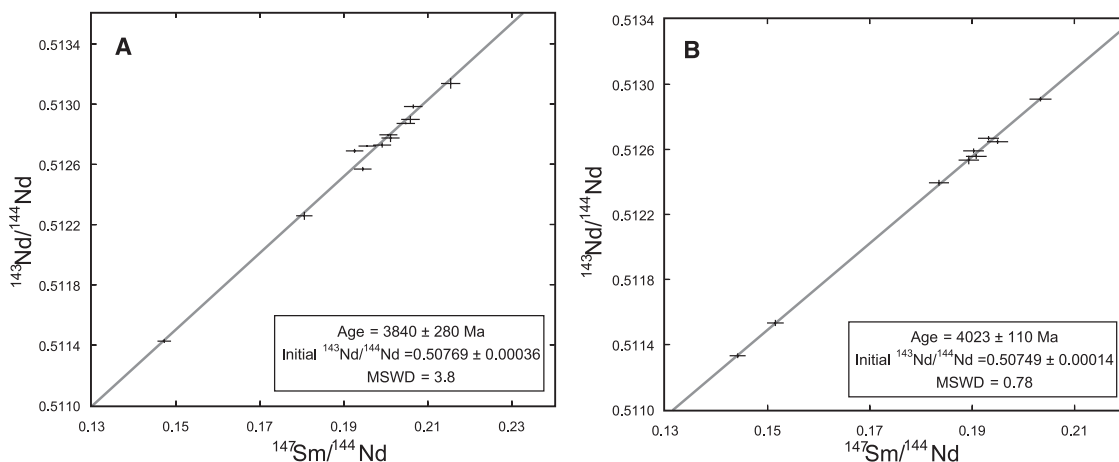


Fig. 4. ^{147}Sm - ^{143}Nd isochron diagrams. (A) Ultramafic to gabbroic samples from one differentiated sill. (B) Samples from the gabbro sills that show a strong gneissic metamorphic texture.



perhaps not as depleted as suggested by the Greenland data (7, 17, 19). As a result, the calculated ^{143}Nd depleted-mantle model ages (T_{DM}) for the faux-amphibolite, except PC-129, range from 4.1 to 4.4 Ga, consistent with the age suggested by ^{142}Nd systematics and in contrast to the 3.2 to 3.6 Ga T_{DM} values of the gabbros and sample PC-129 (table S2).

Whether or not the faux-amphibolite is 4.28 Gy old, its compositional characteristics may provide clues to the process of crust formation in the Hadean (>4.0 Ga). The basaltic major and compatible (e.g., Ni) trace element composition of the faux-amphibolite is consistent with derivation from a peridotitic mantle. Compared to the gabbros and to modern mid-ocean ridge basalts, the most unusual compositional characteristic of the faux-amphibolite is its low Ca content, high K and Rb contents, and LREE enrichment. Because elements like K and Rb are easily affected by alteration, however, it is unclear whether these are magmatic features of the faux-amphibolite. The LREE enrichment could reflect relatively low degrees of mantle melting, but this explanation is not supported by the relatively low concentration of elements such as Ti and Nb in the faux-amphibolite. The high LREE to Nb ratios of the faux-amphibolite, however, is similar to that of modern calc-alkaline melts produced in convergent margin settings. The Hadean crust, represented by the faux-amphibolite, was intruded at 4.0 and 3.8 Ga by gabbro and ultramafic sills that have the ^{143}Nd and ^{142}Nd isotopic composition of the depleted mantle at the time of their intrusion. The low $^{143}\text{Nd}/^{144}\text{Nd}$ ratios of tonalites and felsic bands that were replaced between 3.8 and 3.6 Ga, well after ^{146}Sm was extinct (9–11), suggest that they formed by the partial melting of the faux-amphibolite.

