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Resilience of temporal processing to early and extended visual deprivation

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Abstract

Early visual deprivation is known to have profound consequences on the subsequent development of spatial visual processing. However, its impact on temporal processing is not well characterized. We have examined spatial and temporal contrast sensitivity functions following treatment for early and extended bilateral visual deprivation in fifteen children born with congenital cataracts in rural India. The results reveal a marked difference in post-treatment spatial and temporal sensitivities. Whereas spatial processing in newly sighted children is significantly impaired relative to age-matched controls, temporal processing exhibits remarkable resilience and is comparable to that in the control group. This difference in spatial and temporal outcomes is especially surprising given our computational analyses of video sequences which indicate a strong linkage between the spatial

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CRediT authorship contribution statement

Jie Ye: Formal analysis, Writing - original draft, Writing - review & editing. **Priti Gupta:** Investigation, Writing - review & editing. **Pragya Shah:** Formal analysis, Funding acquisition, Investigation, Writing review & editing, Writing - original draft. **Kashish Tiwari:** Investigation. **Tapan Gandhi:** Investigation, Writing - review & editing. **Suma Ganesh:** Investigation. **Flip Phillips:** Formal analysis, Writing - original draft, Writing - review & editing. **Dennis Levi:** Formal analysis, Writing - review & editing. **Frank Thorn:** Formal analysis, Writing - review & editing. **Sidney Diamond:** Formal analysis, Writing - original draft, Writing - review & editing. **Peter Bex:** Formal analysis, Writing - review & editing. **Pawan Sinha:** Writing - review & editing, Conceptualization,, Formal analysis, Funding acquisition, Writing - original draft.

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and temporal spectral content of natural visual inputs. We consider possible explanations for this discrepancy.

Keywords

Visual deprivation; Temporal contrast sensitivity; Spatial contrast sensitivity

1. Introduction

Children with congenital blindness, who are deprived of medical care despite having treatable conditions present an unusual opportunity, when they finally receive surgery, to study whether and how vision develops late in life. Thus, the humanitarian mission of identifying and treating such children, who often languish in remote rural areas of developing countries, also has direct and compelling scientific relevance. We launched Project Prakash in 2004 to advance these twin objectives, one rooted in service and the other in science. The project provides sight surgeries to children in rural India suffering from dense bilateral congenital cataracts, and studies their post-operative visual development (Sinha, 2013).

We have previously reported results showing that children treated for congenital cataracts several years after birth exhibit persistent deficits in spatial acuity and contrast sensitivity functions (CSFs) relative to their normally developing peers (Ganesh et al., 2014; Kalia et al., 2014). This is likely a manifestation of a critical period in visual development: Denied patterned imagery during early development, the visual system apparently is unable to gain normal spatial function even when visual input is later restored (Regal et al., 1976; Daw, 2014).

Beyond its impact on spatial vision, it is important to consider how early visual deprivation affects the temporal dimension of post-operative vision, given that humans inhabit dynamic environments. The data so far address this issue for monocular deprivation (Harwerth et al., 1983; Hess et al., 1981) or limited durations of binocular deprivation. A study of children treated for congenital cataracts within the first few months of life, and assessed several years later (Ellemberg et al., 1999) showed that short durations of visual deprivation (averaging 4.5 months), followed by long periods of typical visual experience (averaging 9.5 years), result in near-normal temporal perception. However, the consequences of extended bilateral deprivation, lasting several years, and well beyond putative critical periods, are not known. Also unknown is the status of temporal processing soon after sight treatment, rather than many years later, and any longitudinal changes therein. The findings presented here address these issues.

2. Methods

The study protocol was approved by COUHES, MIT's Institutional Review Board, and the Ethics Committee of the Shroff Charity Eye Hospital in New Delhi. Informed consent was obtained from all participants.

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Subjects:

Our experimental group comprised 15 individuals who underwent cataract extraction and intraocular lens implantation at ages ranging from 7 to 21 years (mean 11.7 years; table appended to the end of the manuscript presents information for each subject). All had dense bilateral cataracts since before one year of age. Assessment of congenitality of deprivation was based on parental reports, ophthalmic examination, and the presence of nystagmus, which is known to be induced by profound visual impairment very early in life (Tusa et al., 1991). The children were provided surgeries, which involved cataract extraction and intra-ocular lens implantation.

