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Science **331**, 750 (2011);

DOI: 10.1126/science.1201463

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25. We thank M. S. Dresselhaus for encouragement, M. T. Lee and S. H. Shen for their assistance, and R. Greif for

discussions and critical reading of the manuscript. This research has been supported by the Office of Energy Efficiency and Renewable Energy of the U.S. Department of Energy. S.S.M. and X.C. also acknowledge support from the King Abdullah University of Science and Technology–University of California Academic Excellence Alliance. TEM work was performed at the National Center for Electron Microscopy, which is supported by the Office of Science, Office of Basic Energy Sciences of the U.S. Department of Energy.

Supporting Online Material

www.sciencemag.org/cgi/content/full/science.1200448/DC1
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References

15 November 2010; accepted 11 January 2011
Published online 20 January 2011;
10.1126/science.1200448

Complete Fourth Metatarsal and Arches in the Foot of *Australopithecus afarensis*

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The transition to full-time terrestrial bipedality is a hallmark of human evolution. A key correlate of human bipedalism is the development of longitudinal and transverse arches of the foot that provide a rigid propulsive lever and critical shock absorption during striding bipedal gait. Evidence for arches in the earliest well-known *Australopithecus* species, *A. afarensis*, has long been debated. A complete fourth metatarsal of *A. afarensis* was recently discovered at Hadar, Ethiopia. It exhibits torsion of the head relative to the base, a direct correlate of a transverse arch in humans. The orientation of the proximal and distal ends of the bone reflects a longitudinal arch. Further, the deep, flat base and tarsal facets imply that its midfoot had no ape-like midtarsal break. These features show that the *A. afarensis* foot was functionally like that of modern humans and support the hypothesis that this species was a committed terrestrial biped.

Although *Australopithecus afarensis* was primarily a terrestrial biped, there continues to be debate over the nature of its bipedality and the extent to which its morphology represents a compromise between terrestrial bipedality and arboreal locomotion. One of the key adaptations to a human-like striding bipedal gait is the evolution of permanent transverse and longitudinal pedal arches (1, 2). The arches, supported by bone and soft tissue, provide an important mechanism for shock absorption during the stance phase of gait (3) and a rigid lever at heel-off, as well as permit flexibility during locomotion at different speeds and across irregular terrain (3–6). Muscles that in apes adduct the hallux (such as the m. adductor hallucis and m. fibularis longus), in humans primarily support the pedal arches (1, 5). Permanent plantar arches are a key component of human bipedal walking and running because they contribute to the rigidity of the foot and provide an enhanced mechanical advantage during the propulsive phase of gait (1, 7–9). Extant apes, in contrast, exhibit pronounced midtarsal dorsiflexion during heel-off as a result of a mobile midfoot, which permits flexibility for negotiating variably oriented arboreal substrates [(8, 9) and a

recent review in (10)]. This break is greater in magnitude and is kinematically and anatomically distinct from the medial collapse seen in some humans (7, 11, 12). Therefore, determining the extent to which the foot of *A. afarensis* had permanent longitudinal and transverse pedal arches is key to deciphering the extent of its commitment to terrestrial bipedality.

Skeletal evidence for the presence of pedal arches in *A. afarensis* has been ambiguous, because

key bones from the midfoot have been lacking. The talus (specimens AL 288-1 and AL 333-147) shows a distinct facet for plantar calcaneonavicular (13) and cubonavicular ligaments (9, 13, 14), which are indicative of a human-like medial longitudinal arch. However, unlike in humans, a groove is present for the m. fibularis longus tendon on the plantar surface of the ectocuneiform (AL 333-79) in *A. afarensis*, as seen in apes, perhaps related to the lack of a transverse arch. Dorsal inclination of the tarsal facets has been interpreted to suggest the lack of longitudinal arches in *A. afarensis* (11, 12), and the well-developed navicular tuberosity is argued to be a weight-bearing structure in these hominins (15, 16).

Here we describe AL 333-160, a complete, nearly perfectly preserved fourth metatarsal of *A. afarensis* from Hadar, Ethiopia (Fig. 1). This specimen was recovered from the Hadar locality AL 333 in 2000 during sieving of eroded Denen Dora 2 submember surface deposits of the Hadar Formation. Since 1975, these deposits at the 333 locality have yielded more than 250 hominin fossils that eroded from an in situ horizon dated to ~3.2 million years ago (17). We assign AL 333-160 to *A. afarensis*, the only hominin species in an assemblage of >370 hominin specimens so far recovered from the Hadar Formation (18). Other partial metatarsals attributed to *A. afarensis* are known from Hadar (19), but none is complete enough to address the question

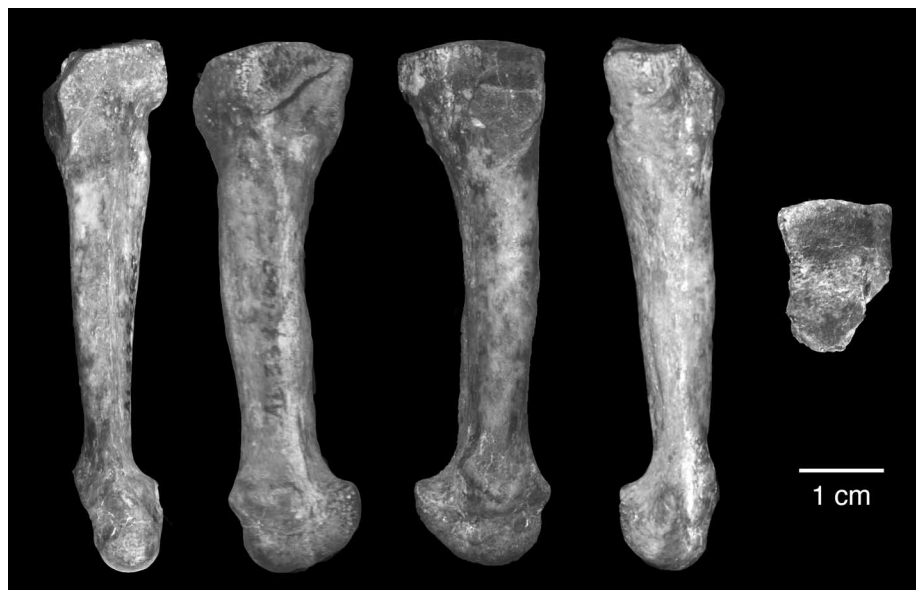


Fig. 1. AL 333-160 left fourth metatarsal in dorsal, lateral, medial, plantar, and proximal views.

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of pedal arches. The anatomy of a fifth metatarsal of *A. africanus* from Sterkfontein, South Africa (20, 21), is consistent with the presence of perma-

nent pedal arches, but the fourth metatarsal is the key element along the lateral column of the foot that differs between apes and humans and is

therefore the best test of the presence of permanent longitudinal and transverse arches in the foot.

