Psychological Science

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Tapan K. Gandhi, Suma Ganesh and Pawan Sinha Psychological Science published online 9 January 2014 DOI: 10.1177/0956797613513906

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What is This?

Improvement in Spatial Imagery Following Sight Onset Late in Childhood

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Psychological Science 201X, Vol XX(X) 1–9 © The Author(s) 2014 Reprints and permissions: sagepub.com/journalsPermissions.nav DOI: 10.1177/0956797613513906 pss.sagepub.com



Abstract

The factors contributing to the development of spatial imagery skills are not well understood. Here, we consider whether visual experience shapes these skills. Although differences in spatial imagery between sighted and blind individuals have been reported, it is unclear whether these differences are truly due to visual deprivation or instead are due to extraneous factors, such as reduced opportunities for the blind to interact with their environment. A direct way of assessing vision's contribution to the development of spatial imagery is to determine whether spatial imagery skills change soon after the onset of sight in congenitally blind individuals. We tested 10 children who gained sight after several years of congenital blindness and found significant improvements in their spatial imagery skills following sight-restoring surgeries. These results provide evidence of vision's contribution to spatial imagery and also have implications for the nature of internal spatial representations.

Keywords

cognitive development, mental models, visual memory

Received 3/6/13; Revision accepted 10/22/13

Being able to imagine and reason about the spatial structure of the environment is a crucially important skill. People rely on it for various tasks, such as handling and manipulating objects, and planning routes through complex layouts. However, the factors that contribute to the development of spatial imagery and reasoning skills are still unclear.

Sensory input across multiple modalities (vision, audition, touch, and proprioception) is rich with information about the spatial structure of the environment and the objects therein (Lacey & Sathian, 2011; Woods & Newell, 2004). The redundancy of these multiple sources, and their strong interactions (Deneve & Pouget, 2004; Stein & Meredith, 1993), provides robustness, but also makes it difficult to titrate their individual contributions to spatial imagery. One way of gaining insight into this issue is to determine whether spatial skills change after the introduction of a sensory stream that an individual had been deprived of since birth. Obvious ethical considerations rule out forced sensory deprivation as an experimental manipulation with human subjects. The individual contributions of the various sensory modalities to spatial skills have, therefore, remained largely unexplored thus far.

One promising way forward is to study those rare cases in which people have not received treatment for disorders that cause profound sensory loss in a particular modality, even though their conditions are curable. Previous studies have demonstrated the effectiveness of using samples of people who have received sight-restoring surgeries to study various aspects of visual development (Chatterjee, Kalia, Gandhi, & Sinha, 2013; Gandhi, Kalia, Chatterjee, & Sinha, 2013; Kalia et al., 2013; Maurer, Lewis, & Mondloch, 2005). However, the influence of vision on performance of spatial imagery tasks is not well researched. In the study reported here, we attempted to begin filling in this gap by investigating whether the spatial imagery skills of congenitally blind children change after they receive sight-restoring surgeries.

Our work builds on earlier studies by other investigators who have compared spatial imagery skills of normally sighted and blind individuals. Although these experiments

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could not reveal the influence of sight initiation on spatial skills after a lifetime of blindness, they do provide interesting cross-sectional data on whether long-term visual deprivation affects spatial abilities. The basic finding from these studies is that people born without sight are able to mentally experience spatial representations (Arditi, Holtzman, & Kosslyn, 1988; Forrest, 1984; Haber, Haber, Levin, & Hollyfield, 1993; Vecchi, 1998; Zimler & Keenan, 1983). Their abilities are similar to those of sighted individuals in generating pictures by means of haptic stimuli (Carreiras & Codina, 1992; Klatzky, Golledge, Loomis, Cicinelli, & Pellegrino, 1995) and in performing classic mental rotation tasks (Marmor, & Zaback, 1976), mental scanning tasks (Kerr, 1983), and motor imagery tasks (Imbiriba, Rodrigues, Magalhaes, & Vargas, 2006). Moreover, it appears that blind and sighted participants rely on similar processes while carrying out imagery tasks, as a spatial interference task causes similar disruptions in their ability to analyze the shape of a series of mentally generated objects or follow a pattern on a mentally generated matrix (Aleman, van Lee, Mantione, Verkoijen, & de Haan, 2001).

