

Growing up blind does not change the neural bases of Theory of Mind

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Edited by Nancy G. Kanwisher, Massachusetts Institute of Technology, Cambridge, MA, and approved May 8, 2009 (received for review January 11, 2009)

Humans reason about the mental states of others; this capacity is called Theory of Mind (ToM). In typically developing adults, ToM is supported by a consistent group of brain regions: the bilateral temporoparietal junction (TPJ), medial prefrontal cortex (MPFC), precuneus (PC), and anterior temporal sulci (aSTS). How experience and intrinsic biological factors interact to produce this adult functional profile is not known. In the current study we investigate the role of visual experience in the development of the ToM network by studying congenitally blind adults. In experiment 1, participants listened to stories and answered true/false questions about them. The stories were either about mental or physical representations of reality (e.g., photographs). In experiment 2, participants listened to stories about people's beliefs based on seeing or hearing; people's bodily sensations (e.g., hunger); and control stories without people. Participants judged whether each story had positive or negative valence. We find that ToM brain regions of sighted and congenitally blind adults are similarly localized and functionally specific. In congenitally blind adults, reasoning about mental states leads to activity in bilateral TPJ, MPFC, PC, and aSTS. These brain regions responded more to passages about beliefs than passages about nonbelief representations or passages about bodily sensations. Reasoning about mental states that are based on seeing is furthermore similar in congenitally blind and sighted individuals. Despite their different developmental experience, congenitally blind adults have a typical ToM network. We conclude that the development of neural mechanisms for ToM depends on innate factors and on experiences represented at an abstract level, amodally.

blindness | development | plasticity | temporoparietal junction | experience

Consider the following scenario: “While cleaning out her dorm room, Abigail sees an old love-letter lying under the bed. The handwriting looks like her beloved boyfriend’s.” Based on this short description we can make inferences about Abigail’s mental states, emotions, and actions. We infer that Abigail knows the letter is from her boyfriend; we recognize that she may feel happy to be reminded of him; and we might predict that she will put the letter away for safekeeping. This ability to reason about the mental states of others is called Theory of Mind (ToM).

A strikingly consistent group of brain regions supports ToM reasoning in a variety of tasks (1–3). These regions are located in right and left temporoparietal junction (TPJ), medial prefrontal cortex (MPFC), precuneus (PC), and anterior temporal sulci (aSTS). The distinct contribution of each of these regions is still controversial (2, 4–6) but this pattern of activation is highly reliable across a range of tasks involving ToM, presented both verbally (7, 8) and nonverbally (1, 9). Consequently, these regions are sometimes collectively called the ToM (or mentalizing) network.

Two key open questions remain: How do these functional regions develop in the life of an individual, and what processes lead to the typical location and functional profile of regions involved in ToM? One possibility is that the emergence of these

regions is controlled by intrinsic biological factors, such as genes. However, a large body of research has shown that the function of cortical regions is at least partly determined by patterns of input from the environment received during development. For example, temporary visual deprivation of one eye in kittens leads to permanent under-representation of that eye in their visual cortices (10). Striking effects of visual deprivation are also observed in humans. The occipital cortices of congenitally blind adults support performance of language and tactile tasks (for review, see refs. 11 and 12).

One possibility is, therefore, that the functional organization of ToM regions is in part determined by experience during development. Which aspects of experience might play a role? Developmental psychologists have identified at least 3 kinds of experience that affect cognitive ToM development: visual, first-person, and linguistic. Children use these types of experience to learn about the invisible contents of other minds and to formulate a ToM. First, through vision children perceive the external consequences of other people’s internal states: facial expressions as well as head, eye, and body movements. To explain these behaviors, children may formulate a causal model of the internal states that drive human actions (13–16). Second, children have their own first-person experiences of mental states. Upon observing the similarity between their own and other people’s external actions and circumstances, children may infer that other people also experience internal states similar to their own (17–19). Third, children hear how other people talk about the mind, including descriptions of mental states like beliefs and emotions.

Would changes in these aspects of experience lead to changes in the neural mechanisms that support ToM? We begin to address this question by investigating the brain regions recruited for ToM in a group of adults who have had different developmental experiences: congenitally blind individuals.

Congenital blindness alters 2 sources of information about other minds. First, congenitally blind children cannot learn about other people’s minds via visual observation of other people’s facial expressions, head and eye movements, or hand and body movements. Second, congenital blindness alters first-person experiences of mental life. For sighted people, like Abigail in our example above, many mental states begin with visual experience: seeing the letter, recognizing the handwriting, etc. Another sighted person could imagine having the same experiences. By contrast, congenitally blind adults can understand Abigail’s experience and could share its more abstract features (e.g., feeling happy to be reminded of her boyfriend) but could not literally have the same experience.

