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Development of Visual Memory Capacity Following Early-Onset and Extended Blindness

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Abstract

It is unknown whether visual memory capacity can develop if onset of pattern vision is delayed for several years following birth. We had an opportunity to address this question through our work with an unusual population of 12 congenitally blind individuals ranging in age from 8 to 22 years. After providing them with sight surgery, we longitudinally evaluated their visual memory capacity using an image-memorization task. Our findings revealed poor visual memory capacity soon after surgery but significant improvement in subsequent months. Although there may be limits to this improvement, performance 1 year after surgery was found to be comparable with that of control participants with matched visual acuity. These findings provide evidence for plasticity of visual memory mechanisms into late childhood but do not rule out vulnerability to early deprivation. Our computational simulations suggest that a potential mechanism to account for changes in memory performance may be progressive representational elaboration in image encoding.

Keywords

cognitive development, visual memory, impact of early visual deprivation, late sight onset

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Given the crucial role visual memory plays in enabling many aspects of cognitive function, it is not surprising that visual memory develops very rapidly. Visual memory capacity increases significantly over the first year of life (Rose et al., 2001; Ross-Sheehy et al., 2003) and continues to increase with age in childhood (Cowan et al., 2011; Riggs et al., 2006; Simmering, 2012; Walker et al., 1994). Children as young as 4 years of age spontaneously encode a high degree of visual detail. They exhibit high fidelity in their visual memory capacity over a large set of items not only for basic-level categories but also for unique details and information about the position and arrangement of parts (Ferrara et al., 2017). By adulthood, humans come to possess the ability to remember several thousand images, which manifests as high accuracy in immediate recognition tests (Brady et al., 2008; Madigan, 2014; Nickerson, 1965; Shepard, 1967; Standing, 1973; Standing et al., 1970). This impressive performance has even led some

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researchers to speculate that picture-memory capacity may be essentially unlimited (Yuille, 2014).

Notwithstanding evidence of excellent picture-memory capacity, several questions about the development of this ability remain open. One of these concerns the role of early visual experience: Can visual memory develop even if visual experience is precluded in the first several years of life? Past research on animals has shown that early visual deprivation can cause dramatic changes in neural organization that have a profound impact on many visual functions (Hubel & Wiesel, 1970). Human studies of recovery after congenital blindness have shown similar trends (Lewis & Maurer, 2005; Ostrovsky et al., 2006). Early visual deprivation is found to have profound consequences on the subsequent development of various low-level visual functions, such as acuity, contrast sensitivity, and motion coherence (Braddick et al., 2003; Cobb & MacDonald, 1978; Ellemberg et al., 2002; Kalia et al., 2014; Sinha & Held, 2012). Other studies of visual function after treatment of congenital blindness suggest that early deprivation also impairs high-level aspects of vision, such as object and face recognition (Fine et al., 2003; Gregory & Wallace, 1963; Sacks, 1995; Valvo, 1971; von Senden, 1960). Even relatively short periods of deprivation ranging in duration from 2 to 6 months after birth have been shown to have significant detrimental consequences on face-recognition skills (Le Grand et al., 2001; Lewis & Maurer, 2005; Maurer et al., 2005, 2007). Given this evidence of compromised visual perception after late sight onset, and the suggestion from several studies (reviewed in Slotnick, 2004) that visual memory and visual perception recruit common neural substrates, it is possible that visual memory may be vulnerable to early deprivation in the same way that visual perception is. However, there are also plausible reasons to expect resilience of memory resources. A notable one is the possibility of memory being amodal, catering to and sustained by incoming information from multiple sensory modalities. In this perspective, visual deprivation leads to a diminution, rather than elimination, of input to the amodal memory store. Reports such as those of Wolbers et al. (2011) point to the biological feasibility of such a proposal. Taken together, the mixed nature of past results highlights the difficulty of definitively predicting how visual deprivation would impact the subsequent development of image memory. Accordingly, our goal here was to examine this question empirically by investigating whether the development of visual memory capacity is impacted by early and extended visual deprivation.

We have had an opportunity to address this question as part of a humanitarian and scientific initiative, Project Prakash (Sinha, 2013), that is intended to alleviate curable childhood blindness in the developing world while also addressing scientific questions about visual development. As part of this effort, we provide free surgical treatment to congenitally blind children and study changes in their visual skills and associated neural reorganization as the children gain visual experience. Working with this unusual population provides a glimpse into the impact of early visual deprivation on visual skill acquisition and the interplay between nature and nurture during that process.

In the present study, we followed the development of visual memory in 12 newly sighted Prakash patients. Participants performed an old/new task that involved memorizing a set of images and then completing a recall task in which they were asked to identify the memorized items from a larger collection that included previously seen images and novel distractors. The sets to be memorized differed in their cardinalities (i.e., the number of images to be memorized) and the semantic information that they contained (images of natural scenes vs. abstract paintings). The real and abstract sets were comparable in low-level image properties such as luminance and spatial frequency. We were thus able to examine the posttreatment development of visual memory capacity and, using the two types of stimulus sets that differed in their semantic content, also focus the investigation to study the potential emergence of meaning as a modulator of this capacity.

Statement of Relevance

Humans exhibit impressive visual memory from early in life. What are the roots of this proficiency? Specifically, does its development depend on early visual experience? These fundamental questions have proven difficult to answer given the challenges of working with neonates and the ethical impossibility of limiting their visual experience. We had the opportunity to address this issue through our work with an unusual group of children, those who had been born blind and did not receive treatment for several years. We provided them with sight surgeries and then longitudinally studied the development of visual memory capacity. Our results revealed a steady improvement in their memory performance and indicated the feasibility of neural change even late in childhood. We also describe computational simulations that provide hints about the possible nature of neural changes underlying the observed improvements in visual memory performance.

Previous studies that investigated whether meaning influences memory have typically done so with linguistic stimuli; relatively few studies have examined this issue purely in the visual domain. Notably, Bellhouse-King and Standing (2007) compared visual memory performance of concrete, regular abstract, and diverse abstract pictures. The investigators found that meaningfulness is not necessary for effective picture memory but does appear to facilitate it. They found that even quite meaningless visual designs can be recognized at well above chance level, provided that they are sufficiently distinctive so that they are not confused with each other. However, the abstract images used in the study were pictures of snowflakes (*regular abstract*) and groupings of simple geometrical figures such as triangles, rectangles, and circles (*diverse abstract*), so all patterns belonged to the same conceptual class (snowflakes) or shared the same small set of constituent elements.

Building on this past work, we sought to address the primary question of whether visual memory capacity could develop even after several years of congenital blindness and, secondarily, whether and to what extent image semantics contribute to memory capacity.

