
This copy is for your personal, non-commercial use only.

If you wish to distribute this article to others, you can order high-quality copies for your colleagues, clients, or customers by [clicking here](#).

Permission to republish or repurpose articles or portions of articles can be obtained by following the guidelines [here](#).

The following resources related to this article are available online at www.sciencemag.org (this information is current as of December 23, 2010):

Updated information and services, including high-resolution figures, can be found in the online version of this article at:

<http://www.sciencemag.org/content/330/6012/1830.full.html>

Supporting Online Material can be found at:

<http://www.sciencemag.org/content/suppl/2010/12/20/330.6012.1830.DC1.html>

This article **cites 12 articles**, 4 of which can be accessed free:

<http://www.sciencemag.org/content/330/6012/1830.full.html#ref-list-1>

This article appears in the following **subject collections**:

Psychology

<http://www.sciencemag.org/cgi/collection/psychology>

pollen rejection. In progeny of some interspecific tomato hybrids, distorted segregation ratios for *CUL1*-linked markers are consistent with the selective elimination of pollen bearing the nonfunctional *SICUL1* allele (*15*). Distorted transmission of *CUL1* is only observed in progeny of crosses between SC cultivated tomato and SI wild species, and only when the F_1 hybrid is used as pistillate parent. Moreover, two SC accessions of mostly SI species that either accumulate no S-RNase in the pistil [*S. pennellii* LA0716 (*11*)] or express a mutant protein lacking RNase activity [*S. arcanum* LA2157 (*24*)] exhibit normal F_2 segregation for *CUL1*-linked markers in hybrids with cultivated tomato (*25*, *26*). These observations suggest that selection against *CUL1*-deficient pollen requires S-RNase activity in the pistil. If so, loss of *CUL1* function in the red- or orange-fruited species was likely preceded by a loss of S-RNase expression [styles of *S. lycopersicum* do not accumulate S-RNase (*11*)]. On the other hand, pistils of LA0716 and LA2157 reject pollen from cultivated tomato (*9*, *27*) without expressing functional S-RNases, which suggests that pollen rejection by UI can also be mechanistically distinct from SI. Although our results are from an analysis of interspecific *Solanum* hybrids, they may be relevant to UI in other solanaceous plants, and possibly to other families that use the S-RNase-based SI system.

References and Notes

- B. A. McClure, *J. Exp. Bot.* **60**, 1069 (2009).
- B. A. McClure *et al.*, *Nature* **342**, 955 (1989).
- P. Sijacic *et al.*, *Nature* **429**, 302 (2004).
- D. Lewis, L. K. Crowe, *Heredity* **12**, 233 (1958).
- R. T. Chetelat, J. W. DeVerna, *Theor. Appl. Genet.* **82**, 704 (1991).
- D. Bernacchi, S. D. Tanksley, *Genetics* **147**, 861 (1997).
- J. Murfett *et al.*, *Plant Cell* **8**, 943 (1996).
- N. G. Hogenboom, *Euphytica* **22**, 219 (1973).
- J. J. Hardon, *Genetics* **57**, 795 (1967).
- B. E. Liedl, S. McCormick, M. A. Mutschler, *Sex. Plant Reprod.* **9**, 299 (1996).
- P. A. Covey *et al.*, *Plant J.* **64**, 367 (2010).
- C. M. Rick, in *Plant Evolutionary Biology*, L. D. Gottlieb, S. K. Jain, Eds. (Chapman & Hall, London, 1988), pp. 133–147.
- M. A. Mutschler, B. E. Liedl, in *Genetic Control of Self-Incompatibility and Reproductive Development in Flowering Plants*, E. G. Williams, A. C. Clarke, R. B. Knox, Eds. (Kluwer, Dordrecht, Netherlands, 1994), pp. 164–188.
- C. M. Rick, J. W. De Verna, R. T. Chetelat, M. A. Stevens, *Proc. Natl. Acad. Sci. U.S.A.* **83**, 3580 (1986).
- W. Li, S. Royer, R. T. Chetelat, *Genetics* **185**, 1069 (2010).
- Z. Hua, T. H. Kao, *Plant Cell* **18**, 2531 (2006).
- L. Zhao *et al.*, *Plant J.* **62**, 52 (2010).
- C. Cenciarelli *et al.*, *Curr. Biol.* **9**, 1177 (1999).
- D. Twell, J. Yamaguchi, S. McCormick, *Development* **109**, 705 (1990).
- C. M. Rick, J. F. Fobes, M. Holle, *Plant Syst. Evol.* **127**, 139 (1977).
- N. Zheng *et al.*, *Nature* **416**, 703 (2002).
- H. Qiao *et al.*, *Plant Cell* **16**, 582 (2004).
- K. Kubo *et al.*, *Science* **330**, 796 (2010).
- J. Royo *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **91**, 6511 (1994).
- A. W. van Heusden *et al.*, *Theor. Appl. Genet.* **99**, 1068 (1999).
- T. M. Fulton, R. Van der Hoeven, N. T. Eannetta, S. D. Tanksley, *Plant Cell* **14**, 1457 (2002).
- C. M. Rick, in *Solanaceae Biology and Systematics*, W. G. D'Arcy, Ed. (Columbia Univ. Press, New York, 1986), pp. 475–495.
- J. Y. Ho *et al.*, *Plant J.* **2**, 971 (1992).
- A. J. Monforte, S. D. Tanksley, *Genome* **43**, 803 (2000).
- M. A. Canady, V. Meglic, R. T. Chetelat, *Genome* **48**, 685 (2005).
- We thank J. DeVerna, P. March, K. Smith, and the C. M. Rick Tomato Genetics Resource Center (TGRC) staff for providing seed or cuttings of key genotypes; P. March for photos of fruit; B. McClure and P. Bedinger for comments on the manuscript; and S. Tanksley for providing seed of *S. habrochaites* introgression lines. Supported by NSF grant DBI 0605200. Sequence data have been deposited in GenBank under accession numbers HQ610200 and HQ610201. Seed requests submitted to the TGRC are subject to a material transfer agreement (<http://tgrc.ucdavis.edu/MTA/TGRC-MTA.pdf>).