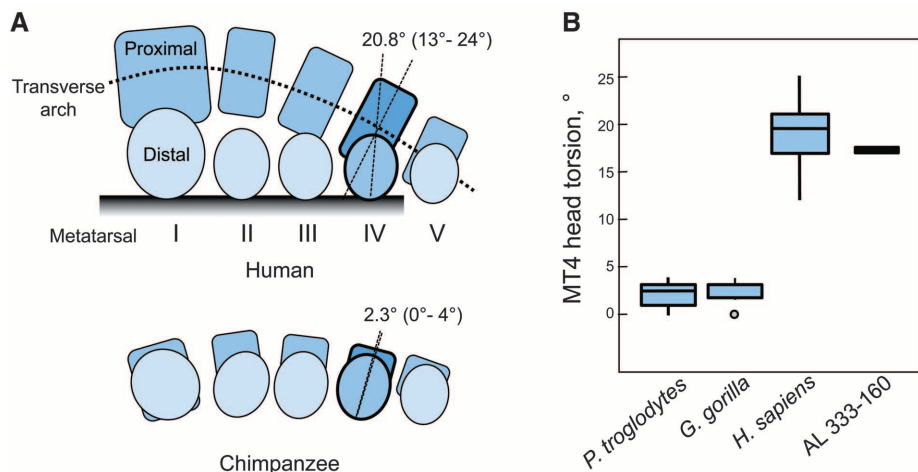
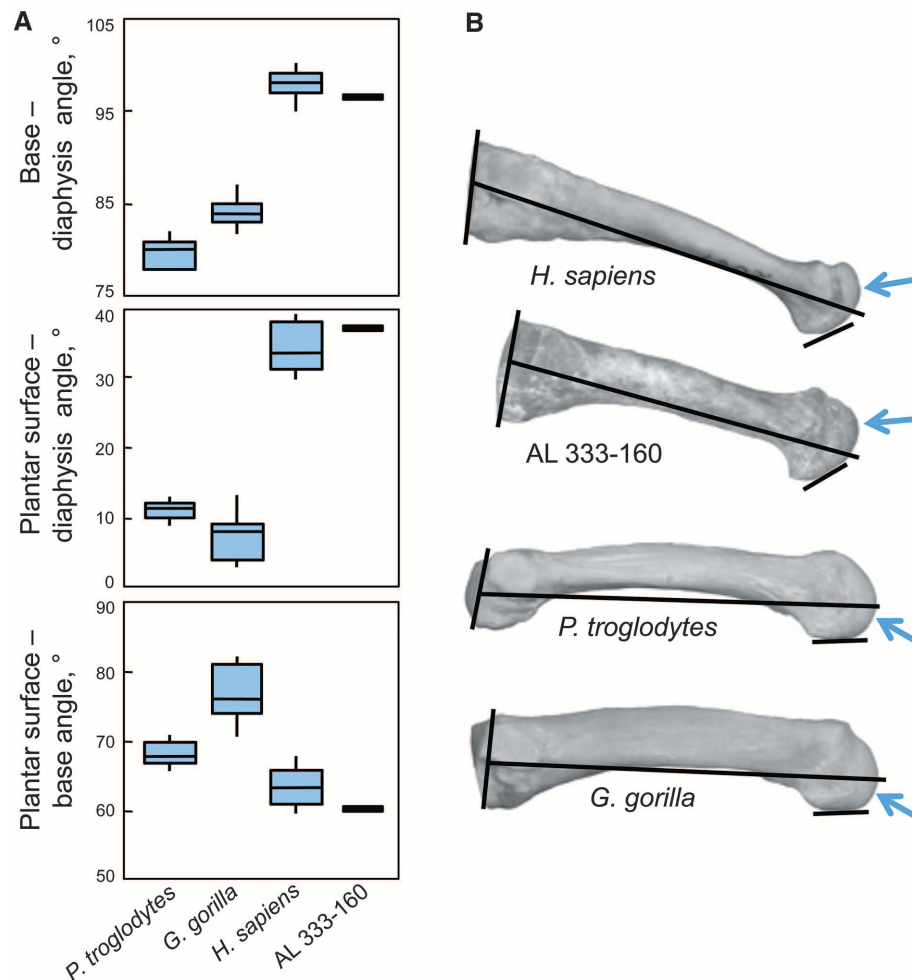


Fig. 2. (A) Schematic representation of metatarsal proximal (rounded rectangles) and distal (ovals) ends seen in distal view in a human above and a chimpanzee below. In both species, the metatarsal heads are in contact with the substrate. Because of the arch, the proximal ends of the human metatarsals are higher and situated in a transverse arch configuration (indicated by the dashed line). This results in axial torsion within the human fourth metatarsal of the head relative to the base, whereas this is not found in apes. [Modified from (23)] (B) Box plot of torsion values for chimpanzees, gorillas, humans ($N = 10$ individuals each), and AL 333-160, showing the distinct torsion in both hominins that is lacking in the apes. MT, metatarsal. Data are in table S1.

In AL 333-160, the metatarsal head is twisted laterally relative to the base, producing shaft torsion characteristic of modern humans (2) and later fossil hominins, including *Homo habilis* specimen OH 8 (22, 23) and the *H. erectus* foot bones from Dmanisi, Republic of Georgia (24). This torsion contrasts with the ape condition, in which the head and base exhibit minimal relative rotation (Fig. 2). Torsion allows the plantar surface of the metatarsal head to contact the ground in a foot with a strong skeletally supported transverse arch (2, 25, 26), an everted posture characteristic of a foot adapted for the modern human terminal-stance phase of gait, rather than the inverted foot postures of apes used in climbing. This degree of torsion of the AL 333-160 metatarsal demonstrates that a permanent bony transverse arch must have been present in the foot of *A. afarensis*.

In AL 333-160, the diaphysis is angled plantarily, rather than dorsally, relative to the base, as in humans and *H. habilis* [OH 8; see (11)] and unlike in African apes (Fig. 3). This morphology further indicates a permanent longitudinally arched posture of the foot, because the fourth metatarsal makes an angle of about 8° to the ground in a

Fig. 3. (A) Box plots of angular relations of the proximal and distal metatarsal ends to the diaphysis in chimpanzees, gorillas, humans, and AL 333-160. The proximal ends of hominin metatarsals are angled plantarily relative to the diaphysis, reflecting the average 8° of inclination of the metatarsal in normal arched posture, whereas that of the apes is oriented slightly dorsally. The flattened plantar portion of the hominin distal articular surface is inclined distally, also reflecting this posture and the habitual extension at this joint during bipedal locomotion, something also not seen in the apes who have this surface oriented directly plantarily. This distal plantar surface is also more distally oriented relative to the base in both hominins. In every case, AL 333-160 resembles humans only, strongly supporting the presence of arches in the *A. afarensis* foot. (B) Left fourth metatarsals of human, AL 333-160, chimpanzee, and gorilla in medial view, showing the orientation of bone ends and diaphysis. The blue arrows indicate the domed portion of the head. AL 333-160 resembles humans in having the doming along the dorsal articular margin, whereas the distal articular surface is domed more plantarily in the apes.



normal human foot (5). The metatarsal head in AL 333-160 is flattened along the plantar portion of its articular surface, which faces distally relative to the diaphysis rather than being parallel to the diaphysis as in extant apes, forming a large plantar surface-diaphyseal angle (Fig. 3). This reflects the overall more extended posture of the metatarsophalangeal joints in the hominins (2, 5, 23).

The AL 333-160 head exhibits another set of distinctive hominin apomorphies observed also in *Ardipithecus ramidus* (25), *Australopithecus* (14, 19, 27), and later hominins [reviews in (1, 22)]. It is domed dorsally in medial and lateral views (indicated by arrows in Fig. 3B), and there is a deep transverse gutter along the dorsal margin of the subchondral surface. In chimpanzees and gorillas, the domed portion of the head inclines plantarly, reflecting habitual loading in flexion. The hominin configuration seen in AL 333-160, and also in the AL 333-115 partial metatarsals (14, 19), would allow an increased range of dorsiflexion at the metatarsophalangeal joint as compared with apes, as well as habitual loading of the joint in extended postures that occur during the push-off and terminal phases of striding bipedal gait.

The lateral column of the human midfoot is relatively stiff, so that the mid- and hindfoot lift off the ground during gait simultaneously (1). In apes, however, dorsiflexion in the midfoot

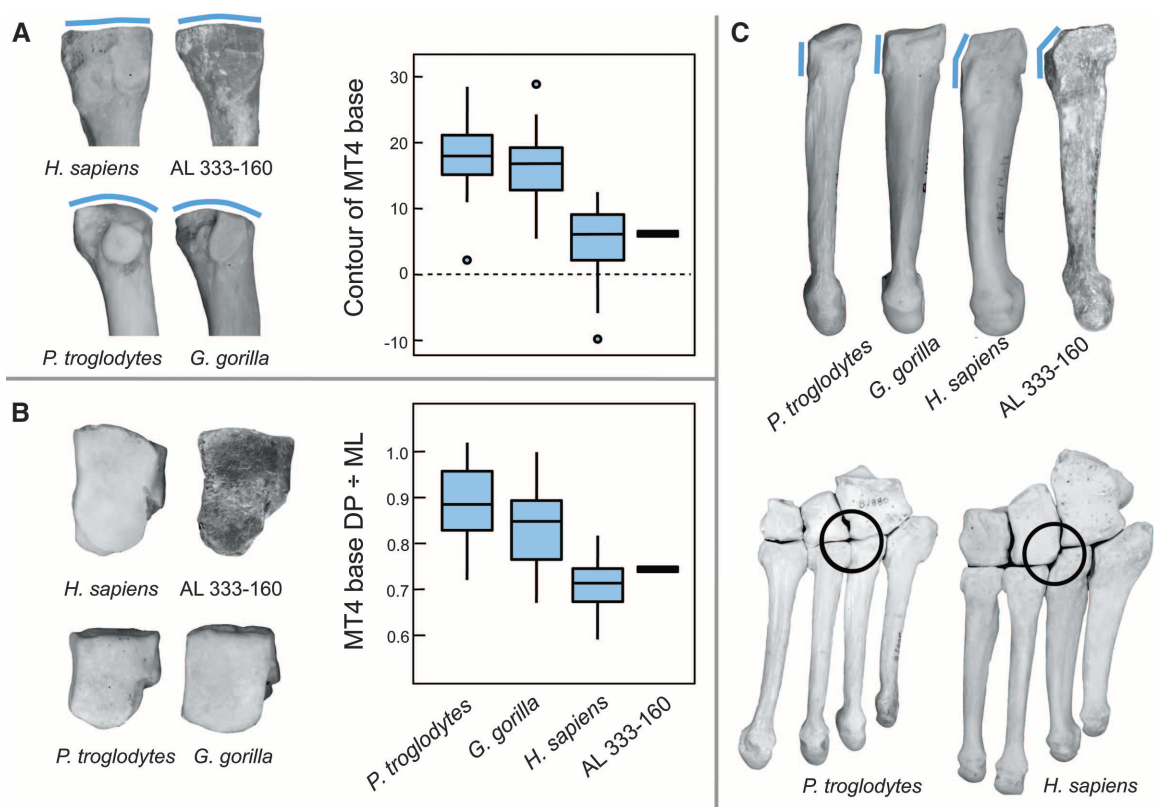
ensures that the heel leaves the substrate before the midfoot, a condition known as a “midtarsal break,” which can be up to 28° in magnitude (28). This dorsiflexion occurs primarily at the cuboid-metatarsal joints (10, 26, 29) and is distinct from the medial collapse in some human feet, which is far less pronounced and occurs to a variable degree at multiple joints (7, 11, 12). The transverse and longitudinal pedal arches and metatarsophalangeal dorsiflexion inferred from AL 333-160 signal an osteological pattern of midfoot stability and lateral foot rigidity unknown in the apes.