Pre-operative assessments:

We tested for light perception in all four quadrants. Anterior segment was evaluated on slit lamp and type of cataract and any associated ocular pathology were noted. Given the patients' dense bilateral cataracts which precluded fundus viewing via ophthalmoscopes, B scan ultrasound was done in all cases preoperatively to check for any posterior segment pathology.

Intervention:

Keratometry and biometry of all children was performed under general anesthesia just before the surgery. All surgeries were performed by a single surgeon (SG). A complete circular capsulorhexis was done after instilling methyl cellulose in the anterior chamber and nucleus aspirated with bimanual irrigation and aspiration technique or by phaco aspiration in calcified thick plate cataracts. All children underwent a primary posterior capsulorhexis through the anterior route with capsulorhexis forceps or vitrector in cases with thick fibrous posterior capsule plaques. A foldable acrylic posterior chamber intra-ocular lens (PCIOL) was implanted in the bag. The scleral tunnel and the side-ports were closed by 10–0 interrupted sutures. Patient information is provided in Table 1.

Control data were obtained from two normally-sighted children aged 10 and 11 years.

There was no history of neurological or psychiatric illness in any of the subjects.

2.1. Procedure

The spatial and temporal contrast sensitivity functions for each subject were measured with a modified quick CSF method (Lesmes et al., 2010) implemented on an iPad Pro 9.7 (Dorr et al., 2013, 2017, 2019) with mean luminance of 185 cd/m2, spatial resolution of 14.8*19.7 cm (2048*1536 pixels), 60 Hz refresh rate, which subtended 27.7*21.0 degrees at 40 cm viewing distance.

Observers were seated 40 cm from the screen and were required to indicate the orientation of band-pass filtered (Hou et al., 2015) Landolt C targets (NRC, NAS, 1980) in a 4 alternative forced choice (AFC) task. Stimuli were present until the observer made a response by touching the region of the display containing the gap in the Landolt C. Stimuli were digitally filtered with a raised cosine filter with 4.5 cycles per letter peak spatial frequency and 1 octave FWHH bandwidth (Chung et al., 2002). Peak filter spatial frequency

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covaried with size of the presented Landolt C. For the spatial CSF, the temporal frequency of the stimuli was fixed at 0 Hz and the spatial frequency and contrast adaptively changed each trial. For the temporal CSF, the spatial frequency of the stimuli was fixed at 1.25c/deg and the temporal frequency and contrast adaptively changed each trial. Temporal frequency was controlled by reversing the contrast of the stimuli sinusoidally over time, so the mean luminance was held constant across the frames. Stimuli were presented within a temporal window of 1 s, so the lower frequency cut-off was 1 Hz. The display was 60 Hz, so the upper cut-off frequency was 30 Hz.

The quick CSF algorithm utilizes the functional form of the spatial CSF (a truncated log parabola; Watson and Ahumada, 2005) or temporal CSF (an asymmetric log parabola; Kosovicheva et al., 2019), each with 4 parameters for peak sensitivity, peak frequency, high frequency fall-off and low frequency fall-off. On each of 50 trials, the quick CSF algorithm selected the contrast and either the spatial frequency or temporal frequency that maximized information gain about the subject's spatial CSF or temporal CSF. After each trial, the subject's correct or incorrect response is used update information about the CSF parameters using Bayesian inference. At the end of 50 trials, the CSF is estimated by resampling from the posterior distributions of the four parameters.

Prakash subjects were assessed longitudinally before, and at multiple time-points after, surgery (−2 days, +1 week, +2 weeks, +2 months, +6 months, and + 12 months).

3. Results

Fig. 1a shows spatial CSF data for each of the 15 children. All Prakash children exhibited improvements in their spatial contrast sensitivity from before to after surgery, but had marked deficits relative to controls especially at high spatial frequencies (high-frequency cut-off<5 cycles per degree while that of the controls was > 40 cpd) which persisted even a year after treatment.

A very different pattern of results is evident for temporal contrast sensitivity (Fig. 1b). The Prakash children had significant deficits relative to controls prior to their surgery, but post-operatively, the temporal contrast sensitivity improved markedly, even at high temporal frequencies. We quantified the total gain in contrast sensitivity by computing the area under the log contrast sensitivity function (AULCSF; Applegate et al., 1997). Pre-operatively, both the spatial and temporal AULCSFs of the patients were markedly less than control subjects' (Fig. 2a). Their AULCSF increased following surgery and showed progressive improvements over time. Of particular interest here is the finding that the patients exhibited high temporal AULCSF soon after surgery and reached stability within two months. Spatial AULCSF, on the other hand, continued to show persistent large deficits. A 2-way ANOVA with the ratio of AULCSF of patients versus controls as the dependent variable reveals significant effects of condition (temporal versus spatial) ($p < 0.001$) and time from surgery ($p < 0.01$).

