

Lack of Automatic Imitation in Newly Sighted Individuals

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Abstract

Viewing a hand action performed by another person facilitates a response-compatible action and slows a response-incompatible one, even when the viewed action is irrelevant to the task. This automatic imitation effect is taken as the clearest evidence for a direct mapping between action viewing and motor performance. But there is an ongoing debate whether this effect is innate or experience dependent. We tackled this issue by studying a unique group of newly sighted children who suffered from dense bilateral cataracts from early infancy and were surgically treated only years later. The newly sighted children were less affected by viewing task-irrelevant actions than were control children, even 2 years after the cataract-removal surgery. This strongly suggests that visually guided motor experience is necessary for the development of automatic imitation. At the very least, our results indicate that if imitation is based on innate mechanisms, these are clearly susceptible to long periods of visual deprivation.

Keywords

vision, cognitive neuroscience, perceptual learning, mirror neuron system, social behavior, visual development

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Humans have a natural tendency to mimic observed actions (Chartrand & van Baaren, 2009), even when they are irrelevant to the task at hand (Heyes, 2011). In the original study investigating this automatic imitation phenomenon (Stürmer, Aschersleben, & Prinz, 2000), participants were asked to open or close their hand in response to a color cue that was superimposed on a video clip depicting a task-irrelevant hand action (opening or closing). Correct responses were initiated faster when the viewed action was response compatible than when it was response incompatible. This automatic imitation effect (AIE) suggests a direct mapping between action viewing and motor performance, a key notion of the mirror-neuron-system hypothesis (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Iacoboni, 2009; Wohlschläger & Bekkering, 2002).

Are the foundations for mirror system function available from birth, or do they require substantial visual experience throughout early childhood to develop? Meltzoff and Moore's (1977) classical work suggested that mirror system function must be innate because infants imitated facial expressions immediately after birth. However,

others pointed out that this mimicry behavior was limited to tongue protrusion (Anisfeld et al., 2001), a neonate action response that can be triggered by a broad range of stimuli (Jones, 2006) and therefore cannot be attributed to imitation. Indeed, in a recent study, scholars examined mimicry of various gestures in neonates and failed to uncover any evidence for imitation (Oostenbroek et al., 2016).

The response of the mirror system can also be modified with training. For example, in an fMRI study (Catmur et al., 2008), an observed hand action was used as a cue to perform the same hand action in the congruent-imitation group, whereas it required response with a foot action in an incongruent-imitation group. Following training, in the incongruent-imitation group, mirror system areas that were usually activated during observation of hand actions responded more vigorously to observation

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of foot actions. These results indicate that mirror system properties change through sensorimotor learning.

In our study, we tested automatic imitation behavior in newly sighted children. If mimicry is innate, we expected to find an immediate or fast recovery of imitation behavior after sight retrieval. If, on the other hand, the mirror system acquires its mirroring properties from learned associations between seen body parts and motor outcomes, we might expect to find slow learning dynamics or a constant deficit implying a critical period for these associations to be acquired.

Method

Participants

Fifteen Ethiopian children (age: $M = 12.5$ years, $SD = 2.9$) with early-onset bilateral cataracts participated in the experiment. Our sample size was severely limited because of the rareness of the condition (untreated congenital bilateral cataracts). Furthermore, our participants had to be able to recognize others' hand actions to be included in the study. Their dense bilateral cataracts were most likely congenital or developed within a few months after birth, as all had clear nystagmus, a telltale sign of early-onset blindness. Thirteen of the children underwent cataract-removal surgery and an intraocular lens implant. The children's guardians gave their written consent for the operation and for participating in the behavioral testing. The procedures were approved by the ethics committee of the Hebrew University of Jerusalem and Hawassa University. The children performed the behavioral tests in Hawassa Referral Hospital or in their blind schools 2 weeks to 4 years after the operation ($M = 18.2$ months, $SD = 13.3$). For more information regarding the newly sighted participants, see Table S1 in the Supplemental Material available online. Fourteen typically developing Ethiopian children (age: $M = 11.6$ years, $SD = 2.1$) and 24 typically developing Israeli children (age: $M = 11.5$ years, $SD = 2.8$) were also tested and served as a control group.