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Infants' Perseverative Search Errors Are Induced by Pragmatic Misinterpretation

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Having repeatedly retrieved an object from a location, human infants tend to search the same place even when they observe the object being hidden at another location. This perseverative error is usually explained by infants' inability to inhibit a previously rewarded search response or to recall the new location. We show that the tendency to commit this error is substantially reduced (from 81 to 41%) when the object is hidden in front of 10-month-old infants without the experimenter using the communicative cues that normally accompany object hiding in this task. We suggest that this improvement is due to an interpretive bias that normally helps infants learn from demonstrations but misleads them in the context of a hiding game. Our finding provides an alternative theoretical perspective on the nature of infants' perseverative search errors.

Human infants' abilities for understanding the physical world are often tested in hide-and-search tasks. First demonstrated by Piaget (1), the perseverative search error (some-

times called the A-not-B error) is a well-known and robust mistake that infants close to 1 year of age normally commit. In the standard A-not-B task, a demonstrator repeatedly places an object

under one (A) of two opaque containers (A and B) in full view of the infant. After each hiding event, the infant is allowed to retrieve the object. This is followed by test trials where the demonstrator places the object under container B and allows the infant to search for it. Despite just having seen the object being hidden at the new B location, infants between 8 and 12 months of age frequently look for it under container A where it had been previously hidden. This perseverative search error continues to be of theoretical interest for researchers of cognitive development (2–6).

A wide range of explanations have been proposed to account for this response bias. According to Piaget's original hypothesis (1), the A-not-B error reflects young infants' as yet incomplete comprehension of object permanence. Piaget believed that the infant conceives the appearance of the object under container A to be an inherent consequence of the search response itself. More recent accounts of the perseverative bias have focused on the motor response involved in searching at location A, which has been primed during its repeated execution after the initial hiding trials. In these accounts, the A-not-B error is usually ascribed to a deficit in inhibitory control over a previously rewarded motor response (7) or to constraints on short-term memory (8), or both (9). Alternatively, the perseverative response has been seen as driven by a response bias established in the visuomotor response execution system during repeated A-trials (10). Others point out that simply observing another person reaching to location A repeatedly is in itself sufficient to elicit the A-not-B error. In this view, infants' errors do not reflect their difficulty with response inhibition,

but are due to an attentional bias to the location where the previously observed manual responses have been directed (11). A more recent explanation suggests that observing repeated hiding events at location A leads to automatic motor simulation (covert imitation) of the action through the activation of the mirror neuron system (12).

In contrast to the focus of such accounts on infants' repeated responses directed at container A, we have examined the perseverative error from a different perspective by exploring the potential role of the communicative demonstration context of the task. The A-not-B task normally involves face-to-face interaction, in which object hiding is accompanied by the demonstrator's ostensive and referential signals [such as eye contact, infant-directed speech, addressing the baby by name, and pointing at and/or looking back and forth between the hiding location and the infant (13)]. Recent findings indicate that ostensive-referential communicative signals can play an interpretation-modulating role, leading to selective encoding of different aspects of action demonstrations in social learning tasks [e.g., (14–17)]. Csibra and Gergely (13, 18) hypothesized that ostensive signals induce a receptive "pedagogical learning stance" in the infant, involving a built-in interpretive bias of generalizability. This bias assumes that ostensively communicated manifestations are more likely to convey semantic or generic information about the referent than episodic information that obtains only in the here-and-now.

The hiding events in the standard A-not-B task can be interpreted both as indicating episodic information about the referent's current location ("the target object is now under container A") and as communicating information about some generalizable property of the referent kind (e.g., "this type of object is usually found in container A"). We hypothesized that in the A-not-B paradigm, the interpretive bias of generalizability may result in a pragmatic misinterpretation of the object-hiding actions as potential teaching demonstrations. As a result, the infant would tend to

infer and learn some generalizable information, such as "this kind of object is to be found in container A" or "we keep toys in container A." According to this hypothesis, misinterpretation of the ostensibly communicated hiding events leads infants to commit the perseverative search error during B test trials. We therefore predicted that in a noncommunicative action observation condition, which lacks ostensive signals but provides experience with repeated motor search responses directed at container A, the perseverative search error should be reduced.