Dorsoplantar curvature of the lateral tarsometatarsal joint surfaces contributes to the distinctive midtarsal dorsiflexion in great apes (8, 10, 26, 29). These surfaces on the human proximal fourth and fifth metatarsals are flatter. The proximal articular surface of AL 333-160 is nearly flat (Fig. 4B), matching the mean of the modern human sample. Limited dorsiflexion at the lateral tarsometatarsal joints (10, 30), which would contribute to a relatively stiff lateral foot like that of modern humans, can be inferred for *A. afarensis*. AL 333-160 also has dorsoplantarly deep metatarsal bases, a condition also described for *Ardipithecus ramidus* (25) (Fig. 4B). This would limit dorsiflexion and plantarflexion at the lateral tarsometatarsal joints, additional evidence of a human-like relatively stiff lateral foot fundamentally different from that seen in apes.

A rigid lateral foot in *A. afarensis* is further suggested by the orientation of the facet for the lateral cuneiform on the base of the AL 333-160 fourth metatarsal (Fig. 4C), mirroring the complementary facet seen on the lateral cuneiform (14, 19). In *A. afarensis*, as in modern humans, *H. habilis* [OH 8 (31)], and the Dmanisi *H. erectus* feet (24), the lateral cuneiform is elongated, extending distally past the cuboid, so that it articulates with the proximomedial corner of the fourth metatarsal at an obliquely oriented facet (14, 19). In apes, the lateral tarsometatarsal joints are aligned in the same coronal plane in such a way that the distal end of the lateral cuneiform is coplanar with the fourth tarsometatarsal joint, and the oblique facet on the fourth metatarsal for the lateral cuneiform is absent (Fig. 4C), a configuration that facilitates dorsiflexion at the tarsometatarsal joints (10). Thus, even if there was more calcaneocuboid mobility in *A. afarensis* than in modern humans (32, 33), this was evidently not the case for the lateral tarsometatarsal joints [see also (34)].

Most researchers conclude that the 3.6-million-year-old footprints in the Upper Laetoli Beds at Laetoli, Tanzania, evince a medial longitudinal arch [for example, (35, but see (36)]. Although *A. afarensis* is the only hominin species represented by fossil remains in these beds at Laetoli, one objection to this species having made the prints is the purported absence of the medial

Fig. 4. (A) Proximal ends of left fourth metatarsals in medial view, showing the dorsoplantar contour of the distal end. The box plot shows measured curvature, measured as maximum distance of the proximal joint surface from a line drawn between dorsal and plantar articular margins, expressed as a ratio to dorsoplantar length, following (11). Data are from (11). All hominins have relatively flat surfaces, rather than the convex profile of apes. (B) Proximal view of left fourth metatarsals, showing the dorsoplantarly expanded articular surface in hominins as compared with apes. The box plot of the ratio of dorsoplantar to medio-lateral breadth shows the almost square proportion of apes, but the deep shape of the hominins. Data are in table S2. (C) Above, dorsal view of left fourth metatarsals, showing the articular facet for contact with the third metatarsal (vertical line) and the oblique articular facet for contact with the ectocuneiform in the hominins. Below, dorsal view of articulated cuboid, lateral, and medial cuneiforms and lateral metatarsals, showing



the articular configuration of the lateral cuneiform with the third and fourth metatarsals. In apes, the cuneiform is directly medial to the cuboid and does not contact the fourth metatarsal. Both hominins have lateral cuneiform contact and an obliquely oriented facet on the fourth metatarsal for the cuneiform.

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longitudinal arch in the Hadar foot (35, 37). The morphology of the AL 333-160 Hadar fourth metatarsal eliminates that objection.

The 4.4-million-year-old skeleton of *Ardipithecus ramidus* suggests that the transition to terrestrial bipedality occurred in the earliest hominins, while selection maintained adaptations in the foot for arboreal climbing and grasping (25). By at least 3.2 million years ago, the fundamental attributes of human pedal anatomy and function were in place. This includes the transformation of the first toe and associated musculature from a grasping structure to one designed for propulsion and shock absorption [review in (1)]. Evidence from the Hadar fourth metatarsal adds to this human-like portrait of permanent longitudinal and transverse bony arches in the sole of the foot. The evolutionary trajectory suggested by these fossil remains makes it unlikely that selection continued to favor substantial arboreal behaviors by the time of *A. afarensis*.

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The authors thank the members of the Hadar Research Project (1990–2004) and the Hadar Paleoanthropology Field School (2007 and 2009) for their dedication and hard work, and the directors and staff of the National Museum of Ethiopia, Cleveland Museum of Natural History, and National Museums of Kenya for facilitating the analytical research reported here. Fieldwork permissions were kindly granted by the Authority for Research and Conservation of Cultural Heritage, Ethiopian Ministry of Culture and Tourism, and the Culture and Tourism Bureau of the Afar Regional State government. We thank J. DeSilva, J. M. Plavcan, and G. Schwartz for helpful comments. The analytical research was supported by NSF (grants NSF SBR-9601025 and NSF BCS-0333296), the University of Missouri Research Board and University of Missouri Research Council, and the Institute of Human Origins at Arizona State University.

Supporting Online Material

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Tables S1 and S2

9 December 2010; accepted 12 January 2011
10.1126/science.1201463

Embryological Evidence Identifies Wing Digits in Birds as Digits 1, 2, and 3

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The identities of the digits of the avian forelimb are disputed. Whereas paleontological findings support the position that the digits correspond to digits one, two, and three, embryological evidence points to digit two, three, and four identities. By using transplantation and cell-labeling experiments, we found that the posteriormost digit in the wing does not correspond to digit four in the hindlimb; its progenitor segregates early from the zone of polarizing activity, placing it in the domain of digit three specification. We suggest that an avian-specific shift uncouples the digit anlagen from the molecular mechanisms that pattern them, resulting in the imposition of digit one, two, and three identities on the second, third, and fourth anlagen.

The morphology of the hand of tetrapods is derived from a five-fingered plan, the pentadactyl limb. In many tetrapods, some of the digits have been secondarily lost. Consequently, knowing which digits are present is a characteristic used to infer phylogenetic relationships between lineages. Close relationship between theropod dinosaurs and birds is evident, but the identities of avian hand digits remain controversial. Basal omithischian dinosaurs, such as *Heterodontosaurus*,

possessed a five-digit hand. In the process of the tetrapod evolution, the posterior two digits (digits D4 and D5) (1) were lost, such that later theropods like the maniraptoran *Deinonychus* had only D1 to D3 (2–4). Given the known relationship between theropods and early birds, such as *Archaeopteryx*, paleontological evidence suggests that the digit identity of the avian wing is D1, D2, and D3. In contrast, embryological evidence based on condensation patterns of digits suggests that the modern bird wing comprises the D2, D3, and D4 of the pentadactyl ground state (5–8). In general, the fourth digit is the first visible digit (FVD) of tetrapod embryo development and is part of what has been termed the primary limb axis, which is aligned with the extension of the posterior

zeugopod and the posterior basal autopod (6). In the chick embryo, the FVD occupies the posteriormost position in the three-digit chick forelimb but is still spatially aligned with the primary axis. Thus, the embryological view is that the FVD in the chick forelimb bud is designated as the fourth digit (6). To resolve the apparent disagreement between paleontological and embryological views, we investigated the early development of the posteriormost digit in the chick embryo (9).

Recent studies suggest that digit-specific developmental mechanisms determine digit identity. In the five-digit mouse limb bud, D4 and D5 and a posterior portion of D3 originate from descendants of *shh*-expressing zone of polarizing activity (ZPA) cells (10). Thus in the mouse, the FVD is derived from descendants of *shh*-expressing ZPA. In contrast, despite the ability of the ZPA of the chicken forelimb to induce all subsequent digits, it does not contribute to any digits when implanted into the host limb bud (Fig. 1, D and E) (11–13). This discrepancy may be attributable to the difference in digit numbers in mouse and chick limbs and thus provides an opportunity to further explore digit identity in the avian wing.