Supporting Online Material

www.sciencemag.org/cgi/content/full/330/6012/1827/DC1
Materials and Methods
Tables S1 and S2
Figs. S1 to S3
References

17 September 2010; accepted 18 November 2010
10.1126/science.1197908

The Social Sense: Susceptibility to Others' Beliefs in Human Infants and Adults

Ágnes Melinda Kovács,^{1,2,3*} Ernő Téglás,^{1,2,3} Ansgar Denis Endress^{3,4}

Human social interactions crucially depend on the ability to represent other agents' beliefs even when these contradict our own beliefs, leading to the potentially complex problem of simultaneously holding two conflicting representations in mind. Here, we show that adults and 7-month-olds automatically encode others' beliefs, and that, surprisingly, others' beliefs have similar effects as the participants' own beliefs. In a visual object detection task, participants' beliefs and the beliefs of an agent (whose beliefs were irrelevant to performing the task) both modulated adults' reaction times and infants' looking times. Moreover, the agent's beliefs influenced participants' behavior even after the agent had left the scene, suggesting that participants computed the agent's beliefs online and sustained them, possibly for future predictions about the agent's behavior. Hence, the mere presence of an agent automatically triggers powerful processes of belief computation that may be part of a "social sense" crucial to human societies.

Humans are guided by internal states such as goals and beliefs. Without an ability to infer others' mental states, society would

be hardly imaginable. Social interactions, from collective hunting to playing soccer to criminal justice, critically depend on the ability to infer others' intentions and beliefs. Such abilities are also at the foundation of major evolutionary conundra. For example, the human aptitude at inferring mental states might be one of the crucial preconditions for the evolution of the cooperative social structure in human societies (*1*). However, despite their importance for all aspects of social life, the question of how such "theory of mind" (ToM) abilities (*2*) emerge and develop, and what

their functional characteristics are, is still the topic of important debates.

Decades of research seem to suggest that ToM emerges after the age of four. Developmental transitions in ToM have often been assessed using so-called "false-belief tasks" (*3*). In such tasks, children typically have to predict a person's behavior based on the person's false belief while ignoring their own true belief. For example, children are presented with a situation in which another child (say, John) places a toy in a cupboard and leaves the scene. In his absence, the toy is moved to a different location (say, a basket). Three-year-olds typically predict that, upon his return, John will search in the basket rather than in the cupboard, because they themselves know that the toy is in the basket. That is, at least in their overt responses, 3-year olds fail to take into account that John cannot know that the toy is in the basket and must, therefore, (falsely) believe the toy to be in the cupboard. In contrast, older children (and adults) take into account John's false belief and predict that he will search in the cupboard. Based on such findings, it has been argued that ToM requires complex computations and emerges relatively late in development (*4*).

However, such data are not necessarily inconsistent with the possibility that ToM is automatic and innate (*5–8*). Children might possess ToM abilities early on; however, these might be masked by the slower development of other abilities involved in such tasks, such as inhibition and selection (*6*) or problem solving (*8*). That is, young children might well be able to represent

¹Institute for Psychology, Hungarian Academy of Sciences, H-1132 Budapest, Hungary. ²Cognitive Development Centre, Central European University, H-1015, Budapest, Hungary. ³Cognitive Neuroscience Sector, International School for Advanced Studies (SISSA), I-34014 Trieste, Italy. ⁴Department of Brain and Cognitive Sciences, Massachusetts Institute of Technology, Cambridge MA 02139, USA.