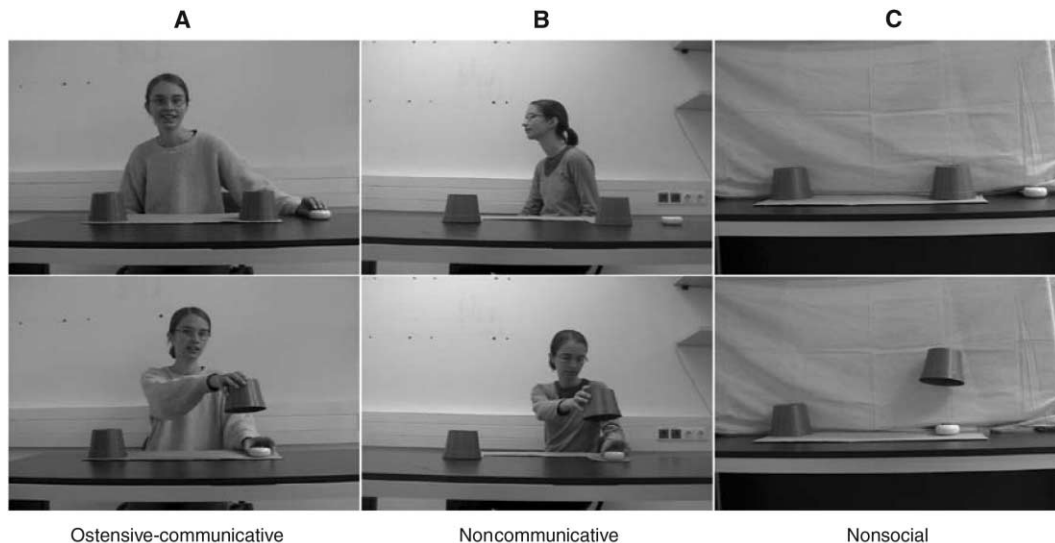
To test this hypothesis, we examined infants' object search behavior in the A-not-B task while varying the presence or absence of the social-communicative context of the hiding events. Three groups of 10-month-old infants (14 in each) were tested. In the ostensive-communicative context (OC) (Fig. 1A), the demonstrator established eye contact with the baby, smiling at and addressing him or her in infant-directed speech (saying "Hello baby, look here!"). Then she repeatedly hid a toy object under container A while shifting her eye gaze back and forth between the infant and the container to direct and share the infant's attention toward the object-hiding action. In the noncommunicative context (NC) (Fig. 1B), the demonstrator's face and torso were oriented 90° away from the infant and, while her hands were just as visible during the repeated hiding actions as in the OC condition, she never looked at or communicated with the infant in any way while hiding the object. In the nonsocial context (NS) (Fig. 1C), the demonstrator acted from behind a curtain and only the object's movements were visible to the infant. In each condition, after a 4-s delay following the hiding events, the demonstrator slid the cardboard sheet with the two containers closer to the infant and then waited until a search response was executed. The toy was hidden four times at the first location (A-trials), then three times at the other location (B-trials) (19).

We analyzed the proportion of correct responses in both the A- and B-trials, as well as the

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Fig. 1. Experimental arrangement in the three hiding contexts: (A) ostensive-communicative task, (B) noncommunicative task, and (C) nonsocial task.



Ostensive-communicative

Noncommunicative

Nonsocial

Fig. 2. Proportion of correct searches (mean + SE) in A- and B-trials as a function of the hiding context. The 10-month-old infants received four A-trials followed by three B-trials. *** $P < 0.0001$, * $P < 0.05$.

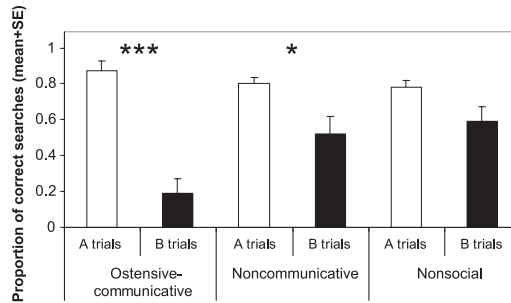


Table 1. Number of infants in the three different hiding contexts (14 in each group) committing at most one or more search errors (searching at location A) in the three B-trials.