Several studies have found that congenitally blind individuals perform less accurately than age-matched sighted participants on spatial imagery tasks (Byrne & Salter, 1983; Cattaneo, Vecchi, Monegato, Pece, & Cornoldi, 2007; Cornoldi, Bertuccelli, Rocchi, & Sbrana, 1993; Cornoldi, Cortesi, & Preti, 1991; De Beni & Cornoldi, 1988; Eimer, 2004; Gandhi, Khurana, Santhosh, & Anand, 2011; Hatwell, 1978; Knauff & May, 2006; Warren, 1977). However, the robustness of these group differences is debatable. Some studies have suggested that visual experience is neither necessary nor sufficient for the development of spatial representations (Afonso et al., 2010; Cattaneo et al., 2008; Cornoldi & Vecchi, 2000; Iachini & Ruggiero, 2010; Millar, 1994; Thinus-Blanc & Gaunet, 1997). Furthermore, the group differences may be tied to specific task scenarios. For instance, Vecchi, Tinti, and Cornoldi (2004) suggested that the difficulty the blind experience may be tied more to the simultaneous maintenance of multiple spatial structures in memory than to manipulating any single one. It is also unclear whether any observed differences in the spatial skills of sighted and blind individuals are due to the lack of visual experience per se or to the long-term (typically several years in duration) limitations on environmental exploration imposed by blindness. Furthermore, even if one accepts that visual experience contributes to spatial skills, it remains an open question whether its influence is subject to a critical time window during development or can be effective much later in life as well.

To summarize, past results on the contribution of vision to spatial imagery skills provide a mixed picture. Blind individuals are able to perform various imagery tasks, and the differences they exhibit relative to sighted participants cannot be definitively attributed to their lack of visual experience. We believe that a more reliable way forward would be to adopt a longitudinal approach and to determine whether the onset of sight in blind individuals leads to changes in their spatial skills.

Method

Subjects

We worked with three groups of subjects:

- The *early-blind group* consisted of 30 children who had been blind from an early age (15 males, 15 females; age range = 12–15 years, mean age = 13 years). All children in this group were enrolled in a school for the blind in New Delhi, India, and knew Braille. (See Table 1 for additional information on individual subjects in this group.)
- The *sighted group* consisted of 30 normally sighted children (15 males, 15 females; age range = 9–11 years, mean age = 10 years).
- The treatable-blind group consisted of 10 congenitally blind children (for the sake of brevity, we refer to all subjects in this group as children, though one was 22 years old) with treatable blindness (all males; age range = 12-22 years, mean age = 15 years). All subjects in this group were blind as a result of dense bilateral congenital cataracts. Determination that the visual deprivation was congenital was based on parental reports and also the presence of nystagmus, which is known to be induced by profound visual impairment very early in life (Tusa, Repka, Smith, & Herdma, 1991). The members of this group were identified via outreach activities undertaken as part of Project Prakash (Mandavilli, 2006; Sinha, 2013; Sinha, Chatterjee, Gandhi, & Kalia, 2013; Sinha & Held, 2012). All were provided surgeries that involved extracting the cataract and implanting an intraocular lens. Postoperative visual acuity ranged from 1.51 logMAR (log of the minimum angle of resolution) to 1.17 logMAR, with a mean of 1.38 logMAR. (See Table 2 for additional information on individual subjects in this group.)

There was no history of neurological or psychiatric illness in any of the subjects. Informed consent was obtained from all subjects prior to our study. The earlyblind and sighted groups were matched in size and gender composition to allow a cross-sectional comparison of their performance. The treatable-blind group was included to provide longitudinal data (before and after sight-restoring surgery) for a within-group analysis.