To examine the contribution of ZPA cells to subsequent digits on ectopic implantation, we performed a swapping transplantation of three-digit forelimb and four-digit hindlimb ZPAs in chick embryos (fig. S1) (13, 14). We used chick embryos at stages 21/22 and 22 as donors for the ZPA grafts, because it is at these stages that autopod specification begins in both forelimb and hindlimb (15–17). Chick hindlimbs that received forelimb ZPA developed only hindlimb digits in a duplicated digit

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ERRATUM

Post date 15 April 2011

Reports: "Complete fourth metatarsal and arches in the foot of *Australopithecus afarensis*" by C. V. Ward *et al.* (11 February, p. 750). In Fig. 4B, the y axis should have been labeled "MT4 base ML/DP," not "MT4 base DP/ML."

LETTER TO THE EDITOR

A rare anatomical variation newly identifies the brains of C.F. Gauss and C.H. Fuchs in a collection at the University of Göttingen

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Sir, Recently, Falk *et al.* (2013) analysed original photographs of the brain of Albert Einstein in an article published in *Brain*. The authors state that

'...we also hope that our identifications will be useful for workers interested in comparing Einstein's brain with preserved brains from other gifted individuals, such as the German mathematician Carl Friedrich Gauss (1777–1855)...'

Since 1855 the brain of Carl Friedrich Gauss has been kept as part of a small collection of preserved (elite) brains at the University of Göttingen, currently (since 1995) in the Institute of Ethics and History of Medicine. Shortly after Gauss's death in 1855, his brain was dissected—with authorization and under the restriction to be only used for scientific studies—by a group of experts led by Rudolf Wagner, a friend of Gauss and physiologist at the University of Göttingen. Wagner published two scientific studies, in which he described a variety of brains using different metrics, such as total brain weight or volume (Wagner, 1860, 1862). In the 1860 work he specifically focused on the convolutions of the cortex of 'intelligent men' considering this a novel and promising approach to assess differences between individual brains, rather than the somewhat crude measures of brain weight and volume. The descriptions of both studies are complemented by a set of copper engravings (Wagner, 1860) and lithographs (Wagner, 1862) made by H. Loedel, depicting the studied brains with great precision and naturalistic accuracy.

In 1998, in parallel with a necessary renewal of the fixative used to preserve the brain in a glass jar labelled 'C.F. G__s', structural

MRI was conducted by our group for documentary reasons. A detailed account of the procedures as well as an MRI reconstruction of the cortical surface was reported (Haenicke *et al.*, 1999; Wittmann *et al.*, 1999). In a letter to *Science*, Frewer and Hanefeld (2000) referred to these MRI results in relation to findings from the brain of Albert Einstein, stating that the Gauss brain does not share the lack of the parietal operculum.

Recent high-resolution functional MRI studies of the primary somatosensory cortex in our laboratory (Schweizer *et al.*, 2008) have brought the rare condition of a divided central sulcus to our attention (Alkadhi and Kollias, 2004). It is caused by an elevated *pli de passage fronto-parietal moyen* (Broca, 1888), which normally represents a deep convolution in the fundus of the central sulcus connecting the pre- and postcentral gyrus. In some rare cases this deep convolution extends to the surface of the brain, presenting itself as a connective structure between the two gyri. This infrequent anatomical variation of a divided central sulcus can clearly be seen in the MRI surface reconstruction of the left hemisphere of the brain in our earlier publications (Haenicke *et al.*, 1999; Wittmann *et al.*, 1999).

The historical first description of 'bridges connecting the two central convolutions' was indeed made by Rudolph Wagner (1862). Although these bridges are virtually identical to the divided central sulcus seen in our MRI surface reconstructions of the believed-to-be Gauss brain, Wagner's description was unambiguously assigned to the brain of the famous physician Conrad Heinrich Fuchs (1803–1855), who died in the same year as Gauss (Wagner, 1862).

Subsequent inquiries at the University of Göttingen revealed a glass jar labelled 'C.H. F__s' similar to the glass jar in which the

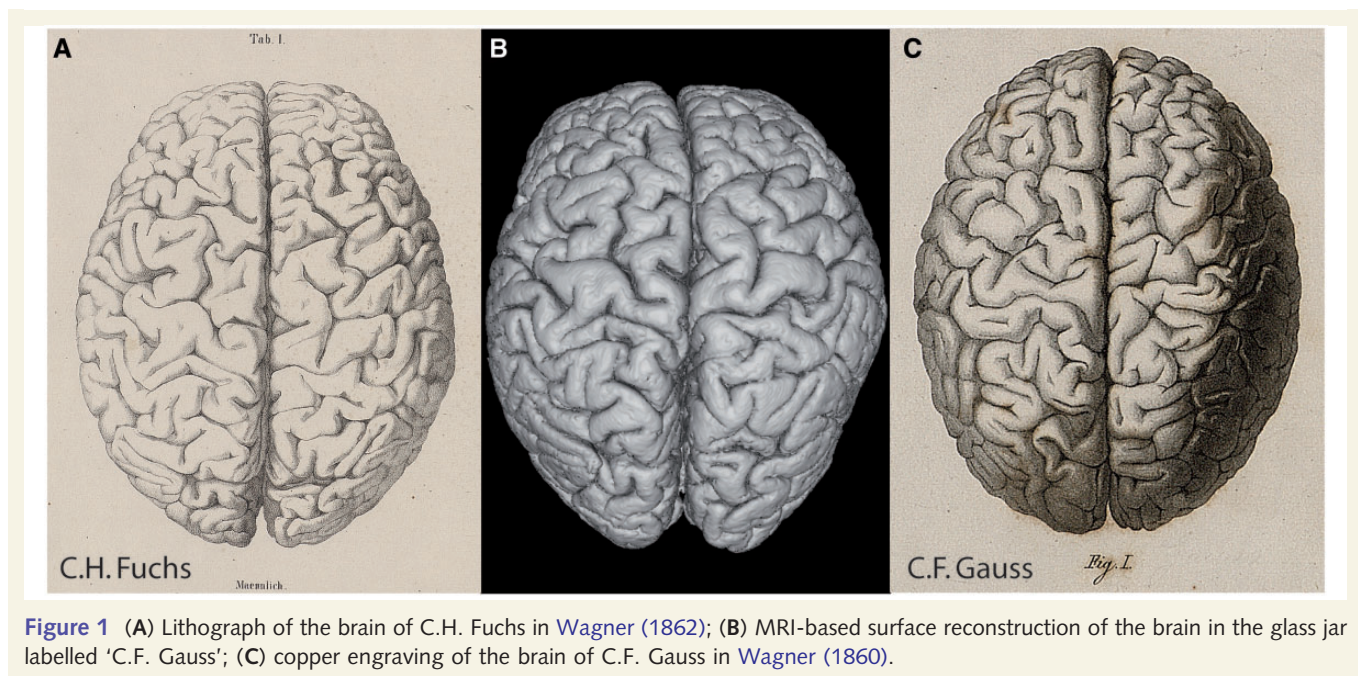


Figure 1 (A) Lithograph of the brain of C.H. Fuchs in Wagner (1862); (B) MRI-based surface reconstruction of the brain in the glass jar labelled 'C.F. Gauss'; (C) copper engraving of the brain of C.F. Gauss in Wagner (1860).

brain of C.F. Gauss is kept, both most likely originally labelled by Rudolf Wagner. Meticulous comparison of the two brains in these jars with the original copper engravings and lithographs of Wagner (1860, 1862) have now demonstrated that the brain in the jar labelled 'C.F. Gauss' is identical to the brain of C.H. Fuchs as shown in the lithographs of Wagner (1862) (Fig. 1). Moreover, the brain in the jar labelled 'C.H. Fuchs' is identical to the brain of C.F. Gauss as documented in the copper engravings of Wagner (1860). These observations prove that the brains have been stored in the wrong jars, and that, consequently, our MRI data recorded in 1998 (Haenicke *et al.*, 1999; Wittmann *et al.*, 1999) do not show the brain of C.F. Gauss, but rather the brain of C.H. Fuchs.

At this stage, it is still unclear when and under which circumstances the brains were placed in the wrong jars. Circumstantial evidence points to a mistake very early in history. In particular, the son of Wagner, Hermann Wagner, studying mathematics, published his doctoral thesis (Wagner, 1864) about a new approach to determine the dimension of the cortical brain. The data for his thesis were gathered from the brains of C.F. Gauss, C.H. Fuchs, a woman, and a craftsman. This situation would certainly favour an accidental mix-up of the two brains.

Our serendipitous finding now allows for a proper identification of the two brains in agreement with the detailed copper engravings of the brain of C.F. Gauss in Wagner (1860) and the detailed lithograph of the brain of C.H. Fuchs in Wagner (1862). Both of our earlier publications (Haenicke *et al.*, 1999; Wittmann *et al.*, 1999) will need to be corrected, in the sense that the investigated brain was not the brain of C.F. Gauss but that of C.H. Fuchs. The 'rediscovery' of the brain of C.H. Fuchs also provides the opportunity to conduct a more detailed investigation of the historical

first description of a divided central sulcus (Schweizer *et al.*, in preparation).