Preliminary tests

Previous studies have shown that early-onset visual deprivation is associated with great difficulty in shape and face recognition (Le Grand, Mondloch, Maurer, & Brent, 2001; McKyton, Ben-Zion, Doron, & Zohary, 2015; Ostrovsky, Andalman, & Sinha, 2006; Ostrovsky, Meyers, Ganesh, Mathur, & Sinha, 2009; Putzar, Hötting, & Röder, 2010), but shape recognition from biological motion is spared (Bottari et al., 2015; Hadad, Maurer, & Lewis, 2012). We focused here on the imitation abilities of newly sighted children rather than on their

impaired perception. Thus, newly sighted children were included only if they could recognize hands and imitate hand gestures in two preliminary independent tests (15 of an initial group of 21 patients). In the first test, they were shown short video clips of moving body parts (hands, legs, or head) and were asked to move the body part matching the one appearing in the clip. In the second test, they were shown a hand-tapping video clip (as used later in the main experiment) and were asked to imitate the tapping movement.

We also evaluated each participant's visual acuity by assessing his or her contrast sensitivity function (CSF) in a separate experiment. The participants saw gratings of specific spatial frequencies at various contrast levels and were asked to report the grating orientation (horizontal or vertical) on each trial. Their performance at the various contrast levels was used to assess the contrast threshold for each spatial frequency. Plotting the contrast threshold as a function of the spatial frequency yielded the CSF of the participant. The cutoff frequency, the highest frequency that can still be seen by the viewer (using the maximal contrast), was also assessed by fitting the CSF with the truncated log-parabola form (Lesmes, Lu, Baek, & Albright, 2010). For more information about the preliminary tests and the CSF experiment, see the Supplemental Material.

Stimuli, design, and procedure

Participants viewed short videos (800 ms) of red or blue hands tapping on a table (Fig. 1a), presented on a computer screen at a viewing distance of 40 cm. In the beginning, participants had a red and a blue sticker placed on their right hand and left hand, respectively. Participants were instructed to tap with their right hand if the hands in the video were red and with their left hand if the hands were blue, regardless of which hand did the tapping in the video. Crucially, the hand that performed the tapping action in the video either mirrored the hand the participant was instructed to tap with (compatible condition) or did not (incompatible condition). The stickers facilitated fast acquisition of the arbitrary mapping rule between color and required action. After 10 consecutive correct trials, the stickers were removed. To make sure participants remembered the required mapping rule without the stickers, we started the main experiment after another 10 consecutive correct trials.

In the main experiment, there were 168 trials, half of which were compatible with the required action (videos of a right red hand or a left blue hand tapping) and half were incompatible (right blue or left red hand tapping). The same trial order was used for all participants. Each trial began with the video clip of the tapping hand. The

