. <https://doi.org/10.1002/hup.661>
- Seitz, A. R., Nanez, J. E., Holloway, S. R., & Watanabe, T. (2006). Perceptual learning of motion leads to faster flicker perception. *PLoS ONE*, 1, e28. <https://doi.org/10.1371/journal.pone.0000028>
- Singmann, H., Bolker, B., Westfall, J., & Aust, F. (2018). afex: Analysis of factorial experiments: R package version 0.21-2. <https://CRAN.R-project.org/package=afex>
- Siple, P. (1978). Visual constraints for sign language communication. *Sign Language Studies*, 1019(1), 95–110. <https://doi.org/10.1353/sls.1978.0010>
- Smittenaar, C. R., MacSweeney, M., Sereno, M. I., & Schwarzkopf, D. S. (2016). Does congenital deafness affect the structural and functional architecture of primary visual cortex? *The Open Neuroimaging Journal*, 10, 1–19. <https://doi.org/10.2174/1874440001610010001>
- Srinivasan, R., Russell, D. P., Edelman, G. M., & Tononi, G. (1999). Increased synchronization of neuromagnetic responses during conscious perception. *The Journal of Neuroscience*, 19(13), 5435–5448. <https://doi.org/10.1523/JNEUROSCI.19-13-05435.1999>
- Stapells, D. R., Linden, D., Suffield, J. B., Hamel, G., & Picton, T. W. (1984). Human auditory steady state potentials. *Ear and Hearing*, 5(2), 105–113. <https://doi.org/10.1097/00003446-198403000-00009>
- Stevens, C., & Neville, H. (2006). Neuroplasticity as a double-edged sword: Deaf enhancements and dyslexic deficits in motion processing. *Journal of Cognitive Neuroscience*, 18(5), 701–714. <https://doi.org/10.1162/jocn.2006.18.5.701>
- Tobimatsu, S., Zhang, Y. M., & Kato, M. (1999). Steady-state vibration somatosensory evoked potentials: Physiological characteristics and tuning function. *Clinical Neurophysiology: Official Journal of the International Federation of Clinical Neurophysiology*, 110(11), 1953–1958. [https://doi.org/10.1016/s1388-2457\(99\)00146-7](https://doi.org/10.1016/s1388-2457(99)00146-7)
- Tyler, C. W. (1987). Analysis of visual modulation sensitivity. III. Meridional variations in peripheral flicker sensitivity. *Journal of the Optical Society of America. A, Optics and Image Science*, 4(8), 1612–1619. <https://doi.org/10.1364/JOSAA.4.001612>
- Vachon, P., Voss, P., Lassonde, M., Leroux, J.-M., Mensour, B., Beaudoin, G., Bourgouin, P., & Lepore, F. (2013). Reorganization of the auditory, visual and multimodal areas in early deaf individuals. *Neuroscience*, 245, 50–60. <https://doi.org/10.1016/j.neuroscience.2013.04.004>
- Wittevrongel, B., Khachatryan, E., Fahimi Hnazaee, M., Carrette, E., de Taeye, L., Meurs, A., Boon, P., van Roost, D., & van Hulle, M. M. (2018). Representation of steady-state visual evoked potentials elicited by luminance flicker in human occipital cortex: An electrocorticography study. *NeuroImage*, 175, 315–326. <https://doi.org/10.1016/j.neuroimage.2018.04.006>
- Zhang, L., Peng, W., Zhang, Z., & Hu, L. (2013). Distinct features of auditory steady-state responses as compared to transient event-related potentials. *PLoS ONE*, 8(7), e69164. <https://doi.org/10.1371/journal.pone.0069164>

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