Method

Participants

We recruited two groups of participants. The first group comprised 12 newly sighted Prakash patients (six females) ranging in age from 8 to 22 years (M = 12.8 years). The size of the experimental group was determined by the number of children who met the inclusion criteria (treatable congenital profound visual deprivation) during the study period. The patients were tested prior to treatment for congenital cataracts and periodically up to a year afterward. The control group comprised 12 normally sighted schoolchildren ranging in age from 8 to 14 years (M = 10.8 years). This study was approved by the Massachusetts Institute of Technology Institutional Review Board (Committee on the Use of Humans as Experimental Subjects) and the Ethics Committee of Dr. Shroff's Charity Eye Hospital, New Delhi, our medical partner.

Patient group. All patients had been identified via our project's pediatric ophthalmic screening program in rural areas of India. All had dense bilateral cataracts since before 1 year of age. Assessment of congenitality of deprivation was based on parental reports, ophthalmic examination of the eyeball and cataract morphology, and the presence of nystagmus, which is known to be induced by profound visual impairment very early in life (Tusa et al., 1991). It should be noted that although these factors render an inference of congenitality highly probable, they are not absolutely definitive.

Preoperative assessments. We tested for light perception in all four quadrants and measured acuity using the Freiberg Visual Acuity Test (Bach, 1996). The patient information table (see Table S1 in the Supplemental Material available online) shows that all individuals were in the category of "Profound visual impairment (20/500–20/1000)" or "Light perception/projection (< 20/1000)," as per classification norms followed by the American Foundation for the Blind (2020). The anterior segment was evaluated with a slit lamp, and the 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 recorded before surgery in all cases to check for any posterior segment pathology.

Intervention. Keratometry and biometry of all children were performed under general anesthesia immediately preceding the surgery. All surgeries were performed by a single surgeon. The patients underwent a primary posterior capsulorhexis through the anterior route, and a foldable acrylic posterior chamber intraocular lens was implanted in the bag. The best refractive correction was prescribed to patients after their sutures were removed.

Control group. Participants in the control group were recruited from a school in New Delhi. They had normal or corrected-to-normal vision. These participants had no history of neurological or psychiatric illness and their socioeconomic status was matched with that of the patients. Informed assent was obtained from all participants, and consent was obtained from their parents.

Stimuli

For the stimulus sets, we compiled a database of 1,200 real-world and 1,200 abstract images. All images were cropped square and scaled to the same size (256 × 256 pixels). Real images depicted a variety of natural scenes including architecture, flora, fauna, vehicles, and people (Fig. 1a). Abstract images were nonrepresentational paintings drawn from several digital art archives (Fig. 1b). In order to determine whether the inherent discriminability of the images in the two sets was comparable, we computed the 2D correlation coefficients of all pairwise comparisons across 100 randomly selected real images and 100 randomly selected abstract images. We found that the two distributions were statistically indistinguishable (Figs. 1c and 1d). An unpaired-samples t test found that the correlation between real and

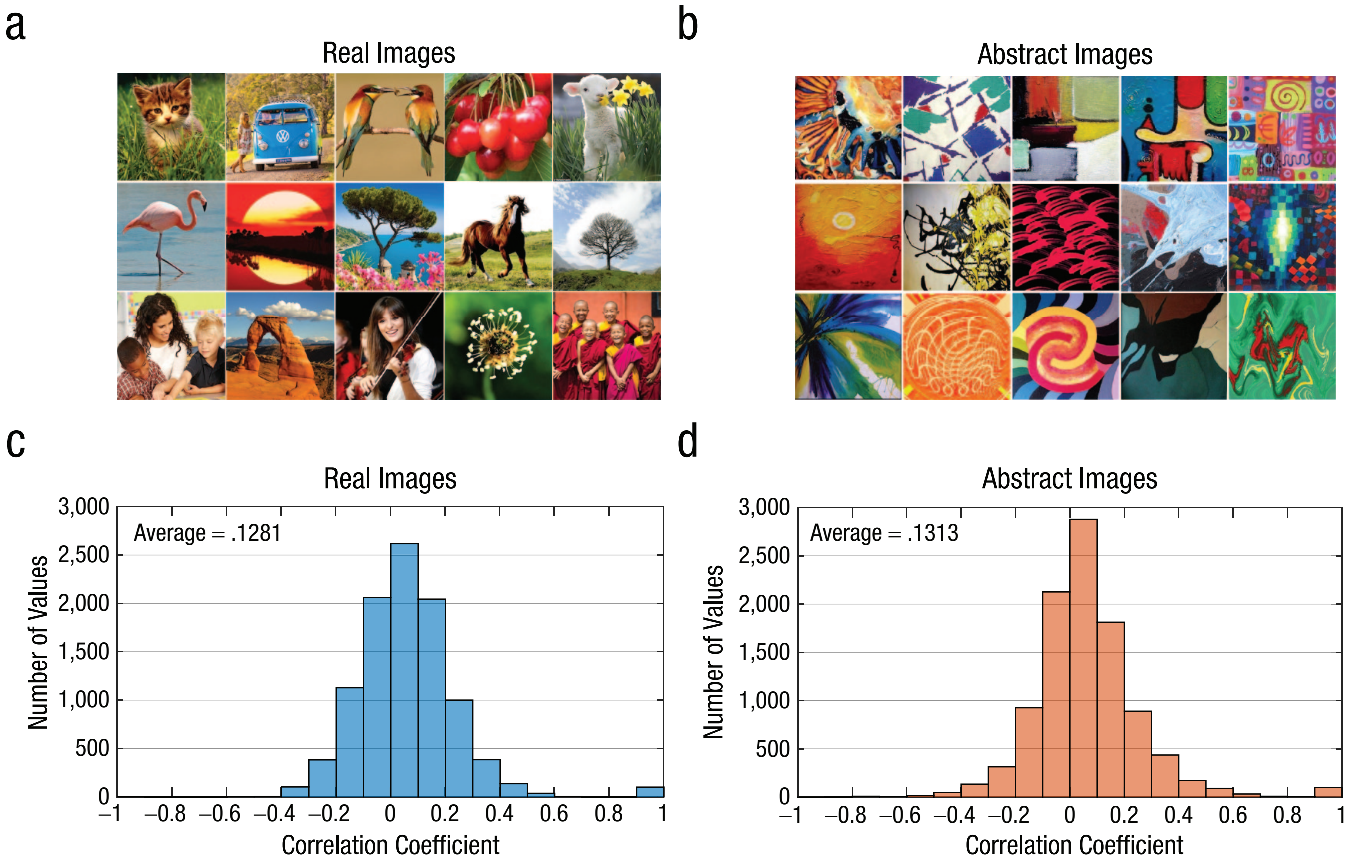

Fig. 1. Example stimuli and stimulus characteristics. The top row shows sample (a) real-world scenes and (b) abstract paintings used in our study. The full stimulus set comprised 2,400 images (1,200 of each type). The distributions in the bottom row show 2D correlation coefficients for all pairwise comparisons across (c) 100 randomly selected real images and (d) 100 randomly selected abstract images.

abstract images was not significant, $t(9898) = -0.9364$, $p = .3491$, $SD = 0.1626$, 95% confidence interval = [–0.0095, 0.0033].