*To whom correspondence should be addressed. E-mail: agneskovacs@mtapi.hu

others' beliefs, but, to correctly predict that, in the example above, John will search for the toy where he (falsely) believes it to be, children also need efficient inhibitory abilities. Specifically, they need to deal with two conflicting representations, namely John's (false) belief that the ball is in the cupboard and their own (true) belief that the ball is in the basket, and to inhibit their own belief when they predict John's behavior. In line with such views, newer research suggests that ToM abilities are present in young children, for instance in 3-year-olds when testing populations with enhanced inhibitory abilities (9), or even in infants in their second year when using simpler testing procedures (10–12).

Although these data suggest that ToM abilities may emerge well before the age of four, another question has received little empirical attention. If such abilities are essentially an innate "social sense," they should be spontaneous and automatic, and others' beliefs should be com-

puted online and effortlessly, just as we compute representations of what we perceive in the environment. The experiments below will address this issue.

Our experiments will also address a second issue that, to our knowledge, has not been investigated directly. Representations about the environment and representations about others' beliefs can differ in many aspects. Most important, unlike most aspects of the environment, others' mental states are not directly observable and are sometimes inconsistent with the true state of affairs. We can represent that "Mary thinks that John is at home" even if we know that "John is not at home." Thus, our knowledge of the environment does not reliably predict the contents of others' beliefs, nor do others' beliefs reliably predict the state of the environment. Accordingly, representations of others' beliefs might be stored in a way reflecting that their content is not referenced to the current state of affairs. Crucially, if

such representations are not referenced to the environment, they should not affect how we interact with the environment either.

Although this conjecture seems consistent with the proposal that representations about others' beliefs are computed by specialized mechanisms (5), there is a more parsimonious hypothesis. We clearly have mechanisms in place to compute representations about what we experience in the environment. Perhaps we use very similar mechanisms to compute others' beliefs based on what they experience. If so, representations about others' beliefs should have fundamentally similar properties as representations about the environment. This hypothesis predicts that representations of others' beliefs should be referenced to the environment just as our own beliefs, and thus can affect our behavior. We test this idea in the experiments below.

Here, we develop a method for investigating ToM mechanisms that, in contrast to variants of the standard false belief task, is implicit, makes no reference to others' beliefs, and requires no behavioral predictions of what agents will do on the basis of their beliefs. Specifically, we use an object detection task to investigate two questions. First, are belief computations automatically triggered by the mere presence of an agent in adults and in infants as young as 7 months, even when the beliefs are entirely irrelevant to the task participants have to perform? Second, are beliefs about others' beliefs stored in a format sufficiently similar to our own representations about the environment that both types of representations can affect our behavior?

In Experiment 1, adults ($N = 24$) performed a visual detection task while watching 40 animated movies (13). As shown in Fig. 1, movies started with an agent placing a ball on a table in front of an occluder. Then the ball rolled behind the occluder. After this, the movies could continue in four ways depending on the experimental conditions. Our critical manipulations involved the participant's beliefs about the ball's presence and the "beliefs" of the agent, such that the agent, the participant, both, or neither could believe that the ball was behind the occluder. This was achieved by varying (i) the final location of the ball and (ii) the time at which the agent left the scene. Specifically, (i) participants saw the ball either staying behind the occluder or leaving the scene and (ii) the agent left the scene either before or after the ball had reached its final location (leading to a true/false belief). That is, the agent had a true belief about the ball's location if he left the scene after the ball had reached its final location; if he left the scene before the ball reached its final location, his belief was false.

At the end of each movie, the agent reentered the scene and the occluder was lowered. The four conditions were paired with two outcomes, in which the ball was either present or absent behind the occluder. Participants were instructed to press a button as soon as they detected the ball. Notably, the agent's beliefs were never mentioned and were irrelevant to the task.