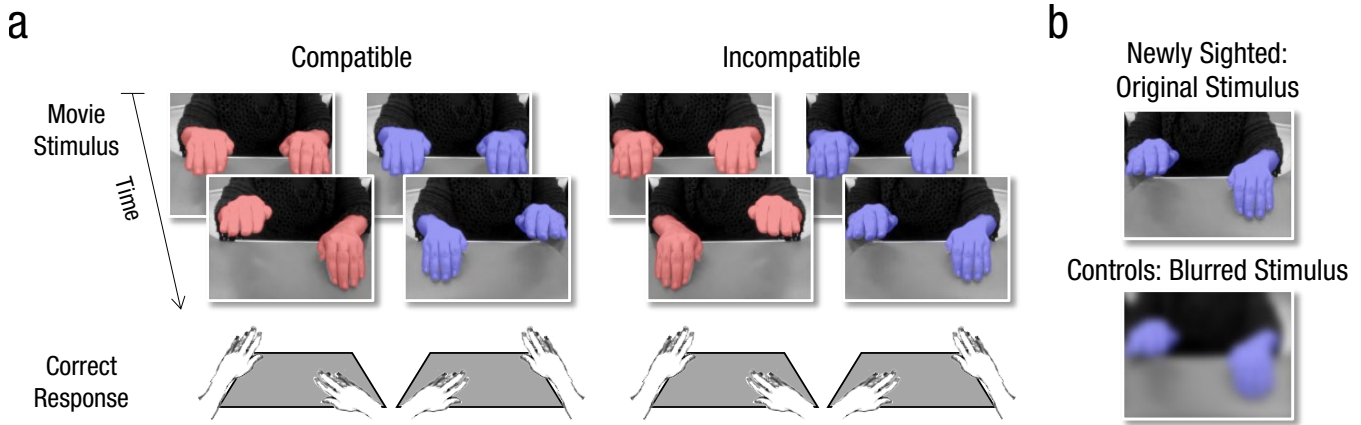


Fig. 1. Experimental procedure. Participants observed short videos of a pair of hands in which either the right or the left hand tapped on a table (a). Participants were asked to tap as quickly and accurately as possible on a touch screen according to the color of the viewed hands, regardless of which hand in the video tapped (blue = tap with the left hand, red = tap with the right hand). The correct tap was either spatially compatible with the observed action (i.e., mirroring the hand action) or spatially incompatible (i.e., tapping with the hand farthest from the tapping hand in the video). Control participants were given blurred versions of the action videos to compensate for the newly sighted group's low visual acuity (b).

participants were asked to tap with their right or left hand on the basis of the viewed hands' color (red: right tap; blue: left tap). They were told to respond as fast as possible, without compromising their success rate, and their responses were recorded via a touch screen placed horizontally under their hands. The last frame was frozen until the tapping response. The tapping triggered a feedback sound (harmonic melody if correct; buzz if wrong) and initiated the next trial. There were two breaks during the experiment.

Typically, as previously reported in the literature (Ganesh et al., 2014), newly sighted individuals have poor visual acuity, resulting in the loss of high-spatial-frequency information. Thus, we showed the control participants blurred versions of the same action clips (Fig. 1b), similar to that experienced by the newly sighted participants (see the Control for Participants' Low Acuity section in the Supplemental Material). Stimuli were presented and responses were recorded using Experiment Builder software (SR Research, Ottawa, Ontario, Canada). See Video S1 in the Supplemental Material for an example of a few experimental trials.

Participants from both groups had almost perfect accuracy (newly sighted: 97% and 96%; control: 99% and 97% correct responses, for the compatible and incompatible trials, respectively). Trials in which the participants made incorrect responses were excluded from the reaction time (RT) analysis. Furthermore, the first two trials in the main experiment, the first trial after each break, and the first trial immediately after an incorrect response were also discarded from the RT analysis, as an analysis showed that RTs on these trials were

typically slower than the average. Thus, the analysis was based on 157 trials, on average.

Results

Figure 2a shows the tapping RT distributions for the compatible and incompatible conditions (on correct trials) in 1 newly sighted and 1 control participant. Both show an AIE, but its magnitude is bigger in the control participant. The CSF of the newly sighted participant was measured using gratings at different spatial frequencies and contrasts, both pre- and postoperation (Fig. 2b). The CSF of the control participants was measured after blurring each grating with a low-pass filter to generate a "modified" CSF similar to that of the newly sighted participants. Obviously, this modified CSF is not a measure of the control participants' normal visual acuity. The same filter was applied to each image in the hand-action videos used in the main experiment to generate a blurry video (Fig. 1b) that mimicked the image quality experienced by the newly sighted participants.

As expected, in control participants (including all 38 control participants because no difference was found between the Ethiopian and Israeli control groups; see the Supplemental Material for statistical analysis), the viewed hand motion facilitated compatible actions and interfered with incompatible actions, despite being behaviorally irrelevant (mean AIE = 61.6 ms, 95% confidence interval, or CI = [46.9, 76.3], $SD = 44.6$, sign-test $p < .0001$). Theoretically, this effect could stem from a spatial compatibility between the tapping hand and the required response (i.e., a "Simon effect"), which is typically associated with