Age (years)	Sex	Cause of blindness	Age at onset of blindness (years)	Visual acuity (left/right)
13 years	Male	Eye infection	< 2 years	0/0
12 years	Male	Eye infection	< 2 years	0/0
12 years	Male	Cataract	1 year 5 months	LP/LP
13 years	Male	Unknown	2 years	0/0
13 years	Male	Eye infection	< 1 year 5 months	0/0
12 years	Male	Optic nerve atrophy	2 years	0/0
12 years	Male	Microphthalmos	Birth	0/0
14 years	Male	Microphthalmos	Birth	0/HM
12 years	Male	Optic nerve atrophy	2 years 5 months	0/0
13 years	Male	Eye infection	2 years	0/0
13 years	Male	Microphthalmos	Birth	0/0
14 years	Male	Fundus coloboma	Birth	0/0
12 years	Male	Glaucoma (postmeasles)	3 years	0/0
13 years	Male	Microphthalmos	Birth	HM/0
12 years	Male	Cataract	2 years	0/LP
14 years	Female	Cataract	< 3 years	LP/LP
14 years	Female	Microphthalmos	Birth	0/0
12 years	Female	Optic nerve atrophy	2 years 5 months	0/0
12 years	Female	Glaucoma (postmeasles)	2 years	LP/0
13 years	Female	Retinal detachment	3 years	0/0
13 years	Female	Unknown	< 2 years	0/0
13 years	Female	Microphthalmos	Birth	LP/0
14 years	Female	Glaucoma	< 2 years 5 months	0/LP
15 years	Female	Optic nerve atrophy	3 years	0/0
14 years	Female	Cataract	2 years	LP/LP
12 years	Female	Eye infection	1 year 5 months	0/0
13 years	Female	Eye infection	2 years	0/0
13 years	Female	Optic nerve atrophy	2 years 5 months	0/0
12 years	Female	Glaucoma	2 years	0/LP
14 years	Female	Eye infection	< 2 years 5 months	0/0

Table 1. Characteristics of the Children in the Early-Blind Group

Note: Numerical values for visual acuity are from the logMAR (log of the minimum angle of resolution) scale. HM = hand movement; LP = light perception.

Age	Gender	Preoperative acuity (both eyes)	Ophthalmic diagnosis	Postoperative acuity (left/right)
17 years	Male	HM	Total cataract	1.50/1.69
12 years	Male	LP, PR	Total cataract	1.47/1.47
22 years	Male	FC at 50 cm	Total cataract	1.42/1.39
16 years	Male	LP, PR	Membranous cataract	1.47/1.51
12 years	Male	LP, PR	Polar cataract (right), membranous cataract (left)	1.32/1.32
12 years	Male	FC at 50 cm	Zonular cataract	1.17/1.47
16 years	Male	LP, PR	Membranous cataract	1.17/1.72
14 years	Male	LP, PR	Total cataract	1.43/1.47
15 years	Male	HM	Membranous cataract	1.51/1.51
12 years	Male	LP, PR	Polar cataract	1.42/1.42

 Table 2.
 Characteristics of the Children in the Treatable-Blind Group

Note: Numerical values for visual acuity are from the logMAR (log of the minimum angle of resolution) scale. HM = hand movement; LP = perception of light; PR = projection of rays (direction of light); FC = finger counting.

Stimuli and procedure

The experimental stimuli were three square matrices with different numbers of elements $(2 \times 2, 3 \times 3, \text{ and } 4 \times 4 \text{ grids})$. The matrices were formed by raised pegs on a flat plastic board, so that their configurations could be conveyed easily by touch (Fig. 1a). Subjects were seated comfortably and asked to tactually explore the matrices for 30 s to become familiar with their arrangement (Fig. 1b).

They were free to use one or both hands to explore the stimuli. The lower-left peg was designated as the origin. The normally sighted subjects were blindfolded throughout the experiment, as were the treatable-blind subjects after sight onset, so they had no visual experience with the peg board.

At the start of the test, the matrices were removed from the reach of the subjects. They were directed to follow chains of directional commands given verbally by

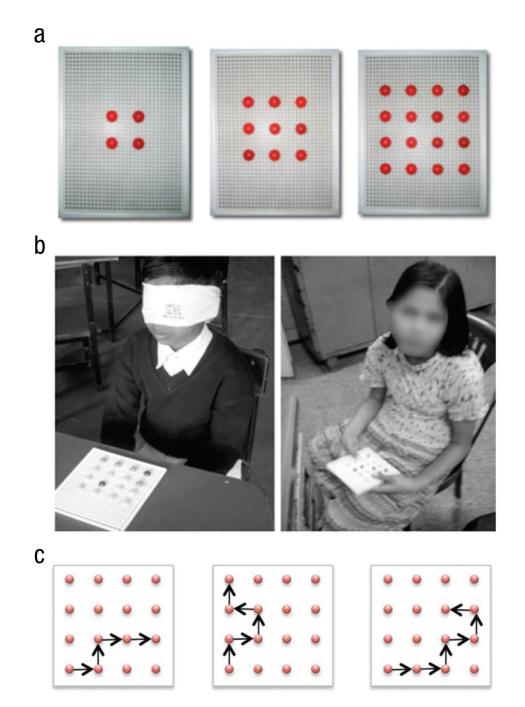


Fig. 1. Illustration of the experimental method: (a) the three peg matrices used in our studies, (b) a sighted child with a blindfold and a congenitally blind child performing a trial of the spatial reasoning task, and (c) sample command chains on a 4×4 grid (from left to right, chains of length 4, 5, and 6).