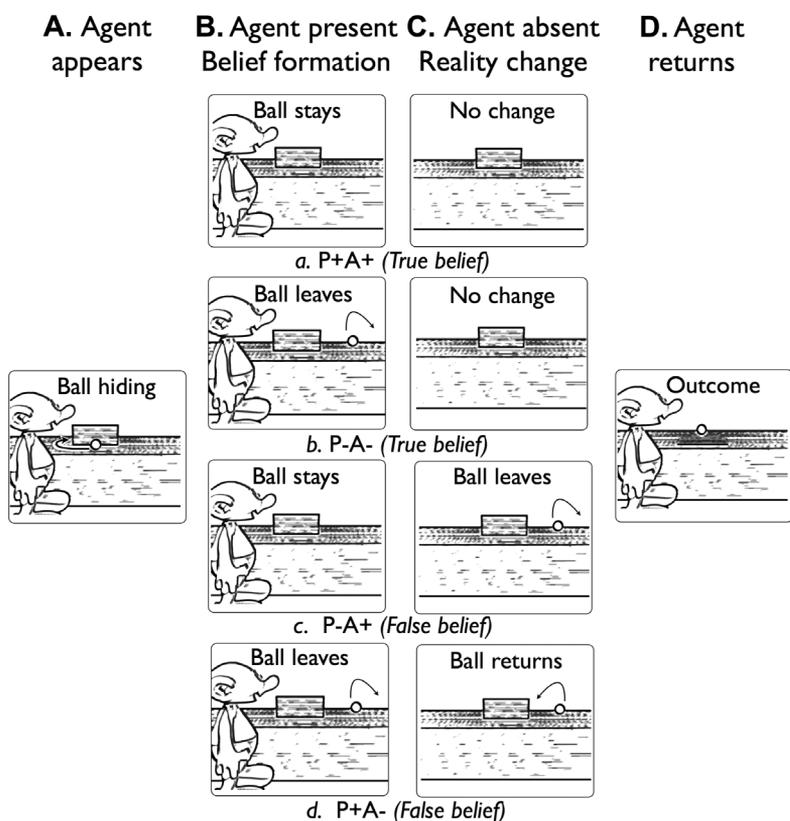


Fig. 1. Logical structure of events in Experiment 1. (A) In all four conditions, the agent enters the scene, placing a ball on a table (13) (Movie S1). The ball then rolls behind an occluder. (B) In the agent's presence, the ball stays behind the occluder (a and c), or leaves the scene (b and d). As a result, the agent (A) "believes" either that the ball is behind the occluder or that there is no ball behind the occluder. Then, the agent leaves the scene. (C) In the agent's absence, the ball leaves the scene (c), returns behind the occluder (d), or does not move (a and b). Thus, the participant (P) either believes the ball to be behind the occluder (a and d), or to have left (b and c). (D) The agent reenters the scene, and the occluder is lowered. In half of the trials of all conditions, participants see the ball behind the occluder. We measure ball detection latencies as a function of (i) the participant's belief (P+, ball behind occluder, versus P-, no ball behind occluder) and (ii) the agent's "belief" (A+, ball behind occluder, versus A-, no ball behind occluder), resulting in two true belief conditions and two false belief conditions. The figure does not reflect the actual timing of the events. To control for the timing differences, we used pairs of conditions matched for their timing properties (13).

We will discuss the experimental conditions in terms of the beliefs of the participant and the agent, respectively, rather than in terms of the events displayed in the animations. (The agent’s “belief” is what he might believe based on what he “experiences” in the scenes if he were a real person.)

We predicted that participants should be faster to detect the ball when they believed that the ball is behind the occluder than when they do not believe so. Crucially, and as mentioned above, the agent’s beliefs were completely irrelevant to the task. As a result, if others’ beliefs are computed through explicit processes requiring effortful computations, the agent’s “beliefs” should have no effect on reaction times (RTs), because participants were not required to perform belief computations. However, if participants automatically compute the agent’s beliefs and store them in a way similar to that of their own representations about the environment, their detection latencies should also be faster when only the agent “believes” that the ball is behind the occluder.

We will compare the experimental conditions to a baseline condition where neither the participant nor the agent believed the ball to be behind the occluder; as a result, there were no belief representations that could speed up RTs. To validate our paradigm, we compared RTs in this baseline condition to the condition where both the participant and the agent believed the ball to be behind the occluder.

Compared to the baseline condition, participants detected the ball faster when they (and the agent) believed that the ball was behind the occluder [$t(23) = 3.47, P = 0.002$] (Fig. 2A) (13). Likewise, participants were faster than in the baseline when they but not the agent believed that the ball was behind the occluder [$t(23) = 3.43, P = 0.002$].

Our critical comparison involves the baseline condition and the condition where only the agent believed that the ball was behind the occluder. Results showed that participants were faster than in the baseline condition when only the agent believed the ball to be behind the occluder [$t(23) = 2.42, P = 0.02$]. This suggests that they computed

the agent’s belief and that this belief influenced their behavior even though it was inconsistent with their own belief. Moreover, RTs did not differ significantly between the condition where the participants themselves believed that the ball was behind the occluder and the condition where only the agent believed so [$t(23) = 0.99, P = 0.33$]. Thus, both types of belief representations speeded up the participants’ RTs to similar extents, a result consistent with the view that the agent’s beliefs are stored similarly to participants’ own representations about the environment.

In Experiment 1, participants simply had to detect a ball after watching a scene involving an agent whose presence was irrelevant to the task. Nevertheless, the agent’s beliefs influenced the participants’ RTs to the same extent as their own beliefs, suggesting that just seeing the agent automatically made participants compute his beliefs and that these beliefs were represented and sustained similarly to participants’ own beliefs.

These results may also provide an important clue to a question that has remained elusive for the last three decades, namely how false beliefs might be computed. In Experiment 1, the agent had a false belief because he left the scene before the ball reached its final position. Possibly, participants compute online the agent’s last belief and, unless there is evidence that he updated it, maintain it in parallel with their own beliefs. If so, the agent’s belief should continue to influence their RTs even in the agent’s absence; if the environment changes, the agent’s beliefs will necessarily become false. We tested this prediction in Experiment 2 with a new group of participants ($N = 24$). This experiment was identical to Experiment 1 except that the agent did not return in the last phase of the movies; instead, a pile of boxes entered the scene before the occluder was lowered (13).