Author contributions: M.B., A.P.-L., and R.R.S. designed research; M.B. and R.R.S. performed research; M.B. and R.R.S. analyzed data; and M.B., A.P.-L., and R.R.S. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

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This article contains supporting information online at www.pnas.org/cgi/content/full/0900010106/DCSupplemental.

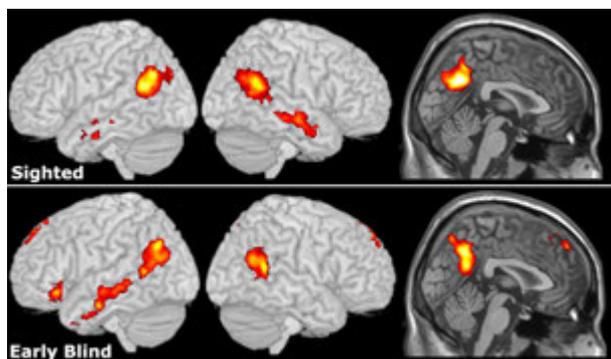


Fig. 1. Belief stories and physical representations stories (experiment 1). There was a greater response to stories about beliefs than stories about physical representations in sighted and EB groups (whole-brain random effects analyses, $P < 0.05$ corrected). Areas of activation are overlaid onto a standardized MNI template.

peak voxels across groups. Sighted and EB participants did not differ in the anatomical loci of any active regions ($P > 0.1$).

No differences in ToM regions were observed between the EB and sighted groups. However, during language comprehension, EB participants had greater activation than sighted participants in the visual cortices (physical story–backwards speech; group-by-condition interaction, $P < 0.05$, corrected) (Fig. S2). There was more language-related activity for EB adults than for sighted adults in the right inferior occipital gyrus, right fusiform gyrus, left middle occipital gyrus, and left fusiform gyrus.

To compare the amount of neural reorganization in the ToM and language networks, we performed a multivoxel pattern analysis to compare activation by group in each task over the entire cerebral cortex. We computed a correlation between voxel-wise t values in the EB and sighted groups' ToM networks (belief–physical; $r = 0.55$) and between the EB and sighted groups' language networks (physical–backward speech; $r = 0.45$). The spatial layouts of the ToM networks were more similar for EB and sighted groups than the spatial layouts of their language networks ($z = 2.07$, $P < 0.05$). To rule out the possibility that the language network was in general more variable across subjects, we compared the language and ToM networks across two halves of our sighted participants. Across the two halves of sighted participants, the language network ($r = 0.61$) was numerically, but not significantly, less variable than the ToM network ($r = 0.58$). Said differently, the similarity between EB and sighted adults on the ToM task is the same as the similarity within the sighted adults. The similarity on the language task, on the other hand, was lower between EB and sighted adults than within sighted adults (Fig. S3).

Experiment 2. Regional specificity across groups. The RTPJ of EB and sighted adults was equally selective for belief content. For EB and sighted participants, stories about people's beliefs activated the RTPJ more than control stories (which were not about people) [EB: $t(9) = 5.17$, $P < 0.001$; sighted: $t(10) = 3.44$, $P < 0.01$] and more than stories about people's bodily feelings [EB: $t(9) = 2.75$, $P < 0.05$; sighted: $t(10) = 2.64$; $P < 0.05$]. Bodily feeling stories and control stories did not differ from each other ($P > 0.2$). There was no difference between groups in the size of the belief–bodily feeling difference (interaction not reliable, $P > 0.3$). Similarly, none of the other ROIs examined were differentially selective across the two groups of participants (LTPJ, PC, vMPFC, and dMPFC) (see Fig. 2). Whole-brain analysis did not reveal any regions that responded differentially across groups in the belief vs. bodily feeling or belief vs. control contrasts.

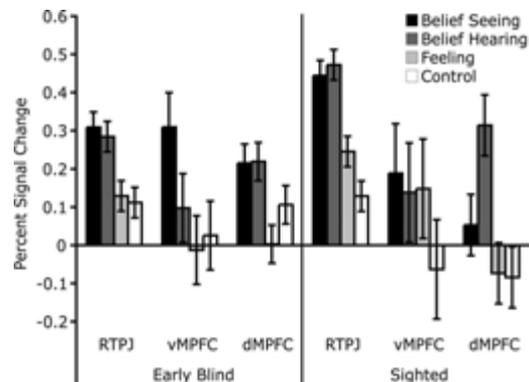


Fig. 2. PSC in RTPJ, vMPFC, and dMPFC ROIs in sighted and EB groups (experiment 2). The graph shows PSC in BOLD signal while participants listened to stories about beliefs based on seeing, stories about beliefs based on hearing, stories about bodily feelings, and stories about events without human protagonists. Error bars represent standard errors of the difference between conditions calculated separately for each group.