Experimental procedure

Our paradigm used an old/new design. During the training phase, participants were asked to memorize multiple successively presented images displayed for 6 s each. In each session, images were randomly selected, without replacement, from the stimulus database. To ensure that participants attended to the images, we also asked participants to rate the perceived beauty of each image on a scale from 1 to 5. During the test phase, the set of training images was augmented with an equal number of novel distractor images. Participants had to indicate whether they had previously seen each of the images in this test set. Participants' verbal responses were recorded by the experimenter. The test session was conducted 5 min after the conclusion of the memorization session. Images were shown on a 17-in. display under program control using MATLAB (The MathWorks, Natick, MA) and the Psychophysics Toolbox (Brainard, 1997). The viewing distance was 40 cm, and stimulus images subtended 15° of visual angle horizontally and vertically.

To assess memory capacity, we progressively increased the number of images a participant was asked to memorize. The cardinalities we used were 10, 20, 40, and 80. At each cardinality, participants went through the memorization and test sessions before proceeding to the next higher cardinality. During the last postoperative check of newly sighted individuals and during recordings on blur-matched controls, each participant was exposed to eight different experimental conditions: four cardinalities (10, 20, 40, and 80) × two image types (real, abstract). Because only a few of the newly sighted patients carried out the experiment on set sizes of 80 at preoperative and early postoperative time points (the high-cardinality task was found to be exceedingly difficult at these time points), longitudinal within-subject analyses were restricted to a combination of three

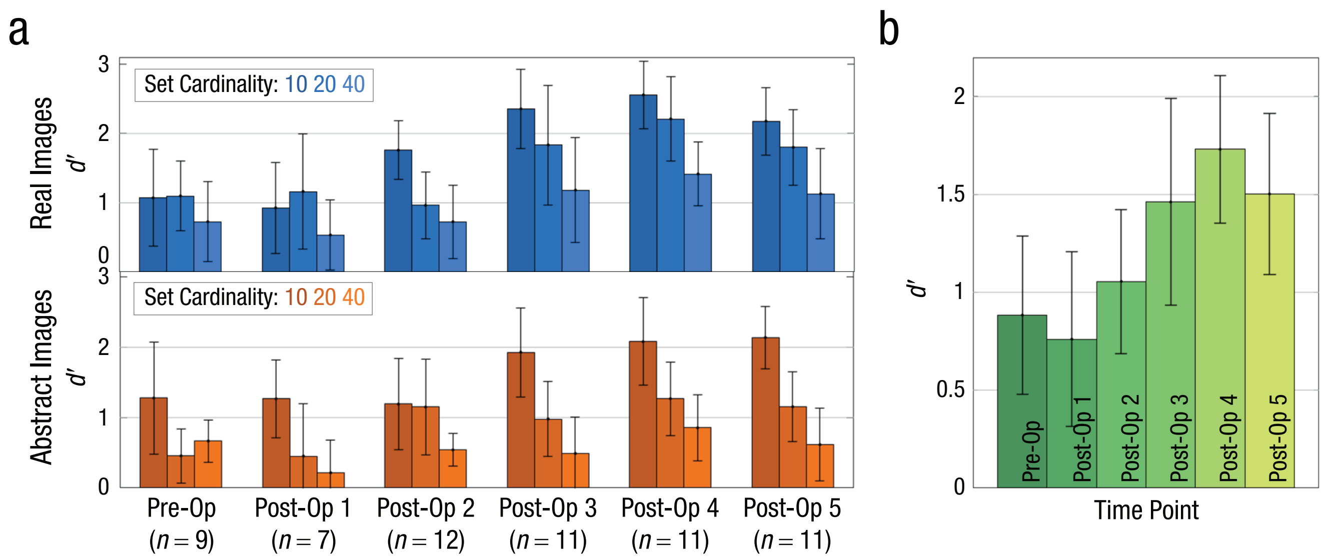

Fig. 2. Recall performance. Averaged sensitivity (d') is shown in (a) for real (top) and abstract (bottom) images as a function of set cardinality (10, 20, 40) and time point relative to surgery for congenital blindness. Participants were tested once before surgery (pre-op), once following surgery on each eye (Post-Op 1 and Post-Op 2, which were typically 1 week apart), and 1 month (Post-Op 3), 6 months (Post-Op 4), and 12 months (Post-Op 5) following surgery. Recall performance is shown in (b) as a function of time point, averaged across set cardinalities and image types. Error bars in both panels represent 95% confidence intervals.

cardinalities (10, 20, and 40) and the two image types. The full combination of four set cardinalities and the two image types were taken into account for a comparison of newly sighted patients 1 year after surgery and control participants. Training and distractor images were unique across all experimental conditions (no images were repeated across cardinalities). No feedback was provided during the testing. The experiment lasted 90 min on average, and participants were free to take breaks between blocks.

The performance of each participant was characterized by calculating d' using the number of hits, misses, correct rejections, and false alarms. Longitudinal-assessment data were collected at six different time points: Once before surgery, once following each eye surgery (which were typically 1 week apart), and 1 month, 6 months, and 12 months following surgery. Not all children contributed data to all longitudinal time points; challenges of travel from their rural domiciles to our center sometimes prevented them from participating in follow-up sessions. When a child was unable to perform the experimental task, as evidenced by unvarying responses to more than 10 stimuli in a sequence, the child's performance for that session was marked as equivalent to chance. Further, when a child was not able to complete all experimental conditions for a given time point, the data were disregarded for our analyses. Control participants were tested while they wore blur goggles simulating Snellen visual acuities of 20/200 and 20/500 (nonoverlapping groups of five and seven children at the two blur levels, respectively). These two acuity values, 20/200 and 20/500, approximated the range of postoperative acuities of the newly sighted patients—nine of the 12 patients were strictly within this acuity range, and three had marginally lower acuities (20/511, 20/524, and 20/543). Relative to 20/500, these three values correspond to differences in the logarithm of the minimum angle of resolution (logMAR) of less than 0.04, or less than one line of acuity measure, which can be considered clinically insignificant (Jones et al., 2003; Smith, 2006). Blurring was achieved by attaching Bangerter occlusion foils (Odell et al., 2008) to clear safety goggles. Assessing the performance of normally sighted participants while they were wearing blurring goggles enabled us to titrate the effects of reduced acuity to be comparable with the newly sighted children's postoperative outcomes, separate from nonoptical factors on visual memory performance.