Context	0 or 1 error	2 or 3 errors
Ostensive-communicative	2	12
Noncommunicative	8	6
Nonsocial	9	5

number of infants who committed the A-not-B error (searched more than once at location A in the B-trials) as a function of the hiding context. We found that the magnitude of the A-not-B error was considerably smaller in the noncommunicative and nonsocial conditions than in the traditional ostensive-communicative context (Fig. 2 and fig. S1). A two-way analysis of variance on the proportion of correct responses, with phase (A- versus B-trials) and hiding context (OC, NC, NS) as factors, showed more correct responses in the A-trials than in the B-trials ($F_{1,39} = 49.376$, $P < 0.0001$) and a significant interaction between these factors ($F_{2,39} = 8.041$, $P = 0.001$). This interaction was because the change of the proportion of correct searches from the A- to the B-trials differed across contexts. Whereas in the OC context the initial success rate of 0.88 in the A-trials dropped to 0.19 in the B-trials ($t_{13} = 8.917$, $P < 0.0001$), the drop was much smaller in the NC context (0.80 to 0.52, $t_{13} = 2.536$, $P = 0.025$) and was not statistically significant in the NS context (0.78 to 0.59, $t_{13} = 1.96$, $P = 0.072$). In addition, although the infants were similarly successful during the A-trials in all contexts ($F_{2,39} = 1.525$, $P = 0.23$), their search performance differed significantly across contexts in the B-trials ($F_{2,39} = 6.660$, $P = 0.005$). In this latter case, post hoc pairwise comparisons (Tukey-Cramer test) showed that infants searched the least correctly in the OC context (OC versus NO, $P < 0.05$; OC versus NS, $P < 0.01$).

Comparison of the number of infants committing the A-not-B error (Table 1) indicated a significant difference between demonstration conditions ($\chi^2 = 8.265$, $P = 0.016$). After having witnessed ostensive-communicative hiding demonstrations during the A-trials, 86% of the infants displayed the perseverative error during the B-trials. In contrast, the majority of infants in the other two contexts (NC, 57%;

NS, 64%) did not show a perseverative response pattern.

These results are not compatible with the currently widely accepted explanations for the A-not-B perseverative response bias, which attribute this robust developmental phenomenon to the dominance (and lack of inhibition) of the prepotent motor search response. Our results also challenge recent proposals that the motor priming of the prepotent response can be induced by simply observing the manual hiding actions directed at location A, mediated by the mirror neuron system (12), because the NC and OC contexts provided the same amount of visual (as well as motor) experience of the repeated manual hiding actions directed at container A.

Rather, we suggest that our results can be explained by the theory of natural pedagogy (13, 14), which proposes a special interpretation-modulating role for ostensive-referential signals in early social learning. The action demonstrations of the A-not-B paradigm can be interpreted either as a hide-and-search game, presenting the infant with episodic (here-and-now) information about the whereabouts of the object (correct interpretation), or as a kind of teaching session that conveys generalizable information about properties of the objects (toys or containers) for the infant to learn (incorrect interpretation). We propose that it is this latter kind of interpretation—mistakenly established during the ostensibly demonstrated A-trials—that remains dominant during the B-trials, leading to the erroneous perseverative search responses.