the experimenter. Each command involved a one-step movement in the horizontal or vertical direction, starting at the origin. Subjects were asked to keep their hands still during the testing to prevent them from using any exogenous tactile reference frames.

Command chains of three lengths were used: 4, 5, or 6 sequential steps on the pegs of the matrix (see Fig. 1c). Each subject was given three trials at each commandchain length for each matrix size. For the treatable-blind group, we additionally included a command chain with 3 steps.

After the experimenter verbalized the command chain for a given trial, the matrix grid was placed in the subject's hands, and he or she was asked to point to the final position of the peg on the grid. No feedback was provided to the subjects.

Members of the treatable-blind group participated in two experimental sessions. The first was conducted prior to their surgery, and the second was conducted after their surgery. The mean time to follow-up was 18 weeks. No training or other visual rehabilitation was provided to

> □ Blind Sighted

100 90

80

70 60

Performance (% correct)

 2×2 Matrix

subjects in this group during this period, which they had spent in their homes.

Results

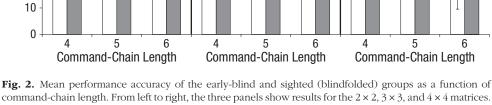
 3×3 Matrix

We report results of two sets of analyses. The first was a cross-group comparison of the performance of sighted and early-blind subjects. The second was a within-group comparison of the performance of treatable-blind subjects before and after surgery. The first comparison served as a precursor to the second, and primary, one. It established differences between blind and sighted individuals and set the stage for an investigation of whether these differences can be bridged longitudinally by the introduction of sight.

Cross-group comparison: sighted versus early-blind children

Figure 2 summarizes the performance of the sighted and early-blind groups. We conducted a three-way analysis of

 4×4 Matrix



command-chain length. From left to right, the three panels show results for the 2×2 , 3×3 , and 4×4 matrices. Asterisks indicate significant differences between groups (*p < .05, **p < .01). Error bars represent ±1 SEM. variance to investigate the main effects of visual status (sighted or blind), matrix size $(2 \times 2, 3 \times 3, \text{ or } 4 \times 4)$, and command-chain length (4, 5, or 6 steps) and their possible interactions. The dependent variable was the percentage of trials in which a subject correctly indicated the terminal position of the command chain.

The main effect of visual status was significant, F(1, 58) = 175.34, p < .001, $\eta^2 = .751$; overall, sighted participants outperformed visually impaired ones. Accuracy averaged across all conditions was 90.3% for sighted participants and 58.4% for the early-blind (visually impaired) subjects. The main effect of matrix size was also significant, F(2, 116) = 46.781, p < .001, $\eta^2 = .446$, with larger matrix sizes eliciting poorer performance. The interaction between matrix size and command-chain length was significant, F(2, 116) = 8.966, p < .001, $\eta^2 = .133$; overall accuracy decreased with increased task complexity. Visual status interacted significantly with both matrix size, F(2, 116) = 45.154, p < .001, $\eta^2 = .437$, and command-chain length, F(2, 116) = 16.693, p < .00, $\eta^2 = .22$.

Blind subjects performed well with small matrices and short command chains. With increasing task complexity, their performance decreased significantly relative to that of the sighted subjects.

The good performance of blind participants on lowcomplexity grids and command chains indicates that they understood the basic task requirements. Differences in performance between the sighted and blind groups replicated previous results (Cattaneo et al., 2007; Cornoldi et al., 1993; Cornoldi et al., 1991; Vecchi et al., 2004) and, more important, set the stage for examining whether the observed differences between the sighted and the blind can be mitigated if sight is initiated in the blind.