Results

As has been observed in previous studies of individuals with late sight onset (Ganesh et al., 2014; Kalia et al., 2017), visual outcomes across members of the experimental group can be quite variable. Despite this variability, however, some general trends are apparent, allowing for statistically meaningful inferences. Figure 2 summarizes the newly sighted individuals' data across time points (preoperative and multiple postoperative

Table 1. Results of Linear Mixed Models Examining Within-Subject Performance Variations of Newly Sighted Patients With Regard to Image Type (Real vs. Abstract), Time Point of Recording, and Set Cardinality (10, 20, 40)

Parameter	Estimate	*SE*	95% CI	*df*	*t*	*p*
Image type	**0.343**	**0.084**	**[0.178, 0.509]**	**348.033**	**4.082**	**< .001**
Time point	**0.020**	**0.005**	**[0.011, 0.029]**	**348.082**	**4.234**	**< .001**
Cardinality	**−0.027**	**0.003**	**[−0.034, −0.020]**	**348.033**	**−8.013**	**< .001**
Time Point × Image Type	−0.001	0.006	[−0.013, 0.011]	348.033	−0.172	.864
Time Point × Cardinality	**−0.0004**	**0.0002**	**[−0.0008, −0.0001]**	**348.033**	**−2.400**	**.017**
Time Point × Image Type × Cardinality	0.0002	0.0002	[−0.0002, 0.0006]	348.033	0.926	.355

Note: The table shows unstandardized estimates of fixed effects. Significant results are indicated in boldface. CI = confidence interval.

assessments), set cardinalities (10, 20, and 40), and stimulus types (real and abstract images).

To assess whether the visual working memory capacity of newly sighted children would longitudinally improve following surgery and whether such improvement may be due to the semantic content of an image, we examined within-subject performance variability as a function of set cardinality, image type, and postoperative recording time (see Table 1). First, we found that performance was significantly higher for real, compared with abstract, images ($p < .001$) as well as for lower, compared with higher, set cardinalities ($p < .001$). Crucially, the analyses revealed a positive relationship between the number of weeks following surgery and overall task performance ($p < .001$), quantifying the learning process visualized in Figure 2. The relationship between postsurgical recording time and performance further showed a significant negative interaction ($p = .017$) with the set cardinality (i.e., the temporal improvement was more salient in lower set sizes) but no significant interaction ($p = .864$) with image type (i.e., not providing evidence for a direct link between learning and the image semantics).

Although the aforementioned tests indicate that for the newly sighted children, visual memory capacity improved after sight onset within the first post-op year, it is particularly noteworthy that postoperative performance soon after surgery shows no improvement relative to preoperative performance: Comparing performance before treatment with performance a week after treatment (“Pre-Op” and “Post-Op 1” in Fig. 2) showed no improvements.[1] The onset of patterned vision, therefore, does not bring about an immediate enhancement of visual memory capacity. Instead, the visual memory capacity develops only over the ensuing months, during which children gain visual experience. To examine whether, despite early deprivation, these performance levels would eventually reach those of participants undergoing normal visual development, we compared the performance of newly sighted participants 1 year after surgery with that of control participants whose acuity was artificially reduced to match that of the newly sighted children.

Figure 3 depicts the data across groups (newly sighted patients 1 year after surgery, blur-matched control participants), set cardinalities (10, 20, 40, 80), and image type (real, abstract). Within- and between-subject analyses revealed similar patterns in both the newly sighted and control groups (see Fig. 3): Performance decreased as a function of cardinalities ($p < .001$; see Table 2) and was higher for real relative to abstract images ($p < .001$). However, no significant difference emerged between the two groups ($p = .609$), and no significant interaction effects between the groups and set cardinality ($p = .928$) or image type ($p = .085$) were found. Thus, although there appear to be differences for specific combinations of image types and set cardinalities (e.g., real images with a set cardinality of 80), these differences did not reach statistical significance.

Thus, although the previous analysis (see Fig. 2 and Table 1) established that sight onset in itself is not sufficient to induce immediate visual memory improvements, here we found that visual experience for 1 year leads to visual memory patterns that are approximately comparable with those of control participants.

We also examined possible links between improvements in memory performance and changes in visual acuity. As documented in previous work, visual acuity shows modest improvements over time following sight-restoring surgery (Ganesh et al., 2014). The same was true of this cohort of children. Figure S3 in the Supplemental Material shows the change in acuity and d' as a function of time after surgery for the 12 newly sighted patients. The dashed red line depicts performance of control participants at a blur level of 20/500. The point to note here is that although patients’ acuity and d' showed an improvement over time, it took several months for their performance (d') to be at par with that of control participants, despite the fact that the induced blur level in the latter was worse than the postoperative acuity of most of the patients. Thus, there is a protracted temporal progression over which visual memory performance develops to a level achievable by control participants with comparable or worse induced acuity. For higher cardinalities, performance of many of the patients remained below that of