This conclusion does not invalidate the contribution of other cognitive factors to the A-not-B error identified by earlier studies. In our study, the perseverative error was reduced but did not completely disappear in the NC and NS contexts, which suggests that infants' search behavior also depends on their inhibitory, information processing, and memory skills (20–21). Had we not inserted a 4-s delay between hiding and searching, infants would have been likely to search for the toy at the correct location (22, 23). Thus, the decay of the accessibility of the short-term memory of target location for search actions is a necessary component of the search error. Similarly, the ostensive hiding demonstration may have generated higher cognitive load to be overcome in search behavior than did the NC and NS contexts (22). Although these accounts could explain why infants did not search at the correct location, they

predict random search rather than perseveration. However, it was only in the NS and NC conditions that infants' search pattern was close to 50%; in the OC condition, they tended to search more often at location A. The theory of natural pedagogy offers an explanation for this baffling tendency to perseverate: The communicative demonstration during the A-trials generates a semantic (and potentially long-term) memory trace that biases infants to search at the old location when they no longer have access to the decayed memory trace of the current location or when their information-processing capacity is overloaded. In addition, the primacy effect of semantic learning (as opposed to the recency effect on episodic memory) made it difficult for the infants to relearn the new location in B-trials.

Human infants are highly social creatures (24) who cannot help but interpret the ostensive communicative signals directed to them. Although such a disposition prepares them to efficiently learn from adults, in certain situations (e.g., the A-not-B task) it can also misguide their performance. Our demonstration of the social communicative determinants of infants' early tendency for perseveration in motor search tasks provides independent support for our general proposal (13) that sensitivity to ostensive-referential communication is a basic evolutionary adaptation that is fundamental to the emergence of human social cognition.

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Antigen Recognition by Variable Lymphocyte Receptors

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Variable lymphocyte receptors (VLRs) rather than antibodies play the primary role in recognition of antigens in the adaptive immune system of jawless vertebrates. Combinatorial assembly of leucine-rich repeat (LRR) gene segments achieves the required repertoire for antigen recognition. We have determined a crystal structure for a VLR-antigen complex, VLR RBC36 in complex with the H-antigen trisaccharide from human blood type O erythrocytes, at 1.67 angstrom resolution. RBC36 binds the H-trisaccharide on the concave surface of the LRR modules of the solenoid structure where three key hydrophilic residues, multiple van der Waals interactions, and the highly variable insert of the carboxyl-terminal LRR module determine antigen recognition and specificity. The concave surface assembled from the most highly variable regions of the LRRs, along with diversity in the sequence and length of the highly variable insert, can account for the recognition of diverse antigens by VLRs.

In the lamprey and hagfish, the only surviving jawless vertebrates, variable lymphocyte receptors (VLRs) play the major role in recognition of foreign antigens (1, 2). In contrast to the variable, diverse, and joining gene segments (VDJs) of immunoglobulins in jawed vertebrates, the jawless vertebrates have solved the receptor diversity problem by somatic DNA rearrangement of diverse leucine-rich repeat (LRR) modules into incomplete *vlr* genes. The resulting mature *vlr* genes encode an N-terminal LRR capping region (LRRNT), the first LRR (LRR1), up to seven 24-residue variable LRRs (LRRVs) (3), a terminal or end LRRV (LRRVe), a connecting peptide (CP), a C-terminal LRR capping region (LRRCT), and a threonine/proline-rich stalk region that connects the protein to a glycosylphosphatidylinositol (GPI) anchor and a hydrophobic tail (Fig. 1A) (1, 2, 4).