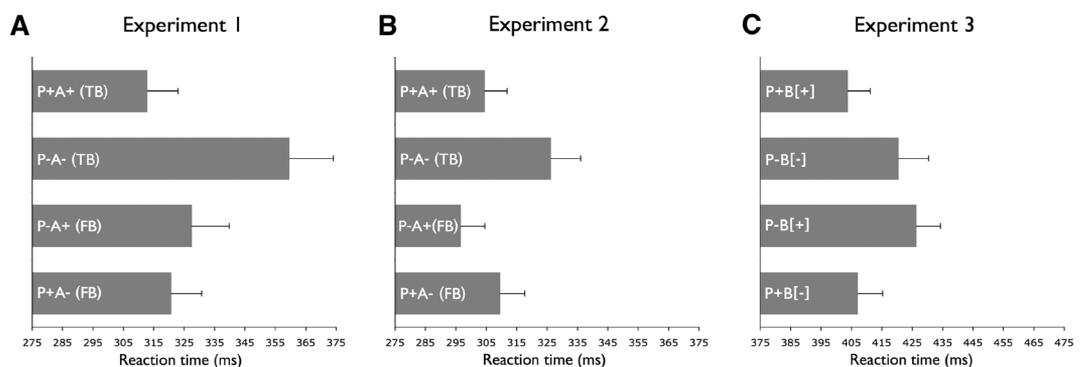
The results of Experiment 2 were similar to those of Experiment 1. Participants were faster than in the baseline condition when they and the agent (who was not present when the occluder was lowered) believed the ball to be behind the occluder [$t(23) = 2.83, P = 0.009$] (Fig. 2B). Likewise, RTs were faster than in the baseline

condition when they but not the agent believed that the ball was there [$t(23) = 3.2, P = 0.004$]. Crucially, RTs were also faster than in the baseline condition when only the agent believed that the ball was behind the occluder [$t(23) = 2.1, P = 0.04$]. Thus, although the agent was not present when participants detected the ball, his beliefs continued to influence participants’ behavior.

Taken together, data from Experiments 1 and 2 show that when participants had to detect the presence of the ball, their RTs were faster not only when they believed the ball to be behind the occluder but also when the agent believed so, irrespective of whether or not the agent was present when participants gave their responses. Although these results appear to reflect computations of the agent’s beliefs, differences in the ordering of events in the different experimental conditions might possibly affect participants’ RTs as well. Specifically, in our experimental design, some conditions required the agent to leave the scene before the ball reached its final location (resulting in a false belief), whereas other conditions required the agent to leave after the ball reached its final location (resulting in a true belief). Despite its plausibility, further analysis of our results did not support this possibility, as the ordering differences (e.g., the number of events that occur after the ball reached its target location) did not predict participants’ RTs in the four experimental conditions (13).

Experiment 3 was designed to further confirm that the RT differences between the crucial conditions in Experiments 1 and 2 were due to the agent’s beliefs and not to other perceptual differences between the conditions. In Experiment 3, participants ($N = 24$) were presented with movies that were similar to those shown in Experiments 1 and 2, except that the agent did not appear in the movies at all. Instead, a stationary pile of boxes was present in all movies during their entire duration. However, all other events (e.g., the movements of the ball) were as in Experiments 1 and 2. Hence, while participants in Experiment 3 could not compute another agent’s beliefs (because there was no agent present), they experienced

Fig. 2. (A) Results of Experiment 1 (adults; agent present in the last scene). Ball detection latencies in adults. Bars represent average latencies, and error bars show SEM (see Fig. 1 for condition labels). (B) Results of Experiment 2 (adults; agent absent in the last scene). Ball detection latencies in adults when a pile of boxes replaced the agent in the very last scene (corresponding to Fig. 1D). (C) Results of Experiment 3 (adults; agent absent in the entire movie). Ball detection latencies in adults when no agent was present at all but a stationary pile of boxes (represented by B in the panel) was present during the entire movie. The signs in square brackets indicate the beliefs the agent would have had if he had been present, as in Experiments 1 and 2. Thus, P+B[–] indicates the



condition where the participant believes that the ball is behind the occluder, and the motion of the ball corresponds to a condition in Experiments 1 and 2 where the agent did not believe that the ball was behind the occluder.

motion paths of the ball identical to those in the different belief conditions from Experiments 1 and 2. If the differences between the critical conditions in Experiments 1 and 2 were due to perceptual differences rather than to belief computations, Experiment 3 should yield the same results, because the motion of the ball is identical. In contrast, if these differences were due to belief computations rather than to perceptual differences, RTs in Experiment 3 should be affected only by participants' own beliefs, since participants never saw an agent and, therefore, could not compute his beliefs.