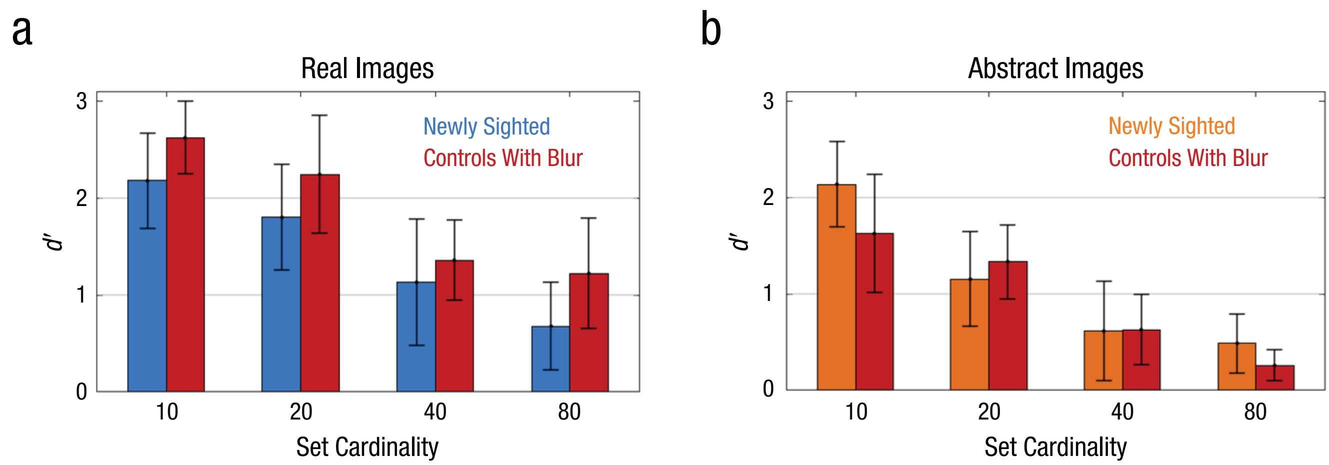

Fig. 3. Recall performance on the final memory task (12 months after surgery). Averaged sensitivity (d') is shown for (a) real and (b) abstract images as a function of set cardinality (10, 20, 40, 80), separately for newly sighted children and blur-matched control participants. Error bars represent 95% confidence intervals.

control participants even though their acuity was better than 20/500. Hence, although the newly sighted Prakash participants did experience longitudinal changes in their postoperative acuity, these changes did not provide an adequate account of the improvement in their visual memory skills. Specifically, memory performance of the Prakash children early in the postsurgical timeline was lower than what was feasible in principle given their acuity.

Figure S1 in the Supplemental Material shows a color-coded matrix of within-subject correlations of acuity and performance over time for all participants in the experimental group. Figure S2 shows the correlations of acuity and recognition performance at the final time point measured for all participants.

Discussion

The current study explored the impact of early visual deprivation on the later development of visual memory recall once sight is restored. The primary finding was that the basic ability to recall previously seen images is initially poor at sight onset but improves significantly in the ensuing months. Despite initially poor posttreatment performance on all image types and cardinalities, the improvements that emerged over time ultimately showed superior recall of real compared with abstract images and an overall pattern that was graded as a function of increased cardinality. Following a year of visual experience, patients' overall performance still fell slightly, though not significantly, short of the typically developing control participants' performance, so we are not ruling out the possibility that early visual deprivation may limit the development of visual memory later in life. However, it is notable that the effects of stimulus type and cardinality were found for both groups of participants, suggesting that some aspects of the functional organization of visual memory that emerge following early visual deprivation may be similar to those that emerge from typical visual development. Importantly, we found that

Table 2. Results of Linear Mixed Models Examining Group-Relevant Performance Variations With Regard to Image Type (Within Subjects), Set Cardinality (Within Subjects), and Group (Between Subjects)

Parameter	Estimate	*SE*	95% CI	*df*	*t*	*p*
Image type	**0.905**	**0.206**	**[0.498, 1.313]**	**155**	**4.389**	**< .001**
Group	0.152	0.295	[−0.439, 0.742]	58.970	0.514	.609
Cardinality	**−0.019**	**0.003**	**[−0.026, −0.013]**	**155**	**−6.103**	**< .001**
Group × Image Type	−0.517	0.298	[−1.106, 0.072]	155	−1.734	.085
Group × Cardinality	−0.0004	0.005	[−0.010, 0.009]	155	−0.091	.928
Group (Experimental) × Image Type × Cardinality	−0.001	0.005	[−0.010, 0.008]	155	−0.228	.820
Group (Control) × Image Type × Cardinality	−0.0002	0.004	[−0.009, 0.009]	155	−0.037	.971

Note: The table shows unstandardized estimates of fixed effects. Significant results are indicated in boldface. CI = confidence interval.

the formation of high-fidelity memory representations for semantically meaningful information emerges slowly and depends on visual experience—a result that is consistent with recent models of visual memory representations in which information about real-world scenes is stored as a hierarchical feature bundle with object-level information at the top and basic features at the bottom (Brady et al., 2011).

The significant longitudinal improvement found in memory capacity suggests that this ability is at least partly resilient to protracted periods of visual deprivation. What might account for this resilience? It is believed that rather than being a localized process, memory is subserved by multiple cortical areas. Candidate areas include the prefrontal cortex (Runyan et al., 2004) and the lateral occipital complex (Gayet et al., 2018), among others. Given this distributed notion of memory as drawing on a distributed network, one possible explanation of the observed resilience is that substrates of visual memory that are located in higher cortical areas may be less susceptible to deprivation than early sensory cortices, such as V1. A related possibility is that at least some memory resources may be amodal, accessible to multiple sensory modalities and cognitive processes (Loomis et al., 2012; McCarthy & Warrington, 1988; Schumacher et al., 1996). Such amodal stores can be maintained by modalities other than vision while an individual is blind and thus lessen their vulnerability to absence of visual information. Additionally, it is worth noting that the newly sighted patients were not entirely denied visual stimulation prior to surgery. Although profoundly visually compromised, they did experience light stimulation and even rudimentary pattern perception. Such experience, however limited, may play a role in sustaining the neural substrates for visual memory. The question of whether total removal of visual stimulation for an extended period after birth can still be followed by the development of visual memory can potentially be investigated with nonhuman animal studies using dark-rearing regimens that have been extensively employed in the past (e.g., Fagiolini et al., 1994).

Beyond the evidence of resilience, a more specific question concerns the nature of mechanisms that might account for the observed enhancement in memory performance. There are at least two broad possibilities. The first involves increases in intrinsic memory capacity, perhaps through the recruitment of greater neural resources for information storage. The second relies on representational elaboration; increasing richness of the representational vocabulary for visual content would render images more discriminable and would become manifest as improved memory performance even without changes in the storage capacity per se. The rapid rate of improvement we observed in the newly sighted children and the relatively advanced age at which such improvements were happening lead us to favor the latter account over the former. We have conducted computational simulations in order to verify the plausibility of the idea that increasing experience with patterned imagery would lead to progressive elaborations of internal representations of individual images, rendering them more discriminable and thereby achieving steadily better performance on the kind of memory task that we have used with the newly sighted children.

To this end, we trained a prototypical convolutional neural network, the AlexNet (Krizhevsky et al., 2012), on the Caltech-101 object database (Fei-Fei et al., 2007), with individual images rescaled and cropped to 100 × 100 pixels. We then analyzed its internal representations throughout training. Specifically, after 1, 5, 10, 20, and 50 epochs of training, we presented 100 new exemplar images to the (partially) trained network and recorded the resulting activations at five different layers of the network (see Fig. 4a). We then applied a multidimensional scaling (MDS) analysis to visualize the activations for each image in a two-dimensional space, separately for each of the five layers and each of the five different numbers of epochs. With this analysis, we investigated representational elaboration: whether, and where in the network, continued training yielded more diverse visual representations that consequently rendered images more discriminable.