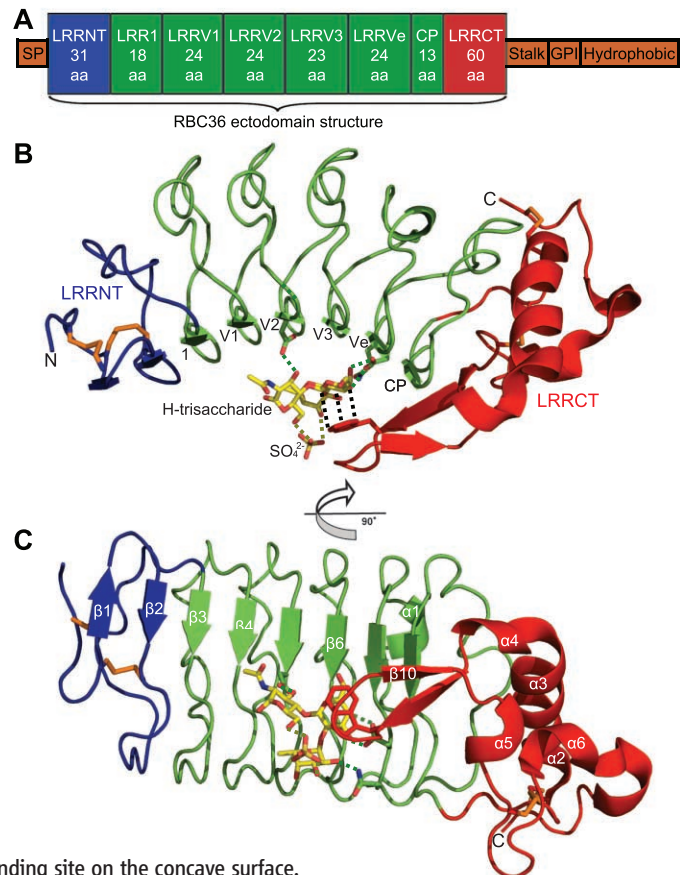
From these somatic gene rearrangements, a potential repertoire of about 10¹⁴ unique VLRs has been estimated (2), which compares favorably with the equivalent diversity attainable through VDJ recombination in antibodies. Different numbers and combinations of LRR modules, coupled with amino acid sequence variation in the LRR segments, thereby contribute to VLR diversity. The LRR repeats form a curved solenoid, as in Toll-like receptors (TLRs) (5, 6), and its concave surface has been suggested as the antigen-binding site from evolutionary, sequence, and mutational analyses (2, 7, 8). Crystal structures of three un-

liganded hagfish VLRs with different numbers of LRRV modules have been determined (7), whereas antigen-binding specificity [erythrocyte H-trisaccharide (9) and *Bacillus* collagen-like protein of *B. anthracis* (BclA) (8)] has been reported only for lamprey VLRs. However, the mode of

antigen recognition has not yet been determined in either system, nor has it been shown whether complementarity-determining region (CDR) equivalents are present in VLRs that would endow them with specificity and affinity for any given antigen, as for antibodies.

We determined the crystal structure of the VLR RBC36 ectodomain (ECD) in complex with the H-trisaccharide derived from the H-antigen of human blood group O erythrocytes at 1.67 Å resolution by molecular replacement, using our lamprey VLR2913 crystal structure [Protein Data Bank (PDB) ID 2R9U]. Lampreys were previously shown to produce high-titer agglutinins against the H-antigens of human O erythrocytes (10, 11). When lampreys were immunized with human blood group O erythrocytes, they elicited VLRs that recognize the dominant H-trisaccharide antigen on Chinese hamster ovary cells transfected with 1,2-fucosyltransferase (9). H-antigens contain the characteristic disaccharide α -L-Fucp-(1 \rightarrow 2)- β -D-Galp-OR, where R is glycoprotein or glycolipid (12). The type II H-antigen trisaccharide, α -L-Fucp-(1 \rightarrow 2)- β -D-Galp-(1 \rightarrow 4)- β -D-GlcNacp-OH, was

Fig. 1. Overall architecture of the VLR RBC36-ECD in complex with the H-trisaccharide. **(A)** Schematic diagram of RBC36. Regions from left to right: signal peptide (SP), N-terminal LRR (LRRNT), five variable LRRs (LRR1, LRRVs), connecting peptide (CP), C-terminal LRR (LRRCT), threonine/proline-rich stalk region, GPI anchor, and hydrophobic tail. **(B)** Ribbon diagram of RBC36-ECD in complex with H-trisaccharide. LRRNT, LRRs, and LRRCT are colored blue, green, and red, respectively. Carbons, nitrogens, and oxygens of the H-trisaccharide are colored yellow, blue, and red, respectively. Disulfide bridges are shown in orange. Green dotted lines represent hydrogen bonds; black dotted lines indicate hydrophobic effects. **(C)** View rotated 90° from (B) that highlights the continuous β sheet and the H-trisaccharide binding site on the concave surface.



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