Results showed that RTs were faster in the two conditions when participants believed the ball to be behind the occluder compared to the two conditions when participants did not believe the ball to be behind the occluder, with no other differences [all P 's < 0.05; see (13) for details] (Fig. 2C). Contrary to Experiments 1 and 2, RTs did not differ between the P-B[-] and P-B[+] conditions [$t(23) = 0.76$, $P = 0.45$], which correspond to the P-A- and P-A+ conditions in the first two experiments. To further confirm that RTs did not differ between these conditions, likelihood ratio analyses showed that the null hypothesis

was about 3 times more likely than the alternative hypothesis (13). Hence, when the agent was not present, participants' RTs were influenced only by their own beliefs about the presence of the ball but not by other perceptual differences between the conditions.

Together, Experiments 1 to 3 suggest that adults automatically compute and store the beliefs of other agents; the resulting representations appear to be similarly accessible to other cognitive processes as are their own beliefs. Once a belief is computed, it seems to remain active even in the absence of the agent, possibly to be used for future predictions about the agent's behavior.

If adults track others' beliefs automatically, such processes may well be present in young infants. We thus asked whether 7-month-olds would automatically compute the beliefs of an agent and whether these beliefs would influence their looking times in a violation of expectation paradigm. We tested this possibility in four experiments involving four different groups of infants ($N = 56$). Whereas Experiments 1 and 2 measured how beliefs about the presence of a ball influenced RTs when adult participants saw the ball, Experiments 4 to 7 measured infants' "sur-

prise" (indicated by longer looking times) when no ball was found, although the participant and/or the agent believed the ball to be behind the occluder. In each experiment, the condition where the participant and/or the agent believed the ball to be behind the occluder was compared to a condition where neither the participant nor the agent believed the ball to be behind the occluder.

In Experiment 4, infants watched two movies from Experiment 1 (13). In the baseline condition, neither the infant nor the agent believed that the ball was behind the occluder. We compared this baseline to a condition where both the infant and the agent believed that the ball was behind the occluder. When the occluder revealed no ball, infants looked longer in this condition than in the baseline condition [$F(1,13) = 5.65$, $P = 0.03$] (Fig. 3A), which suggests that their expectations modulated their looking behavior.

Experiment 5 presents the crucial comparison from Experiment 1. In this experiment, infants' looking times were compared in the baseline condition and in a condition where only the agent believed the ball to be behind the occluder (Movie S1). When no ball appeared behind the occluder, infants looked longer in this condition than in the baseline [$F(1,13) = 7.29$, $P = 0.01$] (Fig. 3B). This suggests that infants computed the agent's belief and looked longer when this belief was not confirmed, possibly also expecting the agent to be surprised. Thus, the beliefs of the agent influenced the infants' looking behavior, even though they clashed with the infants' own beliefs.

Experiment 6 controls for the possibility that infants' looking times in Experiment 5 were not influenced by the agent's beliefs but rather by some visual differences between the movies occurring before the occluder was lowered. (The movies were identical after the occluder was lowered.) We exclude this possibility by replicating Experiment 5, but without lowering the occluder at the end. Thus, infants did not see whether the ball was present behind the occluder, and neither their own nor the agent's beliefs were confirmed or disconfirmed. If the results of Experiment 5 were due to visual differences rather than to belief computations, Experiment 6 should yield the same results. In contrast to this prediction, no differences were observed when the occluder was not lowered [$F(1,13) = 0.05$, $P = 0.81$] (Fig. 3C). This suggests that the differences in Experiment 5 were not due to visual differences between the movies, but rather that infants did indeed compute the agent's beliefs.

In analogy to Experiment 2, Experiment 7 asked whether infants would maintain others' beliefs even in the agent's absence. Specifically, infants were presented with the baseline condition (where both the infant and the agent believed that the ball was not there) and a condition where only the agent believed the ball to be behind the occluder. Before the occluder was lowered, however, a pile of boxes, rather than the agent, entered the scene. As in Experiment 5, infants looked longer than in the baseline condition when the agent