Within-group comparison: before versus after surgery

Figure 3 summarizes the pre- and postsurgical performance of the treatable-blind group. Preoperative performance followed the pattern observed for the early-blind

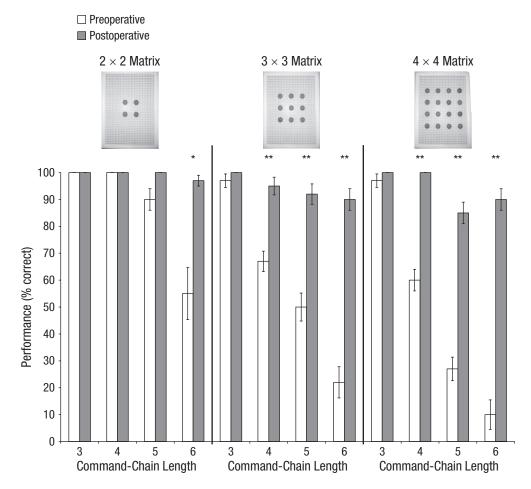


Fig. 3. Mean preoperative and postoperative performance of the treatable-blind subjects as a function of command-chain length. From left to right, the three panels show results for the 2×2 , 3×3 , and 4×4 matrices. Asterisks indicate significant differences between the two testing occasions (*p < .05, **p < .01). Error bars represent ±1 *SEM*.

group: Accuracy was high for small matrices and short command chains, but declined as either of these parameters took on higher values.

This group exhibited marked improvements in performance postoperatively. Subjects were proficient, often near ceiling levels, with the matrix sizes and commandchain lengths that preoperatively had elicited poor performance. A three-way repeated measures analysis of variance with surgical status (preoperative or postoperative), matrix size, and command-chain length as withinsubjects factors revealed a main effect of surgical status, $F(1, 9) = 691.38, p < .001, \eta^2 = .987$; across all matrix sizes and command-chain lengths, postoperative performance (95.8%) significantly exceeded preoperative performance (64.8%). The main effect of matrix size was significant, $F(2, 18) = 42.859, \eta^2 = .988, p < .001$, as was the main effect of command-chain length, F(3, 27) = 220.14, $\eta^2 =$.96, p < .001. Surgical status had significant interactions with both matrix size, F(2, 18) = 34.724, $\eta^2 = .794$, and command-chain length, F(3, 27) = 69.893, $\eta^2 = .885$, both *p*s < .001.

Discussion

Our goal was to examine whether visual experience contributes to spatial imagery skills. We found that a basic level of spatial imagery can be developed even with very limited visual experience, as demonstrated by the ability of the early-blind group and the treatable-blind group preoperatively to perform the task well when the matrices were simple and the command chains were short. However, spatial imagery skills of congenitally blind children improved significantly and rapidly after the onset of sight. Taken together, these results suggest that visual experience can significantly enhance spatial imagery capabilities. This conclusion appears to be consistent with the distinctions among the different senses: Audition, touch, and proprioception convey spatial information (Caclin, Soto-Faraco, Kingstone, & Spence, 2002; Perrott & Saberi, 1990; Pick, Warren, & Hay, 1969), but do not match the richness of spatial detail provided by the visual modality (Kassuba, Klinge, Hölig, Röder, & Siebner, 2013; Warren, Welch, & McCarthy, 1981; Witten & Knudsen, 2005). This difference is echoed in our results showing that the spatial abilities that develop in the presence of profound visual impairment are less able to handle complex imagery tasks than are those that develop following the onset of sight.

Besides demonstrating that internal spatial representations are enriched by visual information, the results reported here also bear on the question of when such enrichment can happen. Much as there are sensory critical periods (Daw, 2006), there could also be a critical period for the development of spatial imagery skills. In other words, perhaps a sensory modality can influence spatial reasoning abilities only during a critical window early in the developmental timeline; if that period elapses without a sensory modality being available, then later restoration of that input will not have an impact on spatial abilities. However, our results provide evidence against such a notion in the context of vision. To the extent that congenitally blind children as old as 22 years of age show significant improvements in their spatial abilities after the onset of sight, we are led to conclude that either the ability of vision to contribute to spatial skills is not subject to a strict critical period or the critical period, if it exists, extends beyond the late teenage years.