Figure 4b shows the results. A modest amount of representational elaboration can be seen in the later convolutional layers, although no such elaboration is evident in the first layer. The elaboration is particularly notable in the fully connected layers; more training renders images more discriminable.

While in the first fully connected layer, continued elaboration can be seen even in comparatively late epochs (e.g., between Epochs 20 and 50), in the second fully connected layer, the representation appears more elaborate from early on. With the softmax operation applied to the last fully connected layer, we see that task-relevant fine-tuning keeps proceeding even until later epochs.

The results from these computational simulations lend credence to the possibility that the progressive improvements in the performance of newly sighted children on the old/new task may have arisen from the increased representational elaborations of images as the children steadily gained more visual experience.

We need to keep in mind some important caveats when interpreting the results of this study. First, although the experimental data clearly show improvements in visual memory performance following sight onset, the

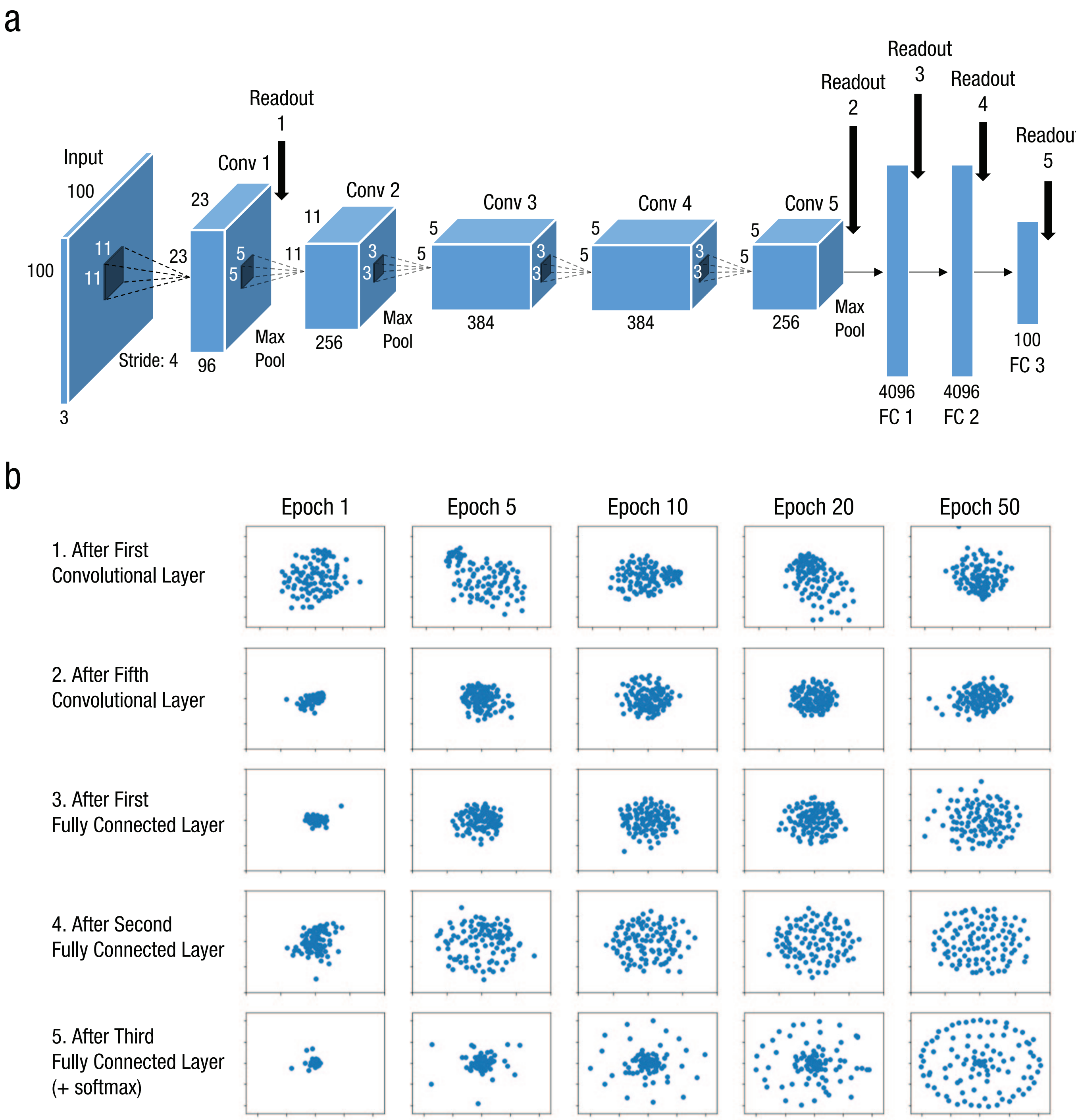

Fig. 4. The convolutional network, the AlexNet, used to conduct computational simulations. The schematic (a) illustrates the functioning of the network. Arrows indicate the five readout sites. "Conv" refers to convolutional layers; "FC" refers to fully connected layers. Multidimensional scaling–derived visualizations of the activities of units in the indicated readout sites are shown in (b). With the exception of the last readout site, to which the softmax operation had already been applied, the activity magnitudes have been normalized. A wider spread in the 2D plots depicting the projected space can therefore not be the result of larger absolute values that may have simply been reinforced during training. The axis scales are identical across epochs but not across layers.

mechanisms underlying this improvement remain unclear. These may include intrinsic changes in the memory subsystems of the brain and/or changes in representational richness of the early visual areas (as suggested by the computational simulations). Related to the second possibility is the potential contribution of acuity improvements. Given the changes in acuity over the same timeline as that of improvements in visual memory performance, we cannot rule out an influence of the former on the latter; increased acuity would permit better discrimination between images by providing access to a richer set of spatial features. Although acuity changes may well contribute to progression in visual memory performance, it is unclear whether they constitute a complete account of the observed improvements. As mentioned in the Results section, newly sighted people exhibit residual deficits in memory performance relative to control participants with induced acuity loss. Control participants' resilience to acuity reduction could arise from the more extensive visual experience they have had with normal resolution imagery, enabling them to better interpret degraded inputs. Not having had the benefit of such experience, the newly sighted group's performance may be more acuity limited than the control group's. Second, accumulating postoperative experience with the real world leads to an increase in categorization abilities (Ostrovsky et al., 2009). The instantiation of visual categories may play a role in organizing visual inputs and thus may impact their memorizability. Third, the patient population we worked with included adolescents and young adults. It is unclear whether these results can be extrapolated to individuals who gain sight much later in life, as was the case with the individuals described in earlier reports (Fine et al., 2003; Gregory & Wallace, 1963; Sacks, 1995; Valvo, 1971).