Examining specific aspects of the contrast sensitivity functions (positions of the function's x-intercept and peak, which correspond to maximum resolution and frequency of peak

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sensitivity), we find marked differences in the spatial versus temporal domains. While spatial acuity remained significantly compromised across the entire span of longitudinal measurements, temporal critical fusion frequency (CFF) of the patients registered large improvements rapidly after surgery (Fig. 2b) and was statistically indistinguishable from that of controls. The position of maximal sensitivity was shifted to low frequencies in the spatial domain, but was comparable to controls in the temporal domain (Fig. 2c).

4. Discussion

These data show that relative to spatial contrast sensitivity, temporal contrast sensitivity is more resilient to extended early-onset visual deprivation. The findings have notable parallels with studies exploring the impact of visual deprivation and amblyopia on the parvo- and magno-cellular systems. The two systems are known to exhibit differential sensitivities to spatial and temporal information, with the parvo stream being more responsive to high spatial frequencies and the magno stream to rapid temporal change (Livingstone and Hubel, 1988). In cats and monkeys, deprivation has been reported to decrease cell sizes in the lateral geniculate nucleus (LGN), with parvocellular laminae being more susceptible to shrinkage than the magnocellular layers (Garey and Blakemore, 1977). Similarly, studies of amblyopia have revealed a greater compromise of the parvocellular rather than magnocellular system (Manny and Levi, 1982; von Noorden and Crawford, 1992; Davis et al., 2006). The higher susceptibility of the parvocellular system to deprivation induced compromise may also help explain an aspect of the results that is evident in the CSF plots in Fig. 1. Specifically, while there is seen to be good recovery of high-temporal frequency sensitivity, low temporal frequency sensitivity shows lingering deficits. How might we account for this result? To the extent that parvo cells do double duty as high spatial-frequency and low temporal-frequency encoders, a deprivation induced compromise of the parvo system would be expected to lead to reduced spatial acuity and reduced low-temporal frequency sensitivity, consistent with our empirical data.

Studies of development of temporal sensitivity in normally sighted infants also provide a notable point of reference for the data we have presented here. Results from infants indicate that temporal contrast sensitivity is quite mature very early in the developmental timeline, even though spatial CSF is quite poor, especially at high spatial frequencies (Braddick and Atkinson, 2009), a difference akin to what we have observed in our data. In the context of these developmental results, the observed resilience of high-frequency temporal processing to extended visual deprivation is consistent with the ‘Detroit Hypothesis’ proposed by Levi & Carkeet (1993), according to which earlier manifestation of a visual function along the developmental timeline may serve to lessen its vulnerability to deprivation related compromise. What could be the factors at work in conferring this resilience to temporal sensitivity?

In addressing this question, we need to consider both exogenous (external stimulus driven) and endogenous (internal processes driven) accounts. The exogenous account has intuitive appeal, especially for explaining the spatial CSF deficits: To a first approximation, a cataract acts as a severe spatial low-pass filter, greatly diminishing or even eliminating, high spatial frequency details from images impinging on the retina (Shandiz et al., 2011). Since a

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cataract deprives the visual system of high-frequency spatial information, it is not surprising that cells tuned to such high-frequencies atrophy, fail to develop, or perhaps are repurposed. By the time the cataract is extracted, the visual system has lost its neural filters capable of processing high-frequency spatial information and hence exhibits the characteristic losses in those spectral regimes in the spatial CSF.

Extending this logic to the temporal domain, an exogenous account for the resilience of the temporal system posits that although a cataract leads to profound reductions in high spatial frequencies, it does not prevent high temporal frequencies from reaching the retina and, thereby, the rest of the visual system. Stimulation arising from movements of large shadows and shapes across the visual field, and temporal fluctuations of overall scene intensity, would not be eliminated by the presence of a cataract. Such stimulation may be the reason why the temporal processing system maintains its function despite the presence of cataracts for several years.