These findings raise several interesting questions that await further study. We highlight three. First, does the nature of spatial imagery change qualitatively when the blind gain sight (Kaski, 2002; Röder, Rösler, & Hennighausen, 1997)? If so, do the newly sighted use an imagery system that is fundamentally different from the one they used preoperatively? Or is the postoperative system a more elaborated version of the same one that they used preoperatively? Perhaps one way of addressing this issue will be by investigating whether and how blind children's tactile exploration changes after sight onset. Functional brain-imaging studies examining neural correlates of mental imagery (D'Esposito et al., 1997; Knauff, Kassubek, Mulack, & Greenlee, 2000; Kosslyn et al., 1999; Kosslyn, Thompson, Kim, & Alpert, 1995) pre- and postoperatively will also be useful in answering this question.

Second, what kinds of learning and representationalchange mechanisms can account for the rapidity with which spatial imagery abilities change after the onset of sight? In this context, some of our other results from Project Prakash deserve mention. While investigating the Molyneux question (Held et al., 2011) with newly sighted children, we found that even though they did not appear to possess a mapping between the spatial information provided by touch and that provided by vision immediately after sight-restoring surgery, this mapping developed rapidly, in some cases over the course of a week. It will be interesting to investigate whether the learning processes that yield cross-modal spatial mapping are related to the ones that enhance spatial imagery abilities, and precisely what their neural substrates might be.

From an applied perspective, our results point to the capacity for improvement in spatial skills well into adolescence. Thus, our third question is, can such improvement be achieved in any way other than through sight-restoring surgeries? This question is of relevance to the many blind individuals whose blindness is currently not treatable.

Author Contributions

T. K. Gandhi and P. Sinha designed the study. S. Ganesh performed the surgical procedures and conducted the ophthalmic assessments. T. K. Gandhi conducted the mental imagery experiments, and both T. K. Gandhi and P. Sinha wrote the manuscript.

Acknowledgments

We wish to thank all the children who participated in this study and the members of the Project Prakash team, who were instrumental in identifying treatable blind children. We are also grateful to Amy Kalia for her help with data analysis and Daphne Maurer for her helpful comments on an earlier draft of this manuscript.

Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

Funding

The research reported here was supported by the James McDonnell Foundation and the National Eye Institute of the National Institutes of Health.

References

- Afonso, A., Blum, A., Katz, B. F. G., Tarroux, P., Borst, G., & Denis, M. (2010). Structural properties of spatial representations in blind people: Scanning images constructed from haptic exploration or from locomotion in a 3-D audio virtual environment. *Memory & Cognition*, 38, 591–604.
- Aleman, A., van Lee, L., Mantione, M. H., Verkoijen, I. G., & de Haan, E. H. (2001). Visual imagery without visual experience: Evidence from congenitally totally blind people. *NeuroReport*, 12, 2601–2604.
- Arditi, A., Holtzman, J. D., & Kosslyn, S. M. (1988). Mental imagery and sensory experience in congenital blindness. *Neuropsychologia*, 26, 1–12.
- Byrne, R. W., & Salter, E. (1983). Distance and directions in the cognitive maps of the blind. *Canadian Journal of Psychology*, 37, 293–299.
- Caclin, A., Soto-Faraco, S., Kingstone, A., & Spence, C. (2002). Tactile "capture" of audition. *Perception & Psychophysics*, 64, 616–630.
- Carreiras, M., & Codina, M. (1992). Spatial cognition of the blind and sighted: Visual and amodal hypotheses. *Current Psychology of Cognition*, 12, 51–78.
- Cattaneo, Z., Vecchi, T., Cornoldi, C., Mammarella, I., Bonino, D., Ricciardi, E., & Pietrini, P. (2008). Imagery and spatial processes in blindness and visual impairment. *Neuroscience & Biobehavioral Reviews*, *32*, 1346–1360.
- Cattaneo, Z., Vecchi, T., Monegato, M., Pece, A., & Cornoldi, C. (2007). Effects of visual impairment on mental representations activated by visual and tactile stimuli. *Brain Research*, *1148*, 170–176.
- Chatterjee, G., Kalia, A., Gandhi, T., & Sinha, P. (2013). Global motion coherence performance after extended congenital blindness: Stretching the window [Abstract]. *Journal of Vision*, *13*(9), Article 22. Retrieved from http://www .journalofvision.org/content/13/9/22.short