In summary, the progressive improvement in memory performance after sight onset leads us to conclude that the substrates responsible for visual memory retain at least some measure of plasticity despite several years of visual deprivation. It is unclear, though, whether these improvements result from increases in storage per se or from enhancements in image encoding, perhaps driven by improvements in visual acuity. Furthermore, additional studies are needed to determine whether the extent of available plasticity is modulated by age at treatment, whether a correlation exists between nonvisual and visual memory capacity, and what neural changes accompany the development of visual memory in the newly sighted.

Transparency

Action Editor: Angela Lukowski

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Author Contributions

P. Gupta and P. Sinha developed the study concept. P. Gupta, S. Gilad-Gutnick, and P. Sinha designed the experimental protocol. P. Gupta, P. Shah, and K. Tiwari collected experimental data. P. Gupta, P. Shah, L. Vogelsang, and P. Sinha analyzed and interpreted the data. M. Vogelsang and L. Vogelsang performed the computational simulations. S. Ganesh conducted the surgical procedures and ophthalmic characterization of Prakash patients. P. Gupta, P. Shah, S. Gilad-Gutnick, M. Vogelsang, L. Vogelsang, T. Gandhi, and P. Sinha drafted the manuscript. All authors approved the final version of the manuscript for submission.

Declaration of Conflicting Interests

The author(s) declared that there were no conflicts of interest with respect to the authorship or the publication of this article.

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Open Practices

Data and materials for this study have not been made publicly available, and the design and analysis plans were not preregistered.

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Supplemental Material

Additional supporting information can be found at http://journals.sagepub.com/doi/suppl/10.1177/09567976211056664

Note

1. It is worth noting that preoperative performance was not exactly at chance level. This is likely because even with dense cataracts, it is possible to get information about overall luminance and average color. This information may have been sufficient for getting some responses correct, especially when the cardinality was low, but this rudimentary characterization of the image was not very useful with larger cardinalities. Indeed, as is evident in Figures 2 and 3, with higher cardinality values, the preoperative d' values dropped close to zero (a similar decrease can be observed in control participants; see Fig. 3).

References

American Foundation for the Blind. (2020). *Low vision and legal blindness terms and descriptions*. https://www.afb.org/blindness-and-low-vision/eye-conditions/low-vision-and-legal-blindness-terms-and-descriptions

Bach, M. (1996). The Freiburg Visual Acuity Test—automatic measurement of visual acuity. *Optometry and Vision Science*, *73*(1), 49–53.

Bellhouse-King, M. W., & Standing, L. G. (2007). Recognition memory for concrete, regular abstract, and diverse abstract pictures. *Perceptual and Motor Skills*, *104*(3), 758–762.

Braddick, O., Atkinson, J., & Wattam-Bell, J. (2003). Normal and anomalous development of visual motion processing:

Motion coherence and 'dorsal-stream vulnerability.' *Neuropsychologia*, *41*(13), 1769–1784. https://doi.org/10.1016/S0028-3932(03)00178-7

Brady, T. F., Konkle, T., & Alvarez, G. A. (2011). A review of visual memory capacity: Beyond individual items and toward structured representations. *Journal of Vision*, *11*(5), Article 4. https://doi.org/10.1167/11.5.4

Brady, T. F., Konkle, T., Alvarez, G. A., & Oliva, A. (2008). Visual long-term memory has a massive storage capacity for object details. *Proceedings of the National Academy of Sciences, USA*, *105*(38), 14325–14329.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436.

Cobb, S. R., & MacDonald, C. F. (1978). Resolution acuity in astigmats: Evidence for a critical period in the human visual system. *The British Journal of Physiological Optics*, *32*, 38–49.

Cowan, N., AuBuchon, A. M., Gilchrist, A. L., Ricker, T. J., & Saults, J. S. (2011). Age differences in visual working memory capacity: Not based on encoding limitations. *Developmental Science*, *14*(5), 1066–1074.

Ellemberg, D., Lewis, T. L., Maurer, D., Brar, S., & Brent, H. P. (2002). Better perception of global motion after monocular than after binocular deprivation. *Vision Research*, *42*(2), 169–179.

Fagiolini, M., Pizzorusso, T., Berardi, N., Domenici, L., & Maffei, L. (1994). Functional postnatal development of the rat primary visual cortex and the role of visual experience: Dark rearing and monocular deprivation. *Vision Research*, *34*(6), 709–720.

Fei-Fei, L., Fergus, R., & Perona, P. (2007). Learning generative visual models from few training examples: An incremental Bayesian approach tested on 101 object categories. *Computer Vision and Image Understanding*, *106*(1), 59–70. https://doi.org/10.1016/j.cviu.2005.09.012

Ferrara, K., Furlong, S., Park, S., & Landau, B. (2017). Detailed visual memory capacity is present early in childhood. *Open Mind*, *2*(1), 14–25.

Fine, I., Wade, A. R., Brewer, A. A., May, M. G., Goodman, D. F., Boynton, G. M., Wandell, B. A., & MacLeod, D. I. A. (2003). Long-term deprivation affects visual perception and cortex. *Nature Neuroscience*, *6*(9), 915–916. https://doi.org/10.1038/nn1102

Ganesh, S., Arora, P., Sethi, S., Gandhi, T. K., Kalia, A., Chatterjee, G., & Sinha, P. (2014). Results of late surgical intervention in children with early-onset bilateral cataracts. *British Journal of Ophthalmology*, *98*(10), 1424–1428.

Gayet, S., Paffen, C. L., & Van der Stigchel, S. (2018). Visual working memory storage recruits sensory processing areas. *Trends in Cognitive Sciences*, *22*(3), 189–190.

Gregory, R. L., & Wallace, J. G. (1963). Recovery from early blindness: A case study. *Experimental Psychology Society Monograph*, *2*, 65–129.

Hubel, D. H., & Wiesel, T. N. (1970). The period of susceptibility to the physiological effects of unilateral eye closure in kittens. *The Journal of Physiology*, *206*(2), 419–436.

Jones, D., Westall, C., Averbeck, K., & Abdolell, M. (2003). Visual acuity assessment: A comparison of two tests for measuring children's vision. *Ophthalmic and Physiological Optics*, *23*(6), 541–546.