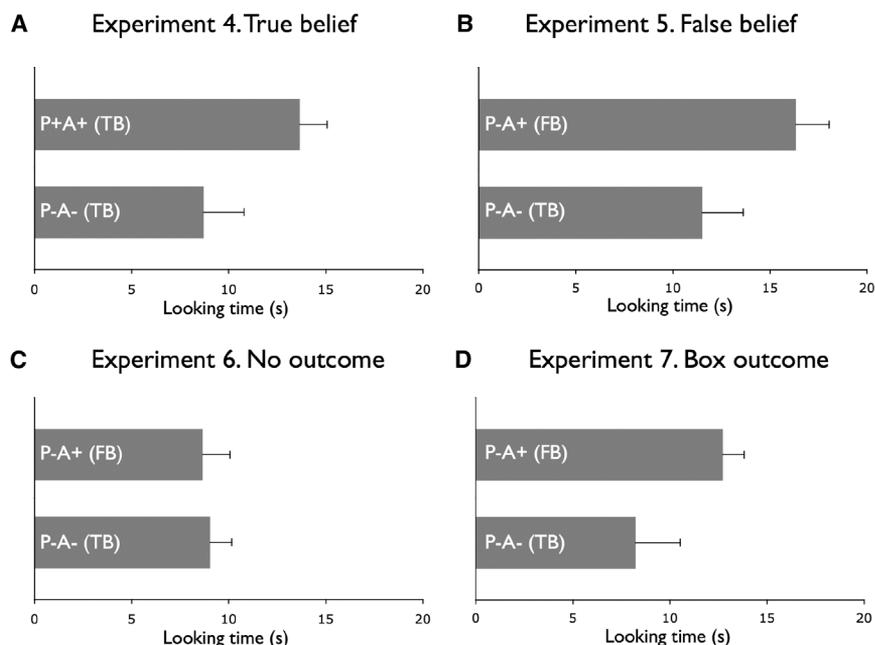


Fig. 3. Results of Experiments 4 to 7. Looking times in 7-month-old infants. Bars represent average looking times, and error bars show SEM (see Fig. 1 for condition labels). (A) Results of Experiment 4 (true belief). Looking times for the condition when infants (and the agent) believed the ball to be behind the occluder (P-A+) and for the condition when neither the infants nor the agent believed the ball to be behind the occluder (P-A-). (B) Results of Experiment 5 (false belief; agent present in the last scene). Looking times for the condition when only the agent (falsely) believed the ball to be behind the occluder (P-A+) (Movie S1), and for the condition when neither the infants nor the agent believed the ball to be behind the occluder (P-A-). (C) Results of Experiment 6 (no outcome control). Looking times for two conditions that were identical to the ones used in Experiment 4, except that the occluder was not lowered at the end of the movies. Thus, infants did not see whether the ball was present behind the occluder. As a result, there were no confirmed nor violated beliefs. (D) Results of Experiment 7 (false belief; agent absent in the last scene). Looking times for the two conditions where the agent was replaced with a pile of boxes in the very last scene (corresponding to Fig. 1D). We compared the condition where only the agent (falsely) believed the ball to be behind the occluder (P-A+) with the condition where neither the infants nor the agent believed the ball to be behind the occluder (P-A-).

(who was not present when the occluder was lowered) believed that the ball was behind the occluder [$F(1,13) = 6.75, P = 0.02$] (Fig. 3D). Hence, like adults in Experiment 2, infants seem to compute others' beliefs online and to maintain them even in the absence of the agent. Possibly, the boxes could have prompted participants to think of the agent and his beliefs, although there was no relation between the boxes and the agent. However, even if the boxes reminded participants the agent, our results can be explained only if participants computed the agent's beliefs and sustained them even though the agent was not present.

Together, our results suggest that the mere presence of social agents is sufficient to automatically trigger online belief computations not only in adults, but also in 7-month-old infants. Once the beliefs have been computed, adults and infants maintain them even in the absence of the agent, presumably for later use in social interactions. Hence, from 7 months on, an age by which infants attribute goals and intentionality (14), humans automatically compute other's beliefs and seem to hold them in mind as alternative representations of the environment. As a result, at

least in implicit tasks like ours, others' (false) beliefs can influence infants' and adults' behavior similarly to their own (true) beliefs. The finding that others' beliefs can be similarly accessible as our own beliefs might seem problematic for an individual, because it may make one's behavior susceptible to others' beliefs that do not reliably reflect the current state of affairs. However, the rapid availability of others' beliefs might allow for efficient interactions in complex social groups. These powerful mechanisms for computing others' beliefs might, therefore, be part of a core human-specific "social sense," and one of the cognitive preconditions for the evolution of the uniquely elaborate social structure in humans.

References and Notes

1. E. Herrmann, J. Call, M. V. Hernández-Lloreda, B. Hare, M. Tomasello, *Science* **317**, 1360 (2007).
2. D. Premack, G. Woodruff, *Behav. Brain Sci.* **1**, 515 (1978).
3. S. Baron-Cohen, A. M. Leslie, U. Frith, *Cognition* **21**, 37 (1985).
4. J. Perner, *Understanding the Representational Mind* (MIT Press, Cambridge, MA, 1991).
5. B. J. Scholl, A. M. Leslie, *Child Dev.* **72**, 696 (2001).

6. A. M. Leslie, O. Friedman, T. P. German, *Trends Cogn. Sci.* **8**, 528 (2004).
7. P. Bloom, T. P. German, *Cognition* **77**, B25 (2000).
8. J. A. Fodor, *Cognition* **44**, 283 (1992).
9. Á. M. Kovács, *Dev. Sci.* **12**, 48 (2009).
10. K. H. Onishi, R. Baillargeon, *Science* **308**, 255 (2005).
11. V. Southgate, A. Senju, G. Csibra, *Psychol. Sci.* **18**, 587 (2007).
12. L. Surian, S. Caldi, D. Sperber, *Psychol. Sci.* **18**, 580 (2007).
13. Materials and methods are available as supporting material on Science Online.
14. G. Csibra, *Cognition* **107**, 705 (2008).
15. This research was supported by the New and Emerging Science and Technology PATHFINDER initiative CALACEI and the Marie Curie Disorders and Coherence of the Embodied Self Research Training Network. We thank G. Csibra, G. Gergely, J. Perner, H. Wellman, M. Hauser, P. Jacob, L. Bonatti, and J. Mehler for comments.