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Young infants have biological expectations about animals

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Contributed by Rochel Gelman, July 29, 2013 (sent for review May 7, 2013)

What are the developmental origins of our concept of animal? There has long been controversy concerning this question. At issue is whether biological reasoning develops from earlier forms of reasoning, such as physical and psychological reasoning, or whether from a young age children endow animals with biological properties. Here we demonstrate that 8-mo-old infants already expect novel objects they identify as animals to have insides. Infants detected a violation when an object that was self-propelled and agentive (but not an object that lacked one or both of these properties) was revealed to be hollow. Infants also detected a violation when an object that was self-propelled and furry (but not an object that lacked one or both of these properties) either was shown to be hollow or rattled (when shaken) as although mostly hollow. Young infants' expectations about animals' insides may serve as a foundation for the development of more advanced biological knowledge.

infant cognition | conceptual development | self-propulsion | agency

By the end of the preschool years, children possess considerable biological knowledge. In particular, they expect the insides of animals to be different from those of artifacts (1, 2); they realize that the insides of an animal are essential for its functioning (e.g., a dog cannot bark after its insides are removed) (3, 4); and they are beginning to understand that certain behaviors, such as eating and drinking, are necessary to maintain the continued functioning of animals and their insides (5, 6). This biological knowledge is often characterized as a vitalistic biology, in which internal organs and their workings sustain the vitality or life force of animals (7–10). A few facets of this vitalistic biology are already in place by the start of the preschool years. Thus, although 3-y-old children lack specific knowledge about the insides of animals (1, 2), they do expect these insides to differ from those of artifacts. When asked whether a pig has the same kinds of insides as a cow or a piggy bank, for example, 3-y-olds are more likely to select the cow (3). Similarly, when told that dogs have “andro” inside, 3-y-olds are more likely to project this novel property to other animals (including mammals and nonmammals) than to artifacts (11).

Does young children's vitalistic biology have roots in infancy? Do infants possess abstract expectations about animals that could lay the foundations for the acquisition of more sophisticated biological knowledge? Below, we consider two broad hypotheses concerning this issue; we refer to them as the “nonbiological” and the “biological” hypotheses.

According to the nonbiological hypothesis, infants do not endow animals with vitalistic or biological properties: animals are simply entities that are self-propelled and agentive [for infants, these two properties are conceptually distinct (12–14); objects may be self-propelled without being agentive, and they may be agentive without being self-propelled]. Proponents of the nonbiological hypothesis differ greatly in their theoretical views on how infants come to understand self-propulsion and agency. To illustrate, consider two such views: the core-domain and image-schema views. According to the core-domain view (15), infants' concept of self-propulsion is part of the skeletal explanatory framework that underlies core physical reasoning: when a novel object gives evidence that it is capable of autonomous

motion (e.g., begins to move on its own), infants attribute to the object an internal source of energy, and they appreciate that the object may use its energy to reverse course, resist efforts to move it, and so on (16). Similarly, infants' concept of agency is part of the skeletal explanatory framework that underlies core psychological reasoning: when a novel object provides evidence that it has autonomous control over its actions (e.g., responds contingently to events in its environment), infants attribute to the object motivational, epistemic, and other internal states, and they use these states to predict and interpret the object's actions (17). In contrast, according to the image-schema view (18), infants' concepts of self-propulsion and agency are formed by a perceptual-meaning-analysis mechanism that redescribes spatiotemporal information into meaningful iconic representations. Thus, self-propelled objects are those that start moving by themselves, without contact with other objects, whereas agentive objects are those that interact contingently with other objects, again without contact. In the image-schema view, infants have no notion of internal energy or internal states; these concepts are acquired later in development as enrichments of primitive spatial concepts. Despite their marked differences, however, both the core-domain and image-schema views assume that animals are, for infants, no more than self-propelled agents.

This assumption contrasts with the biological hypothesis, which admits the possibility that infants ascribe to entities that are self-propelled and agentive additional properties that are vitalistic or biological in nature (19–22). What might these biological properties be? One proposal, put forth by Gelman (19), is that infants are born with an “innards” principle: self-propelled agents have insides that make possible their behavior. According to Gelman (19), “the principle is neutral with respect to the nature of what a child or anyone may think is in the inside.” The innards principle is, of course, consistent with the findings on vitalistic

Significance

We provide an experimental demonstration that young infants possess abstract biological expectations about animals. Our findings represent a major breakthrough in the study of the foundations of human knowledge. In four experiments, 8-mo-old infants expected novel objects they categorized as animals to have filled insides. Thus, infants detected a violation when objects that were self-propelled and agentive were revealed to be hollow, or when an object that was self-propelled and furry rattled when shaken, as though mostly hollow. We describe possible characterizations of infants' expectations about animals' insides, including a characterization that emphasizes human predator-prey adaptations. We also discuss how infants' expectation that animals have insides lays a foundation for the development of more advanced biological knowledge.

Author contributions: P.S., D.W., R.B., and R.G. designed research; P.S., D.W., and R.B. performed research; P.S., D.W., and R.B. analyzed data; and P.S., D.W., R.B., and R.G. wrote the paper.

The authors declare no conflict of interest.

See Commentary on page 15857.

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biology mentioned earlier: children might at first simply expect animals to have insides, and with experience they might gradually learn how the insides of animals differ from those of artifacts (1), how the insides of one kind of animal differ from those of another kind of animal (23), and so on. In line with the innards principle, Gelman (19) found that when children age 3 and older were queried about the insides of various artifacts and animals, they sometimes said that an artifact had nothing on the inside, but they never said that an animal had nothing on the inside (see also refs. 24 and 25).

Is the nonbiological or the biological hypothesis correct? Do infants construe animals simply as self-propelled agents, or do they endow animals with additional, biological properties? One way to address these questions is to examine whether infants expect novel self-propelled agents to have insides, in accordance with the innards principle. Therefore, we used the violation-of-expectation method to test whether infants would detect a violation when a novel object that was self-propelled and agentive—but not an object that lacked one or both of these properties—was revealed to be hollow. Because there is considerable evidence that infants in the second half-year are sensitive to various cues for self-propulsion and agency (12, 26), our experiments focused on 8-month-old infants. We reasoned that positive results would support the biological hypothesis by demonstrating that young infants immediately endow novel self-propelled agents with vitalistic, biological properties. Such results would be unique in providing an experimental demonstration that abstract biological expectations about animals are present in the first year of life.

Although no prior experiment had examined whether infants expect animals to have insides, previous findings with 14-month-olds indicated that, when shown novel objects with eyes and visible insides, infants do notice these insides. Thus, infants assigned perceptually different objects to the same category if they possessed similar insides (27); infants readily formed an association between a transparent object's self-propelled motion and the presence of an internal part (28); and infants also readily associated a transparent object's particular style of self-propelled motion with the color of its internal part (28). Broadly construed, these findings suggested that infants attend to the insides of animals. Building on these findings, we asked in four experiments whether 8-month-old infants would expect novel objects they identified as animals to have insides. All of the experiments followed the same general design. During the familiarization phase, infants were introduced to two novel objects; across conditions, we varied whether or not the objects were capable of self-propulsion and agency. During the test phase, the objects were rotated (Exps. 1–3) or shaken (Exp. 4) to assess infants' expectations about their insides.

In Exp. 1, 8-month-old infants from English-speaking families ($n = 36$) were assigned to a self-propelled/agentive condition or a nonself-propelled/nonagentive condition. Infants watched live events involving two novel objects: a large can covered with alternating stripes of red and gray yarn and a large box covered with beige paper and varying round patches of blue cloth with multicolored dots. All infants received two familiarization trials, two pretest trials, and two test trials, one with the can and one with the box; half of the infants received the can trial first in each pair of trials, and half received the box trial first. Only the familiarization trials differed between the two conditions. Each familiarization trial had an initial phase and a final phase; looking times during the two phases were computed separately. At the beginning of the (76 s) initial phase of the can trial in the self-propelled/agentive condition (Fig. 1*A*), the can rested at the center of the apparatus floor. To start, the can moved in a slight bouncing manner back and forth across the floor and then returned to its original position [this displacement lasted about 16 s and served to establish that the can was self-propelled (16)]. Next, a female experimenter opened a window in the back wall of the apparatus; the can then initiated a "conversation" by quacking at the experimenter, who responded contingently in

English [this exchange lasted about 49 s and served to demonstrate that the can was agentive (17)]. Finally, the experimenter left, closing her window behind her. During the final phase of the trial, the can rested at the center of the apparatus, and infants watched this paused scene until the trial ended. The box familiarization trial was identical except that the box moved in a slight zigzag manner and beeped at the experimenter. Infants in the nonself-propelled/nonagentive condition (Fig. 1*B*) received similar familiarization trials except that the can and box remained stationary [thus providing no evidence that they were self-propelled (16)], and the experimenter remained silent in response to the can's quacks or the box's beeps [thus providing no evidence that they were agentive (14)].