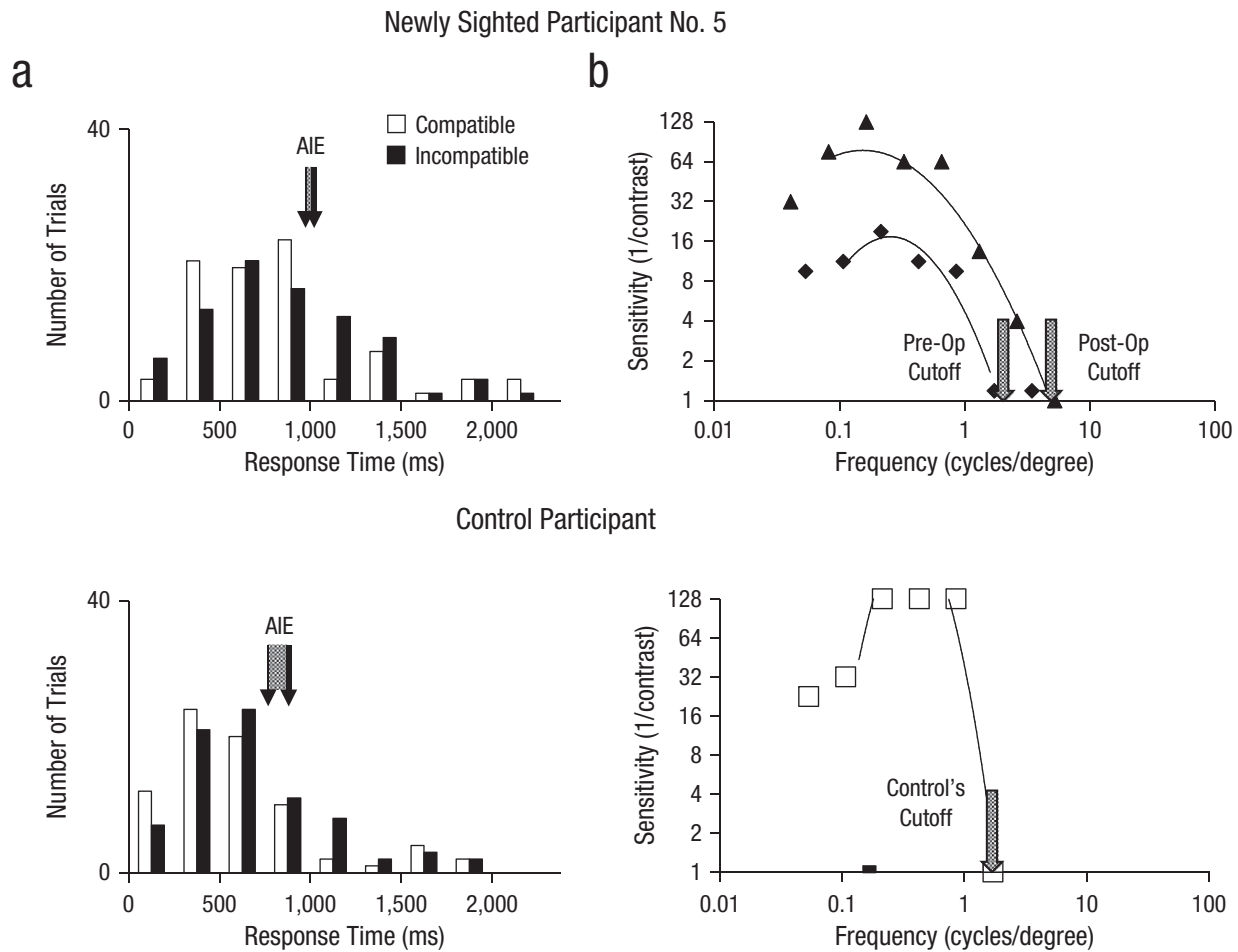


Fig. 2. Exemplars of task performance from the newly sighted and control groups. The response time distribution (a) on correct trials is shown separately for the compatible and incompatible conditions. The mean of each distribution is depicted by an arrow (thin = compatible; thick = incompatible). The automatic imitation effect (AIE) is the difference between the two means. Performance sensitivity in an orientation-discrimination task for a grating is shown (b) as a function of the spatial frequency of the grating (i.e., the contrast sensitivity function, CSF). Data are shown for the newly sighted participant before and after the operation (diamonds and triangles, respectively) and the control participant. The minimum contrast used was 1/128, and therefore the maximal sensitivity that could be measured was 128. The CSF was fitted by a truncated parabola, and the cutoff frequency was calculated by assessing the highest spatial frequency at which the grating could still be perceived (contrast sensitivity = 1; or the required contrast for discrimination is the maximum possible: 100%, as indicated by the gray arrows). Only values on the parabola that were below the maximal sensitivity measure (128) are shown. Note that the control participant's CSF is a modified one, following the blur applied to all stimuli.

a shorter RT. Thus, it may have nothing to do with automatic imitation, which requires recognizing the hands. To minimize this confound, we presented hand action on both sides of the screen during each trial: When one hand moved downward in a tapping action, the opposite hand was raised. Furthermore, 10 of our control participants repeated the experiment using moving blobs (rather than hands) that followed the same motion trajectory as in the main experiment. Unlike the AIE observed in this subgroup in the original experiment ($M = 75.2$ ms, $SD = 50.1$, sign-test $p = .002$), no significant AIE effect was found in this spatial-compatibility control experiment ($M = -30.3$ ms, $SD = 26.5$, sign-test $p = .11$; see the Supplemental Material and Fig. S2 for more details on the control for spatial compatibility). Therefore, we conclude

that the difference in RT between incompatible and compatible trials in the original experiment is truly due to the AIE.