Although this account appears plausible, a closer analysis of the impact of cataracts on temporal content of natural visual inputs argues against its validity. Fig. 3 shows spatial and temporal frequency content analysis of a natural video captured with or without a translucent film that simulates cataracts. Spatial spectra show the expected reduction in high-frequency content with the introduction of a simulated cataract. This is consistent with a key mode in which cataracts compromise vision – a diminishment of spatial detail (Shandiz et al., 2011; Maraini et al., 1994). Of greater interest to us is the impact of cataracts on the temporal content of visual input. As is evident from the temporal spectra in Fig. 3b, cataracts bring about a marked reduction in high-frequency temporal information. Thus, a purely spatial optical pathology has significant temporal consequences too. This empirical observation admits a simple explanation. Setting aside unnatural setups such as high-frequency strobe lights, temporal variations in image intensity at a given image location are determined by the spatial gradients in its neighborhood. This is because variation in a pixel's intensity over time is typically caused by its neighboring pixels in the earlier frame shifting to the current location. Hence, temporal variations are primarily determined by image movements or eye movements. Any filter that smooths out spatial variations will necessarily reduce temporal gradients as well. Hence, a reduction in high spatial-frequency content due to a cataract will inevitably be accompanied by reduced high-temporal frequency content as well, as is borne out by Fig. 3a and b.

This observation is relevant for our interpretation of data from the Prakash children since it highlights the puzzling differential impact of deprivation on spatial and temporal domains. Although both spatial and temporal signals undergo cataract induced diminution in their spectral content, especially at high frequencies, the spatial system shows much greater deficits post-operatively relative to the temporal system. Thus, the resilience of the temporal system relative to the spatial one cannot be ascribed simply to differences in the content of exogenous stimulation; in the presence of a cataract, both systems suffer deprivation, but exhibit markedly different outcomes post-operatively.

Given the limitations of exogenous stimulation-based accounts, it is worth considering potential explanations based on endogenous processes. One possibility in this regard is the

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temporal signal variation introduced by spontaneous activity of retinal ganglion cell (Kuffler et al., 1957; Meister et al., 1991). Such intrinsically generated temporal variability may serve to circumvent the reduction in high temporal frequency content of exogenous stimulation. Another potential endogenous source for enhanced temporal variation is nystagmus. The development of involuntary eye-movements in settings of profound visual impairment is well established (Tusa et al., 1991, 2002), but nystagmus has generally been considered to be a maladaptive consequence of visual pattern deprivation (Chung et al., 2011). A provocative possibility is that nystagmus may, in fact, serve an adaptive purpose by acting to enhance temporal variation at different retinal loci; endogenously generated eye-movement, in this view, compensates for reduced world motion in degraded visual inputs in scenarios such as the presence of cataracts or high refractive errors (Fig. 3c).

This work sets the stage for studies wherein both spatial and temporal modulations exist in the stimuli simultaneously. Doing so would allow us to examine the impact of extended deprivation not only on flicker sensitivity, but on motion perception too. This would have important benefits from the perspective of examining higher visual cortical function. Whereas temporal flicker taps into primarily retinal and geniculate mechanisms, motion perception involves processing in multiple cortical areas. The use of motion stimuli would help reveal how vulnerable these cortical mechanisms are to deprivation, relative to the processes subserving flicker sensitivity. Notably, Ellemberg et al. (2002) have reported that early onset cataracts particularly impair global motion sensitivity, more so than their impact on global form (Lewis et al., 2002).

In summary, our data reveal notable resilience of temporal processing to early onset visual deprivation, even when it lasts several years, well past putative critical periods. Analyses of natural videos as viewed with simulated cataracts show that in such conditions, spatial degradation is accompanied by strong reductions in temporal high-frequency content. Hence, preserved temporal sensitivity after treatment for extended congenital blindness is unlikely to be accounted for by appealing to availability of high temporal frequency content in visual inputs during the period of deprivation. We have considered potential endogenous accounts, although these are yet speculative. The resilience of temporal processing, even in the absence of a definitive understanding of its source, suggests that it may play an important adaptive function. Indeed, studies of visual integration and parsing by newly sighted children underscore the critical role temporal information plays in the genesis of this ability (Ostrovsky et al., 2009).