Supporting Online Material

www.sciencemag.org/cgi/content/full/330/6012/1830/DC1

Materials and Methods

SOM Text

References

Movie S1

12 April 2010; accepted 22 November 2010

10.1126/science.1190792

Siah Regulation of Pard3A Controls Neuronal Cell Adhesion During Germinal Zone Exit

Jakub K. Famulski,*† Niraj Trivedi,* Danielle Howell, Yuan Yang,‡ Yi'ai Tong, Richard Gilbertson, David J. Solecki§

The brain's circuitry is established by directed migration and synaptogenesis of neurons during development. Although neurons mature and migrate in specific patterns, little is known about how neurons exit their germinal zone niche. We found that cerebellar granule neuron germinal zone exit is regulated by proteasomal degradation of Pard3A by the Seven in Absentia homolog (Siah) E3 ubiquitin ligase. Pard3A gain of function and Siah loss of function induce precocious radial migration. Time-lapse imaging using a probe to measure neuronal cell contact reveals that Pard3A promotes adhesive interactions needed for germinal zone exit by recruiting the epithelial tight junction adhesion molecule C to the neuronal cell surface. Our findings define a Siah-Pard3A signaling pathway that controls adhesion-dependent exit of neuronal progenitors or immature neurons from a germinal zone niche.

The migration of neurons from a germinal zone (GZ) to their final laminar positions is essential for morphogenesis of the developing brain (1–3); aberrations in this process are linked to profound neurodevelopmental and

cognitive disorders (4). Although the substrates (5–7), guidance mechanisms (8–10), cytoskeletal elements (11–13), and posttranslational modifications (14–16) required for neuronal migrations are well established, the cell-intrinsic machinery regulating when neurons gain access to permissive migration pathways to exit their GZs are unidentified (17). Developing cerebellar granule neurons (CGNs) are an excellent model to analyze the mechanisms regulating GZ exit and to elucidate migration pathway selection, because they undergo two migration phases (18–20): tangential migration near the cerebellar surface followed by radial migration away from the external granular layer (EGL) where CGNs cross the molecular layer (ML) to eventually reside within the internal

granule layer (IGL). In this study, we examined the roles of the partitioning-defective (PAR) polarity-signaling complex and an upstream regulator in controlling CGN migration from the EGL, a GZ niche (fig. S1).

The PAR complex is an evolutionarily conserved multiprotein complex containing orthologs of partitioning defective-6 (Pard6), partitioning defective-3 (Pard3) and protein kinase C ζ (PKC ζ) that regulates many polarized cellular processes, like cell motility, asymmetric cell division, and epithelial junction formation (21). Because Pard3A protein expression is low in the EGL (Fig. 1, A to C), we examined whether elevated Pard3A activity induces CGN GZ exit. Expression constructs for Pard3A and the fluorescent nuclear reporter H2B-mCherry were co-electroporated into the cerebellar cortices of postnatal day 8 (P8) mice, and cerebellar slices were cultured *ex vivo* (22). Whereas control CGNs remained within the EGL after 24 hours (fig. S2A), CGNs expressing elevated Pard3A entered the ML and IGL (fig. S2B), suggesting that elevated Pard3A expression is sufficient to induce precocious GZ exit.

We next examined the role of Siah, a PAR complex-interacting E3 ubiquitin ligase (fig. S3) expressed in the EGL (Fig. 1D), in regulating Pard3A protein level and PAR complex-dependent GZ exit. The role of Siah ligases in the morphogenesis of the vertebrate nervous system has not previously been examined (23). Epitope-tagged Siah1B immunoprecipitated Pard3A when coexpressed in human embryonic kidney 293 (HEK293) cells (fig. S3B), an interaction that required an intact Siah substrate-binding domain (fig. S3D). Furthermore, Siah1B expression reduced expression of Pard3A, but not Pard6 or PKC ζ , protein (Fig. 1E) and induced Pard3A ubiquitination (Fig.

Department of Developmental Neurobiology, St. Jude Children's Research Hospital, 262 Danny Thomas Place, Memphis, TN 38105, USA.

*These authors contributed equally to this work.

†Present address: Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada.

‡Present address: Department of Physiology, Development and Neuroscience, Anatomy Building, University of Cambridge, Downing Street, Cambridge CB2 3DY, UK.

§To whom all correspondence should be addressed. E-mail: david.solecki@stjude.org