Next, all infants received the can and box pretest trials (Fig. 1*E*), which served to introduce the actions performed in the test trials. In each trial, the experimenter lifted the can or box with both hands, tilted it right and left twice, returned it to the apparatus floor, and then repeated this entire (12 s) sequence until the trial ended. Finally, all infants received the can and box test trials (Fig. 1*F*). These trials were identical to the pretest trials except that, before tilting the can or box from side to side, the experimenter rotated it to reveal its bottom to the infant. When the objects were rotated, infants could see that one was hollow, like an inverted bowl (hollow trial), whereas the other one was closed, like a block (closed trial). For half the infants in each

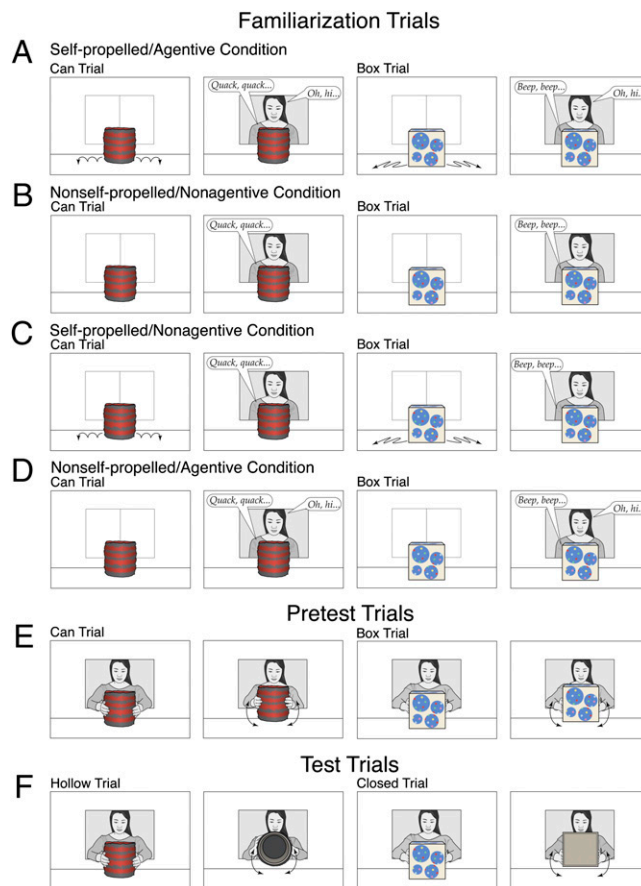


Fig. 1. Schematic drawing of the events shown in Exps. 1 and 2. In Exp. 1, the can and box were either self-propelled and agentive (*A*) or neither self-propelled nor agentive (*B*). In Exp. 2, the can and box were self-propelled and agentive (*A*), self-propelled but nonagentive (*C*), or nonself-propelled but agentive (*D*). Whether the can trial or the box trial was shown first in the familiarization (*A–D*), pretest (*E*), and test (*F*) trials was counterbalanced across infants in each condition; whether the can or the box was hollow in the test trials was also counterbalanced across infants in each condition.

condition, the can was hollow and the box was closed; for the other infants, the reverse was true. Preliminary analyses of the test data in this report revealed no interactions of condition and trial with infants' sex; the data were therefore collapsed across this factor in subsequent analyses.

Infants' looking times during the test trials (Fig. 2) were analyzed by means of an ANOVA with condition and order as between-subject factors and trial as a within-subject factor. The Condition X Trial interaction was significant, $F(1, 32) = 6.11$, $P = 0.019$ [no such interaction was found in an analysis of the final phases of the familiarization trials or in an analysis of the pretest trials, both $F(1, 32) < 1$]. Planned comparisons revealed that in the self-propelled/agentive condition, infants looked reliably longer during the hollow than the closed trial, $F(1, 32) = 10.08$, $P = 0.003$; 14 of 18 infants showed this pattern. In contrast, in the nonself-propelled/nonagentive condition, infants looked about equally during the two trials, $F(1, 32) < 1$; 7 of 18 infants looked longer at the hollow event. Thus, infants detected a violation when the can and box were shown to be hollow, but only if they were self-propelled agents; if the objects were neither self-propelled nor agentive, infants held no expectations about whether they should have insides.

Exp. 2 investigated the specificity of infants' expectations about what objects should have insides. According to the innards principle, infants should expect novel objects that are both self-propelled and agentive to have insides, but they should hold no expectation for objects that are only self-propelled or only agentive. To evaluate this prediction, additional 8-mo-old infants from English-speaking families ($n = 54$) were assigned to one of three conditions. The self-propelled/agentive condition was identical to that in Exp. 1 (Fig. 1A). The other two conditions were similar, except that in the familiarization trials, either the experimenter remained silent [self-propelled/nonagentive condition (Fig. 1C)], or the can and box remained stationary [nonself-propelled/agentive condition (Fig. 1D)].

Analysis of infants' looking times during the test trials (Fig. 2) revealed a significant Condition X Trial interaction, $F(2, 48) = 3.64$, $P = 0.034$ [no such interaction was found in an analysis of the final phases of the familiarization trials, $F(2, 48) < 1$, or in an analysis of the pretest trials, $F(2, 48) = 1.28$, $P = 0.289$]. In the self-propelled/agentive condition, as before, infants looked reliably longer during the hollow than the closed trial, $F(1, 48) = 7.82$, $P = 0.007$; 14 of 18 infants showed this pattern. In contrast, infants looked about equally during the two trials in both the self-propelled/nonagentive and nonself-propelled/agentive conditions, both $F_s < 1$; 8 of 18 infants in self-propelled/nonagentive condition and 9 of 18 infants in the nonself-propelled/agentive condition looked longer during the hollow trial. Thus, infants expected the can and box to have insides only if they were self-propelled and agentive; if they lacked either property, infants held no expectations about their insides.

The results of Exps. 1 and 2 indicated that when a novel object gives evidence that it is capable of both autonomous motion and control, young infants identify it as an animal and immediately expect it to have insides, in accordance with the innards principle. These results provided direct support for the biological hypothesis by demonstrating that young infants possess abstract biological expectations about animals. Exp. 3 sought to provide converging evidence for these conclusions: it examined whether young infants would also expect novel animals identified via learned predictive cues to have insides.

Proponents of both the nonbiological and biological hypotheses assume that, with experience, infants learn to use details of surface appearance and form as cues that novel objects are animals (this cue-learning process enables infants to rapidly identify novel animals without having to wait for evidence of autonomous motion and control). For example, previous research indicates that by 7 mo of age, infants already use fur on a self-propelled object as a cue that the object is an animal (29). When a ball and a furry object with a face moved together in close contact, infants attributed the source of the motion to the furry object; when the two objects later rested stationary side by side, infants looked reliably longer at the furry object as though they anticipated that it would move again. However, no such effect was found when an experimenter moved the ball and the furry object together with her hand. (In a survey we conducted of parents of 35 6- to 9-mo-old infants, 83% reported that their infant had touched a furry animal at least once, and 60% reported that their infant had regular contact with one or more furry animals. These results support the notion that infants in the second half-year have opportunities to identify fur as a predictive cue for animals). Building on these results, we asked in Exp. 3 whether 8-mo-old infants would expect an object that was furry and self-propelled, but not an object that lacked one or both of these properties, to have insides.

Infants ($n = 36$) were assigned to a self-propelled or a nonself-propelled condition and watched events involving a new can that was covered with brown beaver fur and a new box that was covered with tan paper and edged with brown tape (Fig. 3). During the (32 s) initial phase of each familiarization trial in the self-propelled condition, the fur-can or box moved smoothly back and forth across the apparatus floor to demonstrate that it was self-propelled; during the final phase, the object paused at the center of the apparatus until the trial ended. The familiarization trials in the nonself-propelled condition were identical except that the fur-can and box rested on a tray, and the experimenter reached through a window in the back wall of the apparatus to move the tray back and forth. Next, all infants received pretest and test trials identical to those in Exp. 1, except that the fur-can (fur-can trial) and box (box trial) were both revealed to be hollow.

Analysis of infants' looking times during the test trials (Fig. 2) yielded a significant Condition X Trial interaction, $F(1, 32) =$

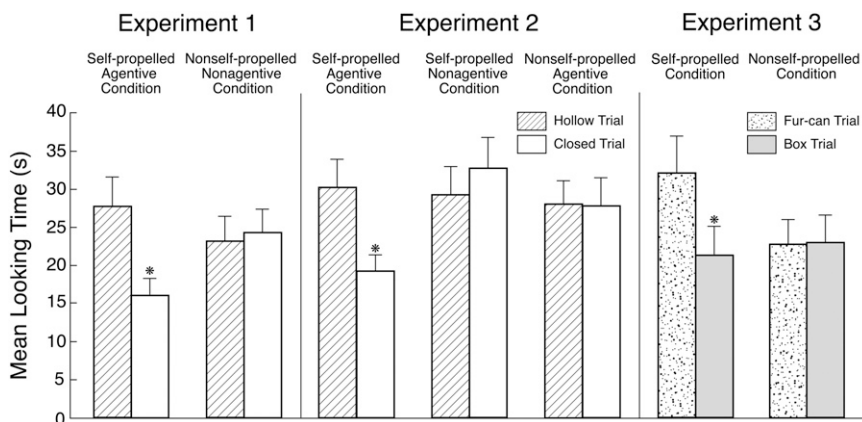


Fig. 2. Mean looking times of infants in Exps. 1–3 during the test trials as a function of condition and trial. Errors bars represent SEs, and an asterisk denotes a significant difference between the trials within a condition ($P < 0.05$ or better).