Figure 3a depicts the AIE in the control participants, the newly sighted participants, and 2 participants who had not yet had cataract-removal surgery as a function of their CSF cutoff frequency (measured on the day of AIE testing). In control participants, the AIE was usually conspicuous regardless of the individual's level of perceived image blur, probably because the key aspect—the moving hands—was always present and recognized as such. In newly sighted participants, the AIE was positive ($M = 24.2$ ms, 95% CI = [6.1, 42.3], $SD = 30.0$, sign-test $p = .023$) but significantly smaller than that of the control group—effect-size $M = 37.4$ ms (control –

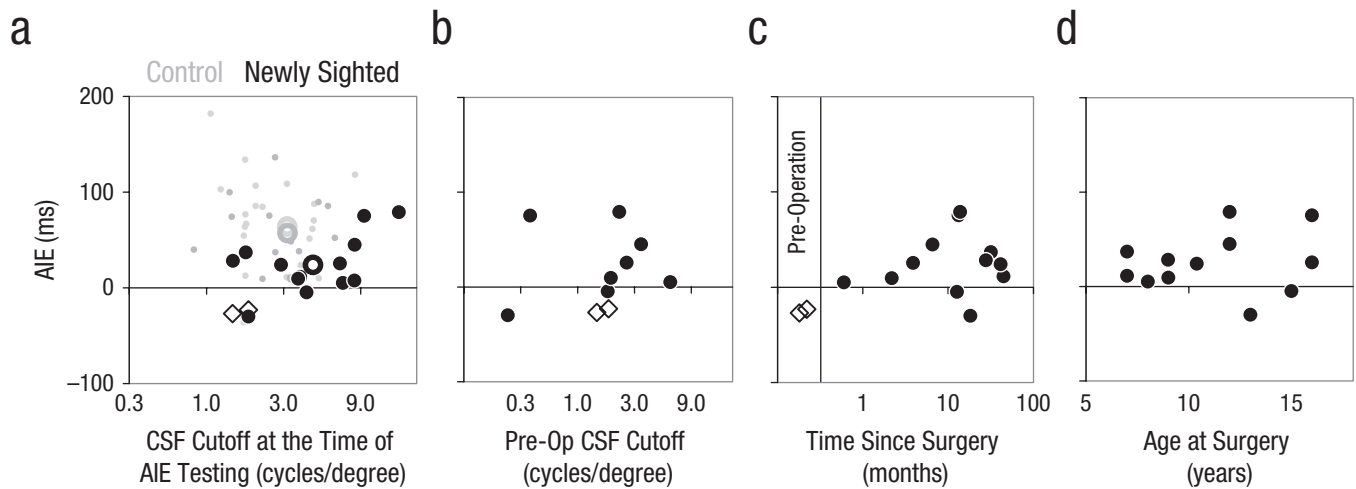


Fig. 3. The automatic imitation effect (AIE). The AIE of each individual (a) is plotted as a function of the individual's contrast-sensitivity-function (CSF) cutoff frequency (at the time of testing). Newly sighted participants ($n = 15$) are denoted by filled black circles, and control participants ($n = 38$) are denoted by filled gray circles (darker = Ethiopians, lighter = Israelis). The open circles denote the mean value of each group. Diamonds represent values for the 2 participants who had not yet undergone cataract-removal surgery. The AIE in the newly sighted participants and the 2 preoperation participants is also plotted as a function of (b) preoperation CSF cutoff frequency and (c) time since surgery. The AIE is also shown as a function of the (d) newly sighted participants' age at surgery.

newly sighted), Mann-Whitney $U = 75$, $p = .010$. Note that the weaker AIE in the newly sighted participants was found despite the fact that, on average, the blur applied to the action videos seen by the control participants was somewhat greater than that perceived by the newly sighted participants. We therefore conclude that, in general, the newly sighted children did not map viewed actions to their own actions as effectively and automatically as did children with typically developed sight.