- Cornoldi, C., Bertuccelli, B., Rocchi, P., & Sbrana, B. (1993). Processing capacity limitations in pictorial and spatial representations in the totally congenitally blind. *Cortex*, 29, 675–689.
- Cornoldi, C., Cortesi, A., & Preti, D. (1991). Individual differences in the capacity limitation of visuo-spatial short-term memory: Research on sighted and totally congenitally blind people. *Memory & Cognition*, *19*, 459–468.
- Cornoldi, C., & Vecchi, T. (2000). Mental imagery in blind people: The role of passive and active visuo-spatial processes.In M. Heller (Ed.), *Touch, representation and blindness* (pp. 143–181). Oxford, England: Oxford University Press.
- Daw, N. (2006). *Visual development*. New York, NY: Plenum Press.
- De Beni, R., & Cornoldi, C. (1988). Imagery limitations in totally congenitally blind subjects. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 14, 650– 655.
- Deneve, S., & Pouget, A. (2004). Bayesian multisensory integration and cross-modal spatial links. *Journal of Physiology-Paris*, 98, 249–258.
- D'Esposito, M., Detre, J. A., Aguirre, G. K., Stallcup, M., Alsop, D. C., Tippet, L. J., & Farah, M. J. (1997). A functional MRI study of mental imagery generation. *Neuropsychologia*, 35, 725–730.
- Eimer, M. (2004). Multisensory integration: How visual experience shapes spatial perception. *Current Biology*, 14, 115– 117.
- Forrest, E. B. (1984). The innate vs. the learned: Visual imagery and the role of experience. *Journal of the American Optometric Association*, 55(1), 43–46.
- Gandhi, T. K., Kalia, A., Chatterjee, G., & Sinha, P. (2013). Emergence of face-localization abilities following extended congenital blindness [Abstract]. *Journal of Vision*, 13(9), Article 23. Retrieved from http://www-mtl.journalofvision .org/content/13/9/23.short
- Gandhi, T. K., Khurana, A., Santhosh, J., & Anand, S. (2011, February). Configurational imagery experience in sighted and visually impaired children. *Journal of the Indian Academy of Applied Psychology*, 37, 128–133.
- Haber, R. N., Haber, L. R., Levin, C. A., & Hollyfield, R. (1993). Properties of spatial representations: Data from sighted and blind subjects. *Perception & Psychophysics*, 54, 1–13.
- Hatwell, Y. (1978). From perception and related issues in blind humans. In R. Held, H. W. Leibowitz, & H. L. Teuber (Eds.), *Handbook of sensory physiology* (pp. 489–519). Berlin, Germany: Springer-Verlag.
- Held, R., Ostrovsky, Y., de Gelder, B., Gandhi, T., Ganesh, S., Mathur, U., & Sinha, P. (2011). The newly sighted fail to match seen with felt. *Nature Neuroscience*, 14, 551–554.
- Iachini, T., & Ruggiero, G. (2010). The role of visual experience in mental scanning of actual pathways: Evidence from blind and sighted people. *Perception*, 39, 953–969.
- Imbiriba, L. A., Rodrigues, E. C., Magalhaes, J., & Vargas, C. D. (2006). Motor imagery in blind subjects: The influence of the previous visual experience. *Neuroscience Letters*, 400, 181–185.