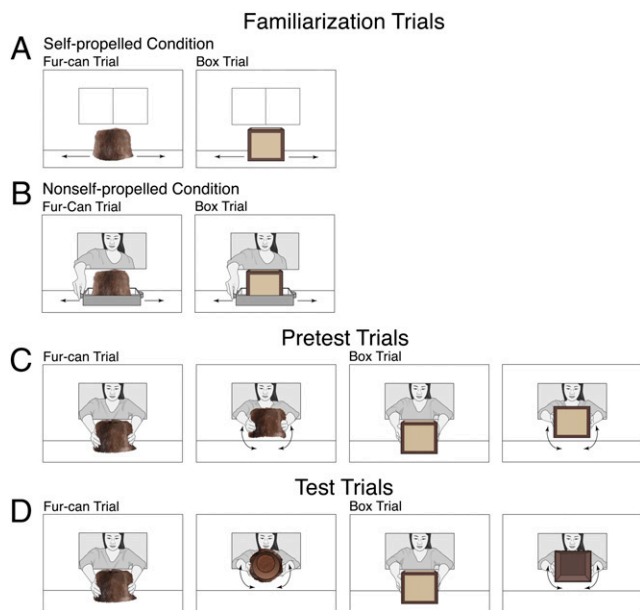


Fig. 3. Schematic drawing of the events shown in Exp. 3. Whether the fur-can trial or the box trial was shown first in the familiarization (A and B), pretest (C), and test (D) trials was counterbalanced across infants in each condition.

6.18, $P = 0.018$ [no such interaction was found in an analysis of the final phases of the familiarization trials or in an analysis of the pretest trials, both $F(1, 32) < 1$]. In the self-propelled condition, infants looked reliably longer during the fur-can than the box trial, $F(1, 32) = 12.00$, $P = 0.002$; 16 of 18 infants showed this pattern. In contrast, infants in the nonself-propelled condition looked about equally during the two trials, $F(1, 32) < 1$; 9 of 18 infants looked longer during the fur-can trial. Thus, infants expected the self-propelled fur-can to have insides, but they held no expectations about the insides of the nonself-propelled fur-can or about those of the box, whether it was self-propelled or not. These results also provide additional evidence that by 8 mo, infants use fur on a self-propelled object as a cue that it is an animal.

In Exps. 1–3, infants detected a violation when an object they had identified as an animal was rotated to reveal that it had no insides. To provide converging evidence for these results, in Exp. 4 we used a different manipulation to assess 8-mo-olds' expectations about insides: instead of rotating the fur-can and box from Exp. 3, the experimenter shook each object to demonstrate that it rattled, as though the shaking caused a few parts to bounce inside the object's largely hollow interior. If infants expected the self-propelled fur-can to have insides, they should detect a violation when it produced a rattling noise when shaken, as though it was mostly hollow inside. (To check our manipulation, we presented 20 adults with the rattling fur-can and the rattling box, and we asked them to estimate based on the sounds they heard how full each object was inside. On average, subjects guessed that the objects were 28% full, supporting our claim that the rattling sounds conveyed that the objects were largely hollow.)

Infants ($n = 51$) were assigned to a self-propelled, a nonself-propelled, or a silent-control condition (Fig. 4). In the self-propelled condition, infants received the same fur-can and box familiarization trials as in the self-propelled condition of Exp. 3 for two pairs of trials. Next, infants received either a fur-can or a box test trial. During the (25 s) initial phase of each trial, the experimenter's gloved hands (which reached through a curtained window in the right wall of the apparatus) first grasped the fur-can or box. Next, the hands lifted the object, shook it (causing it to rattle), and returned it to the apparatus floor; this sequence was repeated two more times, and then the hands rested on

either side of the object. During the final phase, infants watched this paused scene until the trial ended (pilot data indicated that infants tended to look continuously if the rattling persisted, so this nonrepeating procedure was used instead). The nonself-propelled condition was identical, except that in the familiarization trials the fur-can and box rested on a tray and the experimenter's right gloved hand moved the tray back and forth on the apparatus floor. Finally, because infants in the self-propelled condition might look longer when the fur-can rattled not because they expected it to have insides but because they had never seen an animal being shaken before, a silent-control condition was also included. This condition was identical to the self-propelled condition except that in the test trials the objects produced no noise when shaken. In the self-propelled and nonself-propelled conditions, nine infants received a fur-can test trial and eight infants received a box test trial; in the silent-control condition, these numbers were reversed.

Analyses of infants' looking times during the final phase of the test trial (Fig. 5) yielded a significant Condition \times Trial interaction, $F(2, 45) = 4.85$, $P = 0.012$ [no such interaction was found in an analysis of infants' averaged looking times during the final phases of the fur-can and box familiarization trials, $F(2, 45) < 1$]. In the self-propelled condition, infants looked reliably longer if shown the fur-can as opposed to the box trial, $F(1, 45) = 16.08$, $P = 0.0002$. In contrast, in the nonself-propelled and silent-control conditions, infants looked about equally during either trial, both $F(1, 45) < 1$. Thus, infants detected a violation when the fur-can produced a rattling noise when shaken, but only if it was self-propelled. These results provided converging evidence that infants identify self-propelled furry objects as animals and expect their insides to be filled as opposed to hollow.

The present experiments indicate that 8-mo-old infants expect a novel object they identify as an animal to have insides, in accordance with the innards principle. This identification may come about because the object gives evidence of autonomous motion and control, or because it presents cues with learned predictive validity for distinguishing animals from other objects. In either case, upon identifying the novel object as an animal, infants immediately expect it to have insides: they detect a violation if the object either is shown to be hollow or rattles when shaken as although mostly hollow. Taken together, these results

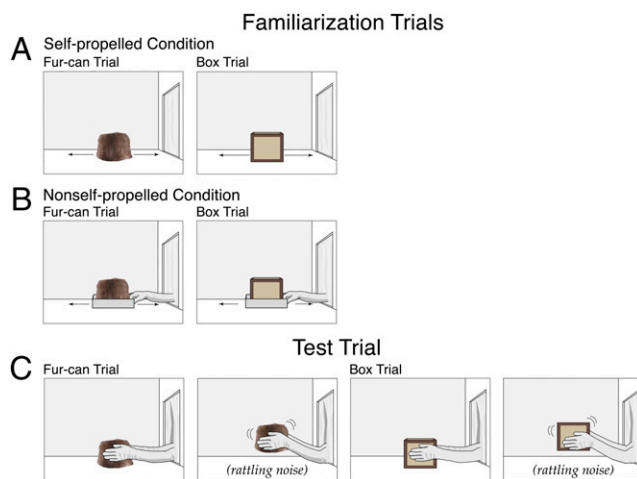


Fig. 4. Schematic drawing of the events shown in Exp. 4. Whether the fur-can trial or the box trial was shown first in the familiarization trials (A and B) was counterbalanced across infants in each condition. In the test trial (C), infants saw either the fur-can or the box trial. The silent-control condition (not shown) was identical to the self-propelled condition except that in the test trial the fur-can or box produced no noise when shaken.

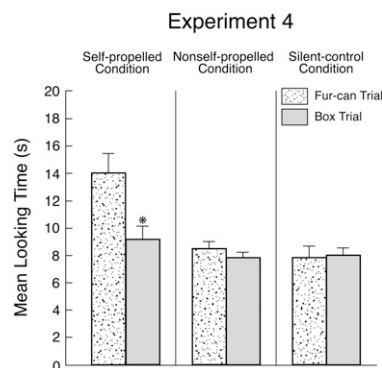


Fig. 5. Mean looking times of infants in Exp. 4 during the final phase of the test trial as a function of condition and trial. Errors bars represent SEs, and an asterisk denotes a significant difference between the trials within a condition ($P < 0.05$ or better).

provide strong support for the biological hypothesis that infants endow animals with vitalistic, biological properties.

At least two broad questions remain for future research. First, what general expectations do infants possess about animals' insides? For example, would infants expect the insides of a novel object that was self-propelled and agentive to differ from those of an object that lacked these properties? Moreover, would infants regard an animal's insides as essential for its functioning? If infants witnessed the removal of the insides of a novel self-propelled agent, would they expect it to no longer be capable of autonomous motion and control?