Reasoning about beliefs based on hearing and seeing in EB and sighted adults. The RTPJ, LTPJ, PC and MPFC responded similarly to the hearing and seeing belief conditions in both EB and sighted participants (all group-by-condition interaction effects and main effects, $P > 0.2$). The dMPFC showed a trend toward a group-by-condition interaction [$F(1,20) = 3.74$, $P = 0.06$]. However, this interaction was primarily driven by a greater response to Hearing Belief trials in sighted participants [$t(11) = 2.78$, $P < 0.05$]. The hearing and seeing conditions were not different in EB subjects ($P > 0.3$). Whole-brain analysis failed to uncover any regions that responded differentially across group in the seeing vs. hearing contrast.

Follow-up memory experiment. Experiment 2 did not reveal any differences between the seeing and hearing conditions across groups. To check that participants did encode the visual or aural source of the protagonists' beliefs, we performed a surprise memory test after the fMRI experiment. Seven of the control subjects performed a forced-choice memory task. They read part of the original story (e.g., Abigail was reminded of her boyfriend) and recalled whether the source of the belief was visual or aural.

Participants were significantly above chance in remembering whether the protagonist experienced the event through seeing or hearing (mean \pm SD: $70 \pm 14\%$; $t(6) = 3.65$, $P < 0.01$; signed-rank test $S = 10.5$, $P < 0.05$). These data demonstrate that participants did encode the modality of the character's experience. (The signed-rank test was used because of the relatively small N .)

Discussion

ToM in the Brains of Blind Individuals. The first key result of the current study is that EB and sighted individuals recruit the same neural network for ToM processing, including the RTPJ, LTPJ, PC, vMPFC, and dMPFC. The components of this network are similarly localized and equally selective for belief content across groups. As in sighted individuals, the ToM network of EB participants responds more to passages about beliefs than passages about nonbelief representations [e.g., photographs (30)] or passages about bodily sensations [e.g., hunger, fatigue (8)].

In contrast to the preservation of the ToM network, we found that visual deprivation leads to reorganization in the neural systems engaged in language comprehension: The visual cortices of EB, but not sighted, individuals are engaged during speech comprehension.

These data illustrate that the ToM network is robust to complete visual deprivation from birth. More generally, our

about others' beliefs by imagining ourselves having the experiences that gave rise to the beliefs. Understanding the beliefs of others would then critically depend on sharing their sensory and action experiences. In contrast, we find that never having seen does not alter how people represent mental states that arise from seeing.

We conclude that thinking about other people's thoughts, in both sighted and blind people, depends on abstract and propositional representations that can be acquired without first-person experience. Of course, our data do not rule out recapitulation of first-person experiences during mentalizing, in some circumstances. Memories of their own specific experiences may help people infer and empathize with another person's current situation (44). Nevertheless, our results suggest that detailed and sophisticated thoughts about thoughts can occur in the absence of such shared experiences.

The Role of Experience in the Development of the ToM Network. We demonstrate that the absence of visual experience during development does not affect the location and functional profile of ToM brain regions. Our results do not resolve, of course, how the brain regions for ToM in the blind (or in the sighted) develop; that is, what mechanisms do lead to brain regions with these functions in these locations.

On the one hand, the brain regions for ToM might be predetermined biologically and not open to the influence of experience in the course of development. The alternative, which we favor, is that the development of neural mechanisms for ToM does depend on experience but that these experiences are represented at an abstract level, linguistically and/or amodally. Thus, blind people's observations of humans through hearing may provide sufficient replacement for sighted people's observations through vision. For example, hearing footsteps or the tone of someone's voice may provide equivalent information to observing actions and seeing faces, as far as development of the ToM mechanism is concerned.

An outstanding question is: How do other kinds of experiential change affect the ToM network? Of particular interest are the effects of changes in linguistic and social environment. As described above, linguistic input may provide a critical source of information for the development of a ToM. Another critical source of relevant experience may be social interactions with caregivers early in life. For example, performance on basic false-belief tasks is delayed in children who were raised in orphanages, even after controlling for IQ and language ability (45). In particular, performance is correlated with the institutional adult-child ratio; children who have fewer opportunities for interaction with adults are more likely to fail false-belief tasks. A number of recent studies have reported the neural effects of institutional rearing (46, 47), but none have directly investigated the ToM network.

In summary, the present data illustrate that the ToM network is remarkably resilient to complete visual deprivation. An important goal of further research should be to establish which aspects of experience are necessary and sufficient for typical development of the ToM network.