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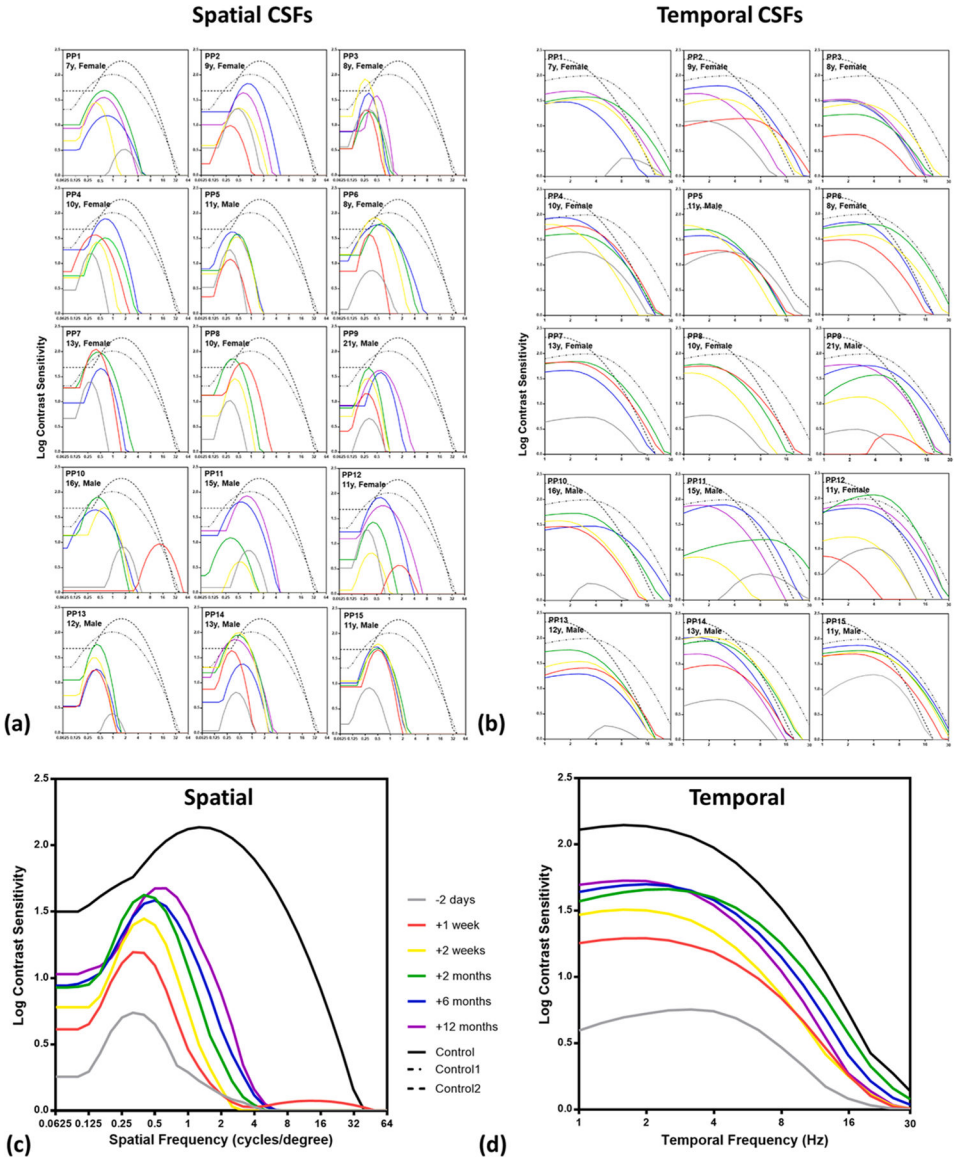

Fig. 1.

(a) Longitudinal spatial CSF results from 15 children who had experienced early and extended visual deprivation. The differently colored traces correspond to CSF measured at different pre- and post-operative time-points (legend between panels (c) and (d)). (b) Longitudinal temporal CSF data from the same set of participants. (c) and (d) Averages across all subjects of spatial and temporal CSFs.