Figure 3 depicts the dependence of the AIE on visual acuity at the time of testing (3a) and before surgery (3b), as well as on the length of time since surgery (3c), and age at surgery (3d). As can be appreciated, none of those factors can clearly explain the variation in the AIE among the newly sighted participants, nor does the combination of those factors (see Statistical Analysis in the Supplemental Material). Incidentally, note that the few newly sighted participants with good visual acuity (> 9 cycles per degree) who had an extended period of visual experience (> 6 months) had a robust AIE, similar to the average of the control group. This may suggest that the two factors in concert afford automatic mirroring functions. However, these trends did not reach statistical significance and may well be due to random noise.

Discussion

We report that newly sighted children who underwent an operation years after birth show clear signs of impaired automatic imitation, even when tested many months after cataract-removal surgery. We interpret this

finding as an indication that newly sighted individuals lack a direct mapping between action viewing and motor performance. To clarify, we do not argue that newly sighted children cannot understand human actions. To the contrary, the newly sighted children qualified for participation in the study only if they could recognize and imitate hands. The issue is whether they imitated the observed actions through a direct mapping strategy or by using an alternative technique.

Direct mapping between observed actions and their internal motor representations is thought to be mediated by mirror neurons that are active when a specific action is observed or performed (Gallese et al., 1996). Such dual-modality activity was found in premotor and parietal regions in the macaque monkey (Gallese, Fadiga, Fogassi, & Rizzolatti, 2002). Importantly, the action-specific activity is also prominent during self-action in the dark, suggesting that it is essentially motor-related rather than vision-based. In humans, some forms of imitation may be based on a similar mirroring mechanism. Indeed, in a seminal article using functional imaging, Iacoboni and colleagues (1999) showed that frontal and parietal regions, composing the human mirror-neuron-system network, were more active when participants tapped their fingers imitating the same viewed action than when they performed the same tapping action in response to a symbolic cue. A later study showed that repetitive transcranial stimulation of the left inferior frontal gyrus (IFG) abolishes the AIE (Catmur, Walsh, & Heyes, 2009). This suggests that the left IFG plays a causal role in the perceptual-to-motor mapping required for automatic imitation.

Our finding has important implications for a hotly debated issue: Are the foundations for mirror system function available from birth, or do they require substantial visual experience throughout early childhood? Studies supporting the innateness of the mirror neuron system (Lepage & Théoret, 2007) rely solely on controversial studies of neonate imitation of tongue protrusion (Abravanel & Sigafos, 1984; Meltzoff & Moore, 1977) and finger actions (Meltzoff & Moore, 1977; Nagy et al., 2005). However, many of these studies have been criticized for various methodological flaws (Anisfeld, 1979; Anisfeld et al., 2001; Masters, 1979). Other researchers have shown that the mapping between observed actions and their compatible motor execution is flexible and influenced by both explicit (Heyes, Bird, Johnson, & Haggard, 2005) and implicit (Wiggett, Hudson, Tipper, & Downing, 2011) learning. It is therefore plausible that automatic imitation behavior develops through experience and stimulus-response associative learning.

Our newly sighted participants, who lacked fine visual experience in the early years, did not show quick recovery of automatic imitation. Innate mechanisms, if they exist, are therefore insufficient to sustain a direct matching without proper visual input in the first years of life. Presumably, to generate such a direct mapping, one must learn to associate self-initiated motor plans with their corresponding visual outcomes. Once a common representational format for perception and action is established, it may allow generalization to map the observed action of other individuals to our own actions, provided that there is enough acuity to recognize these actions. We conclude that visual experience is essential for the development of proper mirror system function. It is currently unclear whether the development of this function is characterized by a critical period (before 7 years) or is simply slow to be acquired at a later age.

Action Editor

Alice J. O'Toole served as action editor for this article.

Author Contributions

A. McKyton and E. Zohary planned the experiments, analyzed the data, and wrote the manuscript. I. Ben-Zion supervised the clinical work, including surgery and postsurgical vision assessment.

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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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Supplemental Material

Additional supporting information can be found at <http://journals.sagepub.com/doi/suppl/10.1177/0956797617731755>

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