Materials and Methods

Participants. Twenty-two sighted (16 females; mean age \pm SD, 40 \pm 19) and 10 EB subjects (5 females; mean age \pm SD, 50 \pm 7) participated in experiment 1. All of the blind participants and 13 of the sighted participants (mean age \pm SD, 52 \pm 16) also took part in experiment 2. All participants were native English speakers. One EB participant was ambidextrous and one was left-handed. One sighted participant was left-handed. The remainder of the blind and all of the sighted participants were right-handed according to self-report. Nine EB participants were congenitally blind and one lost sight between the ages of 2 and 3. All blind participants reported having at most faint light perception and no pattern discrimination (Table S2). None were able to perceive shapes, colors, or motion. None of the participants suffered from psychiatric or

neurological disorders, had ever sustained head injury, or were on any psychoactive medications. The study was approved by the institutional review board. All subjects gave informed consent and were paid \$30 an hour for taking part in the experiment.

Behavioral Procedure. Experiment 1. Participants listened to stories (12 sec) about mental and physical (e.g., photographic) representations of reality. In each story there was an inconsistency between the representation (belief or physical) and reality. Immediately after the story, participants were asked a true/false question (6 sec) that referred to either the situation in reality or to the representation. Prior studies showed no difference between the reality/representation conditions (48). Therefore all analyses collapse across the reality/representation dimension. Story and question pairs were separated by a 12-sec intertrial interval (ITI). On half of the trials the correct response to the question was "true." The belief and physical stories were thus matched on the logical structure as well as the syntactic construction of the statement but differed as to whether they required participants to reason about beliefs. The belief and physical conditions were also matched on average number of words per story and question (all condition differences $P > 0.1$). Additionally, we included a noise control condition that was similar in structure to the story trials. In the noise condition, participants heard a long string of reversed speech followed by a short string of reversed speech. They were asked to determine whether the short string of backward speech was a piece of the long string or a new string. The long strings of reverse speech were created by playing the stories backwards. The short strings were made by playing the questions backwards or by splicing out a piece of a backwards story. The resulting auditory stimuli sounded like unintelligible noise. The task was performed in 6 runs with 12 items per run (4 belief, 4 physical, and 4 backward-speech). Each run was 6 min and 12 sec long.

Experiment 2. Participants heard stories (13 sec) in 4 conditions: seeing belief, hearing belief, bodily feeling, and control. The seeing belief stories described a character coming to believe something as a result of a seeing experience. The hearing belief stories described a character coming to believe something as a result of a hearing experience. The bodily feeling stories described a character experiencing bodily feelings (e.g., aches, exhaustion, relaxation). Seeing, hearing, and bodily feeling conditions were matched on the semantic and syntactic aspects of stories by having each item occur in every condition, across participants. Participants decided whether the main character in the story felt "very bad," "a little bad," "a little good," or "very good" (8 sec). Half of the stories in each condition described an event that might make the character feel bad, whereas half described positive events. The control stories described events without human protagonists that were either positive or negative. Participants were told that if the story they heard did not have a main character (control condition), it was a news clip and they were to rate the story as to whether the news was "very bad," "a little bad," "a little good," or "very good." The control condition was similar in syntactic construction and number of words per story to the belief and bodily feeling conditions ($P > 0.3$). Stories and questions were separated by an 11-sec ITI. The experiment consisted of 4 runs, each 4 min and 34 sec long. There were 8 trials per run, with 2 in each condition. The stimuli for experiments 1 and 2 were digitally recorded by a female speaker at a sampling rate of 44,100 to produce 32-bit digital sound files. See Fig. S4 for examples of stories from experiments 1 and 2.

fMRI Data Acquisition and Analysis. Structural and functional data were collected on a 3-tesla Siemens scanner at the Athinoula A. Martinos Imaging Center at the McGovern Institute for Brain Research (Massachusetts Institute of Technology). For details of data collection and analysis see [SI Materials and Methods](#). Briefly, data analysis was performed with SPM2 (www.fil.ion.ucl.ac.uk) and in-house software. Data were motion-corrected, smoothed, and normalized. BOLD signal differences between conditions were evaluated through random effects analysis both in the whole-brain and in functionally defined ROIs. All reported results are significant at $P < 0.05$ and were corrected for multiple comparisons. Voxel-by-voxel pattern correlation analysis was used to compare the similarity of activations between the sighted and EB groups.

ACKNOWLEDGMENTS. We thank the research participants and the Boston blind community for making this research possible; Lucy Chen, Jonathan K. Scholz, and the Athinoula A. Martinos Imaging Center at the McGovern Institute for Brain Research for help with fMRI analyses and data collection; and Michael Frank, Laura Shultz, and the reviewers for comments on earlier drafts of the manuscript. This research study was supported in part by National Institutes of Health Grants R01 MH067008 and R01 DC006842 (to M.B. and A.P.L.) and K24 RR01887, R01 EY12091, and R21 EY0116168 (to A.P.L.).

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