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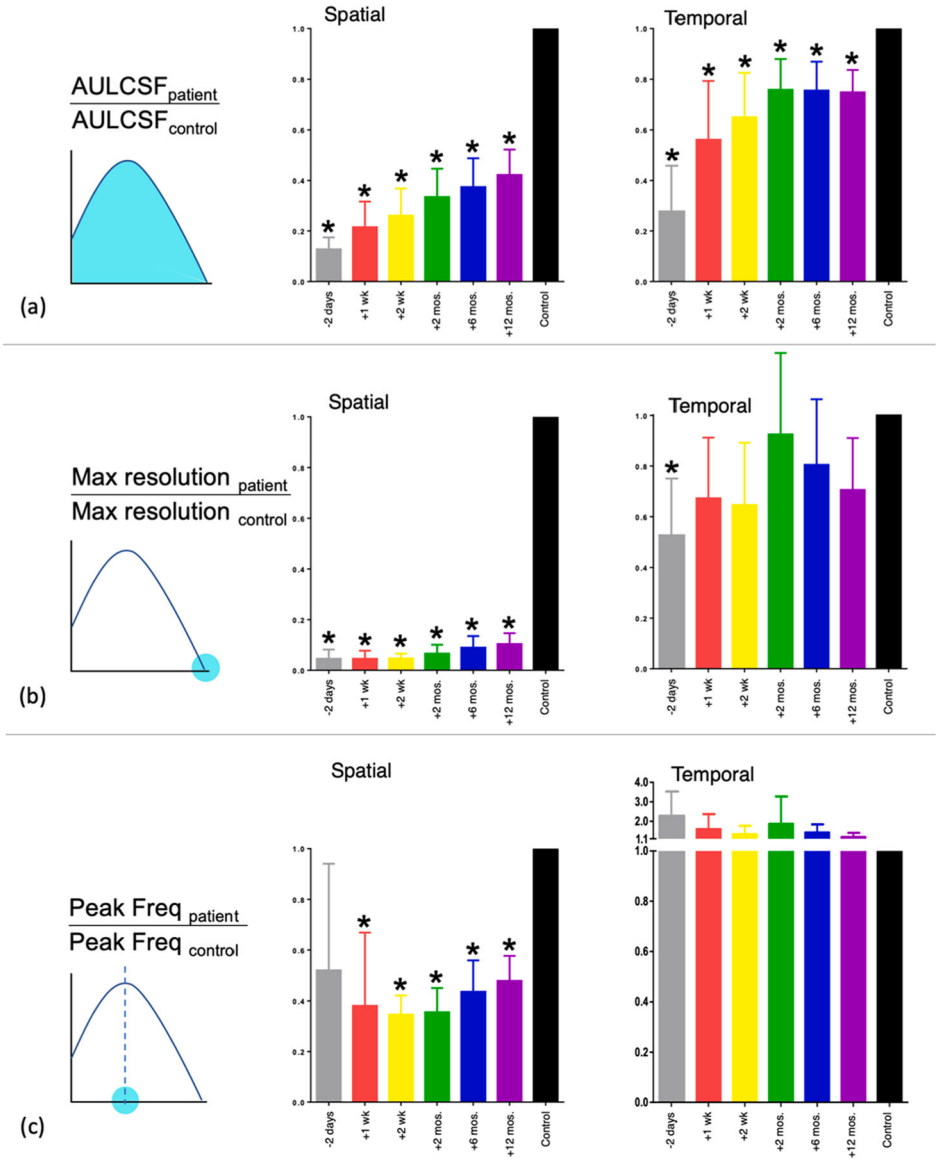

Fig. 2.

(a) Longitudinal data of the spatial and temporal AULCSF ratio for newly-sighted patients relative to controls prior to and following the removal of bilateral congenital cataracts. (b) Longitudinal spatial and temporal resolution limits (spatial acuity and critical fusion frequency) of Prakash patients relative to controls. (c) Longitudinal spatial and temporal peak frequency assessment (For all plots, * indicates $p < 0.05$, when comparing data to controls. Error-bars denote +/− 1 standard deviation.)