- Kalia, A., Lesmes, L., Dorr, M., Gandhi, T. K., Chatterjee, G., & Sinha, P. (2013). Development of contrast sensitivity following extended congenital blindness [Abstract]. *Journal of Vision*, 13(9), Article 281. Retrieved from http://www-mtl .journalofvision.org/content/13/9/281.short
- Kaski, D. (2002). Revision: Is visual perception a requisite for visual imagery? *Perception*, 31, 717–731.
- Kassuba, T., Klinge, C., Hölig, C., Röder, B., & Siebner, H. R. (2013). Vision holds a greater share in visuo-haptic object recognition than touch. *NeuroImage*, 65, 59–68.
- Kerr, N. H. (1983). The role of vision in "visual imagery" experiments: Evidence from the congenitally blind. *Journal of Experimental Psychology: General*, 112, 265–277.
- Klatzky, R. L., Golledge, R. G., Loomis, J. M., Cicinelli, J. G., & Pellegrino, J. W. (1995). Performance of blind and sighted persons on spatial tasks. *Journal of Visual Impairment & Blindness*, 89, 70–82.
- Knauff, M., Kassubek, J., Mulack, T., & Greenlee, M. W. (2000). Cortical activation evoked by visual mental imagery as measured by fMRI. *NeuroReport*, 11, 3957–3962.
- Knauff, M., & May, E. (2006). Mental imagery, reasoning and blindness. *Quarterly Journal of Experimental Psychology*, 59, 161–177.
- Kosslyn, S. M., Pascual-Leone, A., Felician, O., Camposano, S., Keenan, J. P., Thompson, W. L., . . . Alpert, N. M. (1999). The role of Area 17 in visual imagery: Convergent evidence from PET and rTMS. *Science*, 284, 167–170.
- Kosslyn, S. M., Thompson, W. L., Kim, I. J., & Alpert, N. M. (1995). Topographical representations of mental images in primary visual cortex. *Nature*, 378, 496–498.
- Lacey, S., & Sathian, K. (2011). Multisensory object representation: Insights from studies of vision and touch. *Progress in Brain Research*, 191, 165–176.
- Mandavilli, A. (2006). Visual neuroscience: Look and learn. Nature, 441, 271–272.
- Marmor, G. S., & Zaback, L. A. (1976). Mental rotation by the blind: Does mental rotation depend on visual imagery? *Journal of Experimental Psychology: Human Perception* and Performance, 2, 515–521.
- Maurer, D., Lewis, T. L., & Mondloch, C. J. (2005). Missing sights: Consequences for visual cognitive development. *Trends in Cognitive Sciences*, 9, 144–151.
- Millar, S. (1994). Understanding and representing space: Theory and evidence from studies with blind and sighted children. Oxford, England: Oxford University Press.
- Perrott, D., & Saberi, K. (1990). Minimum audible angle thresholds for sources varying in both elevation and azimuth. *Journal of the Acoustical Society of America*, 87, 1728–1731.

- Pick, H. L., Warren, D. H., & Hay, J. C. (1969). Sensory conflict in judgments of spatial direction. *Perception & Psychophysics*, 6, 203–205.
- Röder, B., Rösler, F., & Hennighausen, E. (1997). Different cortical activation patterns in blind and sighted humans during encoding and transformation of haptic images. *Psychophysiology*, 34, 292–307.
- Sinha, P. (2013, July). Once blind and now they see. *Scientific American*, *309*, 48–55.
- Sinha, P., Chatterjee, G., Gandhi, T., & Kalia, A. (2013). Restoring vision through "Project Prakash": The opportunities for merging science and service. *PLoS Biology*, *11*(12), e1001741. Retrieved from http://www.plosbiology.org/ article/info%3Adoi%2F10.1371%2Fjournal.pbio.1001741
- Sinha, P., & Held, R. (2012). Sight restoration. F1000 Medicine Reports, 4, Article 17. Retrieved from http://f1000.com/ prime/reports/m/4/17/
- Stein, B. E., & Meredith, M. A. (1993). *The merging of the senses*. Cambridge, MA: MIT Press.
- Thinus-Blanc, C., & Gaunet, F. (1997). Representation of space in blind persons: Vision as a spatial sense? *Psychological Bulletin*, 121, 20–42.
- Tusa, R. J., Repka, M. X., Smith, C. B., & Herdma, S. J. (1991). Early visual deprivation results in persistent strabismus and nystagmus in monkeys. *Investigative Ophthalmology & Visual Science*, 32, 134–141.
- Vecchi, T. (1998). Visuo-spatial limitations in congenitally totally blind people. *Memory*, 6, 91–102.
- Vecchi, T., Tinti, C., & Cornoldi, C. (2004). Spatial memory and integration processes in congenital blindness. *NeuroReport*, 15, 2787–2790.
- Warren, D. H. (1977). Blindness and early childhood development. New York, NY: American Foundation for the Blind Press.
- Warren, D. H., Welch, R. B., & McCarthy, T. J. (1981). The role of visual-auditory "compellingness" in the ventriloquism effect: Implications for transitivity among the spatial senses. *Perception & Psychophysics*, 30, 557–564.
- Witten, I. B., & Knudsen, E. I. (2005). Why seeing is believing: Merging auditory and visual worlds. *Neuron*, 48, 489– 496.
- Woods, A. T., & Newell, F. N. (2004). Visual, haptic and cross-modal recognition of objects and scenes. *Journal of Physiology-Paris*, 98, 147–159.
- Zimler, J., & Keenan, J. M. (1983). Imagery in the congenitally blind: How visual are visual images? *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 9, 269–282.