Kalia, A., Gandhi, T., Chatterjee, G., Swami, P., Dhillon, H., Bi, S., Chauhan, N., Das Gupta, S., Sharma, P., Sood, S., Ganesh, S., Mathur, U., & Sinha, P. (2017). Assessing the impact of a program for late surgical intervention in early blind children. *Public Health*, *146*, 15–23.

Kalia, A., Lesmes, L. A., Dorr, M., Gandhi, T., Chatterjee, G., Ganesh, S., Bex, P. J., & Sinha, P. (2014). Development of pattern vision following early and extended blindness. *Proceedings of the National Academy of Sciences, USA*, *111*(5), 2035–2039. https://doi.org/10.1073/pnas.1311041111

Krizhevsky, A., Sutskever, I., & Hinton, G. E. (2012). ImageNet classification with deep convolutional neural networks. *Advances in Neural Information Processing Systems*, *25*, 1097–1105.

Le Grand, R., Mondloch, C. J., Maurer, D., & Brent, H. P. (2001). Early visual experience and face processing. *Nature*, *410*(6831), Article 890. https://doi.org/10.1038/35073749

Lewis, T. L., & Maurer, D. (2005). Multiple sensitive periods in human visual development: Evidence from visually deprived children. *Developmental Psychobiology*, *46*(3), 163–183.

Loomis, J. M., Klatzky, R. L., McHugh, B., & Giudice, N. A. (2012). Spatial working memory for locations specified by vision and audition: Testing the amodality hypothesis. *Attention, Perception, & Psychophysics*, *74*(6), 1260–1267.

Madigan, S. (2014). Picture memory. In J. C. Yuille (Ed.), *Imagery, memory and cognition: Essays in honor of Allan Paivio* (pp. 65–89). Psychology Press.

Maurer, D., Lewis, T. L., & Mondloch, C. J. (2005). Missing sights: Consequences for visual cognitive development. *Trends in Cognitive Sciences*, *9*(3), 144–151.

Maurer, D., Mondloch, C. J., & Lewis, T. L. (2007). Effects of early visual deprivation on perceptual and cognitive development. *Progress in Brain Research*, *164*, 87–104.

McCarthy, R. A., & Warrington, E. K. (1988). Evidence for modality-specific meaning systems in the brain. *Nature*, *334*(6181), 428–430.

Nickerson, R. S. (1965). Short-term memory for complex meaningful visual configurations: A demonstration of capacity. *Canadian Journal of Psychology*, *19*(2), 155–160. https://doi.org/10.1037/h0082899

Odell, N. V., Leske, D. A., Hatt, S. R., Adams, W. E., & Holmes, J. M. (2008). The effect of Bangerter filters on optotype acuity, Vernier acuity, and contrast sensitivity. *Journal of American Association for Pediatric Ophthalmology and Strabismus*, *12*(6), 555–559.

Ostrovsky, Y., Andalman, A., & Sinha, P. (2006). Vision following extended congenital blindness. *Psychological Science*, *17*(12), 1009–1014. https://doi.org/10.1111/j.1467-9280.2006.01827.x

Ostrovsky, Y., Meyers, E., Ganesh, S., Mathur, U., & Sinha, P. (2009). Visual parsing after recovery from blindness. *Psychological Science*, *20*(12), 1484–1491. https://doi.org/10.1111/j.1467-9280.2009.02471.x

Riggs, K. J., McTaggart, J., Simpson, A., & Freeman, R. P. (2006). Changes in the capacity of visual working memory in 5- to 10-year-olds. *Journal of Experimental Child Psychology*, *95*(1), 18–26.

Rose, S. A., Feldman, J. F., & Jankowski, J. J. (2001). Visual short-term memory in the first year of life: Capacity and recency effects. *Developmental Psychology*, *37*(4), 539–549.

Ross-Sheehy, S., Oakes, L. M., & Luck, S. J. (2003). The development of visual short-term memory capacity in infants. *Child Development*, *74*(6), 1807–1822.

Runyan, J. D., Moore, A. N., & Dash, P. K. (2004). A role for prefrontal cortex in memory storage for trace fear conditioning. *The Journal of Neuroscience*, *24*(6), 1288–1295.

Sacks, O. (1995). *An anthropologist on Mars: Seven paradoxical tales*. Vintage Books.

Schumacher, E. H., Lauber, E., Awh, E., Jonides, J., Smith, E. E., & Koeppe, R. A. (1996). PET evidence for an amodal verbal working memory system. *NeuroImage*, *3*(2), 79–88.

Shepard, R. N. (1967). Recognition memory for words, sentences, and pictures. *Journal of Verbal Learning and Verbal Behavior*, *6*(1), 156–163.

Simmering, V. R. (2012). The development of visual working memory capacity during early childhood. *Journal of Experimental Child Psychology*, *111*(4), 695–707.

Sinha, P. (2013). Once blind and now they see. *Scientific American*, *309*(1), 48–55.

Sinha, P., & Held, R. (2012). Sight restoration. *F1000 Medicine Reports*, *4*, Article 17. https://doi.org/10.3410/M4-17

Slotnick, S. D. (2004). Visual memory and visual perception recruit common neural substrates. *Behavioral and Cognitive Neuroscience Reviews*, *3*(4), 207–221.

Smith, G. (2006). Refraction and visual acuity measurements: What are their measurement uncertainties? *Clinical and Experimental Optometry*, *89*(2), 66–72.

Standing, L. (1973). Learning 10000 pictures. *The Quarterly Journal of Experimental Psychology*, *25*(2), 207–222.

Standing, L., Conezio, J., & Haber, R. N. (1970). Perception and memory for pictures: Single-trial learning of 2500 visual stimuli. *Psychonomic Science*, *19*(2), 73–74.

Tusa, R. J., Repka, M. X., Smith, C. B., & Herdman, S. J. (1991). Early visual deprivation results in persistent strabismus and nystagmus in monkeys. *Investigative Ophthalmology & Visual Science*, *32*(1), 134–141.

Valvo, A. (1971). *Sight restoration after long-term blindness: The problems and behavior patterns of visual rehabilitation*. American Foundation for the Blind.

von Senden, M. (1960). *Space and sight: The perception of space and shape in the congenitally blind before and after operation*. Methuen.

Walker, P., Hitch, G. J., Doyle, A., & Porter, T. (1994). The development of short-term visual memory in young children. *International Journal of Behavioral Development*, *17*(1), 73–89.

Wolbers, T., Klatzky, R. L., Loomis, J. M., Wutte, M. G., & Giudice, N. A. (2011). Modality-independent coding of spatial layout in the human brain. *Current Biology*, *21*, 984–989.

Yuille, J. C. (Ed.) (2014). *Imagery, memory and cognition: Essays in honor of Allan Paivio*. Psychology Press.