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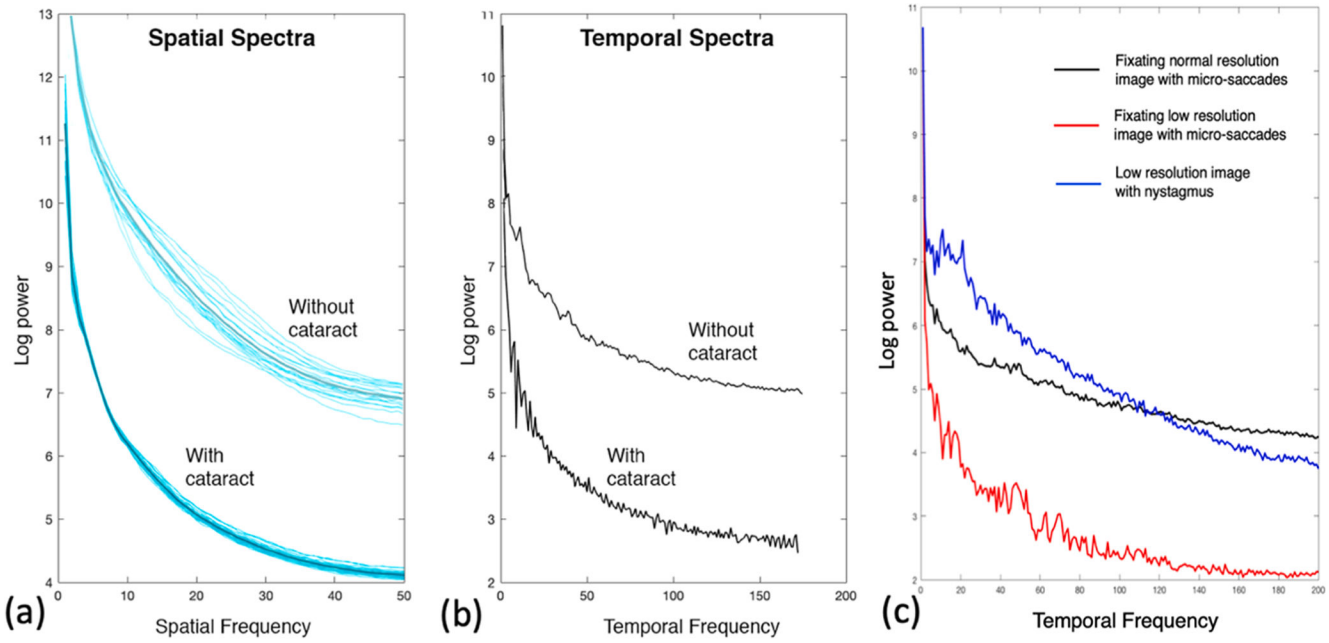

Fig. 3.

Spatial and temporal spectra of a natural dynamic sequence when viewed with or without a simulated cataract. (a) The spatial spectra shown are the radial averages of the 2D Fourier transforms of the individual frames of the video sequence. Light cyan plots correspond to individual frames and the black curves are their averages. (b) Temporal spectra are the averages of 1D FFTs of time-series corresponding to temporal variations in intensity at 1000 randomly placed locations in the video frame stack. (c) Restoration of power in high-temporal frequencies in spatially low-pass filtered visual inputs with the introduction of nystagmus. Cataracts are simulated by a translucent polyethylene filter placed in front of the camera.

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Table 1

Patient information.

Gender	Age of treatment	Detection of blindness	Pre-Treatment acuity	Nystagmus	Type of cataract
F	7	Leukocoria detected within t yr of age; 3 of 5 siblings have cataracts	RE:FC close to face LE: FC at 15cm	Present	Nuclear cataract
F	9	Mother noticed whiteness around 1 year of age when she had started to sit and play	RE:FC close to face LE: FC at 1/2cm	Present	Nuclear cataract
F	8	Parents became aware of child's blindness when she couldn't fetch objects at around 2 years.	BE: FC at 1/2cm	Present	Nuclear cataract with calcified anterior capsule
M	16	Within a month after birth	RE: FC at 20cm LE: HM	Present	Nuclear cataract
M	15	Few days after birth	BE: FC at 1m	Present	Membraneous cataract
F	10	Within a month after birth	RE: FC at 1m LE: FC at 0.5m	Present	Membraneous cataract
M	11	Noticed inability to fixate within 3 months after birth	BE: FC at 1m	Present	Nuclear cataract
F	8	Within 3 months after birth	BE: FC at 1/2 m	Present	Membraneous cataract
F	11	Few days after birth	BE: FC at 1/2 m	Present	Membraneous cataract
M	12	Within a month after birth	BE: Hand movements close to face	Present	Nuclear cataract
F	13	At birth	BE: FC at 1m	Present	Membraneous cataract
M	10	Within 4 months after birth	BE: FC at 20cm	Present	Nuclear cataract
M	21	Within I month after birth	RE: FC at 1m LE: FC at 1/2m	Present	Membraneous cataract
M	13	Noticed inability to fixate in the first month and leukocoria within the first year	BE: FC at 1/2m	Present	Nuclear cataract
M	11	Within 6 months after birth	BE: FC at 1m	Present	Membraneous cataract

Abbreviations: RE/LE: Right eye/Left eye; BE: Both eyes; FC: Finger Counting; HM: Hand Movements.

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