Second, how should we conceptualize infants' expectations about animals' insides? There are at least three possibilities. One is that these early expectations are part of a skeletal explanatory framework that underlies core biological reasoning (21). In this view, infants would possess a naïve theory of biology as well as naïve theories of physics and psychology, although their naïve theory of biology might be less rich. Another possibility is that infants' expectations about insides reflect general biases or modes of construal that are not exclusively tailored for biological phenomena (30, 31). For example, abstract biases for teleology and essentialism, perhaps with sparse conceptual constraints, might lead infants to posit various internal features to explain objects' capacity for self-propulsion (internal energy), for agency (internal states), and for both self-propulsion and agency (innards). Finally, a third possibility is that infants' expectations about insides arise from a quite different source: the cognitive systems that humans evolved to deal with predators and prey and, more generally, to understand animals as a food source (32). As Barrett (32) noted, "Predators are things that systematically try to kill you and eat you. Prey are things you try to capture and eat." From this perspective, it seems plausible that the human mind would have evolved an abstract expectation that animals have filled insides. Damaging the insides of a predator or prey brings about its demise, and consuming these insides provides valuable nutrients. Why would an expectation of filled insides apply to entities that are both self-propelled and agentive, but not to entities that are only self-propelled or only agentive? It could be that in the evolution of predator-prey adaptations, the systems for detecting self-propulsion came first, and those for detecting agency were integrated later as they became available; understanding animals as self-propelled agents would have presented significant advantages for predator evasion and prey capture.

Whichever possibility turns out to be correct, there can be no doubt that infants' expectations about animals are highly primitive and that considerable conceptual elaboration and change must occur for young children to develop a more advanced understanding of biology. Nevertheless, the present research fits well with several developmental results. If infants construe

animals as self-propelled agents with biological properties, then it makes sense that (i) young children initially have difficulty constructing a category of living things that includes plants as well as animals (33, 34); (ii) young children who are taught that plants engage in self-propelled, agentive motion immediately infer that plants are living things (35); and (iii) school-aged children and adults who see computer-animated blobs engage in self-propelled, agentive motion describe them as alive and attribute to them various biological properties (36). All of these results suggest that key components of the interpretive framework that guides infants' expectations about animals persist throughout life.

Methods

Participants. Participants were 177 full-term infants (91 male, range: 6 mo, 17 d to 9 mo, 14 d). Mean ages were 8 mo, 4 d (Exp. 1), 8 mo, 1 d (Exp. 2), 7 mo, 24 d (Exp. 3), and 7 mo, 15 d (Exp. 4). Another 34 infants were tested but excluded because they looked the maximum time allowed in both test trials (16 infants); because they were fussy (6 infants), distracted (2 infants), drowsy (1 infant), inattentive (1 infant), or overly active (1 infant); because the difference in their looking times during the two test trials was over 2.5 SDs from the condition mean (2 infants); because they showed a marked bias during the familiarization trials for one object over the other (2 infants); or because they peeked under one or both objects during the pretest trials (2 infants) or stood too tall to see inside the rotated objects in the test trials (1 infant). Written informed consent was obtained from each infant's parent prior to the test session, and all protocols were approved by the University of Illinois IRB.

Apparatus and Stimuli. The apparatus consisted of a brightly lit display booth (183 cm high \times 100 cm wide \times 57 cm deep) with a large opening (55 cm \times 94 cm) in its front wall; between trials a supervisor lowered a curtain in front of this opening. Inside the apparatus the side walls were painted white, and the back wall (made of foam core) and floor were covered with colored adhesive paper. The experimenter was a female native English speaker. In Exps. 1–3, she wore a green shirt and sat at a window (34 cm \times 48 cm, Exps. 1–2; 25 cm \times 48 cm, Exp. 3) in the back wall of the apparatus; this back window could be closed with two identical doors. In Exp. 4 the experimenter wore long silver gloves and reached through a window (51 cm \times 38 cm and filled with a fringed curtain) in the right wall of the apparatus. In all experiments, a large screen behind the experimenter hid the testing room. In Exps. 1 and 2 the can (18 cm \times 17 cm in diameter) was wrapped with red and gray yarn in alternating stripes; the can had a removable gray felt bottom and its interior was lined with beige felt. The box (18 cm \times 18 cm \times 18 cm) was covered with beige adhesive paper and decorated with varying round patches of blue cloth with multicolored dots; the box had a removable beige felt bottom, and its interior was lined with brown felt. In the familiarization trials, a long flat handle was attached to the bottom of the can or box and protruded through a narrow slit at the bottom of the back wall. In the self-propelled conditions, the experimenter used the handle to move the can (in a slight bouncing manner) and the box (in a slight zigzag manner) along the apparatus floor, between predetermined marks. In the familiarization trials, the can or box also held a small speaker; its wire was tied to the handle and was connected, behind the apparatus wall, to an MP3 player. The can produced varying synthesized quacking sounds and the box produced varying beeping sounds; these sounds were prerecorded on the MP3 player and played through the speaker in the can or box. In the agentive conditions, a small reminder card with the written conversation script was attached to the back of the can or box for the experimenter to follow; in the nonagentive conditions, the can and box produced the same sounds but the experimenter remained silent. In Exps. 3 and 4, the fur-can (about 15 cm \times 22 cm in diameter) consisted of a brown beaver fur hat that was placed over an upright cylinder; in the fur-can pretest and test trials of Exp. 3, the upright cylinder was replaced by an inverted cylinder lined with tan felt. The box (15 cm \times 18 cm \times 18 cm) was covered with tan packing paper and edged with brown tape; in the box pretest and test trials of Exp. 3, an exact copy of the box was used that had no bottom and was lined with brown felt. In the familiarization trials of the self-propelled conditions in Exps. 3 and 4, the fur-can or box was again attached to a long flat handle; behind the wall the experimenter used the handle to move the object smoothly back and forth between predetermined marks. In the familiarization trials of the nonself-propelled conditions, the fur-can or box rested either on a pink tray (5 cm \times 29 cm \times 23 cm) with handles that was moved by the experimenter from the back window (Exp. 3) or on a yellow tray (5 cm \times

23 cm × 29 cm) without handles that was moved by the experimenter's right gloved hand from the right window (Exp. 4); in each experiment, the experimenter moved the tray in such a way that the fur-can and box traveled the same distance as in the corresponding self-propelled condition. In the test trials with rattling sounds, a small plastic bag filled with 22 1-cm metal bells was partly affixed to the interior bottom surface of the fur-can or box; when the object was shaken briskly up and down, the bag bounced against the rigid bottom of the object, producing rattling sounds. During each test session, one camera captured an image of the events and another camera captured an image of the infant. The two images were combined, projected onto a television set located behind the apparatus, and monitored by the supervisor to confirm that the trials followed the prescribed scripts. Recorded sessions were also checked off-line for observer and experimenter accuracy.

Procedure. Infants sat on a parent's lap in front of the apparatus; parents were instructed to remain silent and to close their eyes during the test trials. Two hidden observers helped monitor infants' looking behavior; unless otherwise noted, the primary observers' responses were used in the analyses. In Exps. 1–3, the primary observer left the testing room during the familiarization trials to be naïve during the pretest and test trials about infants' condition and trial order. Interobserver agreement during the test trials averaged 95% per trial per infant. In Exp. 4, observers could use available sounds to determine which test trials were shown; therefore, all final phases of the test trials were recoded frame-by-frame by two independent coders from edited silent videos. The two coders agreed on 97% of coded frames (trials with agreement below 90% were resolved through discussion). In Exps. 1–3 infants were attentive during the initial phases of the two familiarization trials and looked, on average, for 85% of each initial phase. The final phase of each familiarization trial ended when infants (*i*) looked away for 2 consecutive seconds after having looked for at least 2 cumulative seconds or (*ii*) looked for a maximum of 60 cumulative seconds. Each pretest and test trial ended when infants (*i*) looked away for 1 consecutive second after having looked for at least 5 cumulative seconds or (*ii*) looked for a maximum of 50 cumulative seconds; the 5-s minimum value ensured that infants had the opportunity to observe the rotated objects in the test trials. In Exp. 4, infants received two pairs of familiarization trials and one test trial,

and each trial had an initial and a final phase. Across conditions, infants looked, on average, for 82% of each initial phase. The final phase of each trial ended when infants (*i*) looked away for 1 consecutive second after having looked for at least 5 (familiarization) or 6 (test) cumulative seconds, or (*ii*) looked for a maximum of 20 cumulative seconds. Shorter maximum values were used in Exp. 4 because infants received two pairs (instead of one pair) of familiarization trials and because the test trial used a nonrepeating procedure with a final paused scene.

Additional Results. Because in each experiment the two test trials involved different objects, we conducted additional analyses to confirm that the results did not reflect baseline preferences for either object. For Exps. 1 and 2, we examined the test data using ANOVAs with condition, order, and hollow object (can or box) as between-subject factors and trial as a within-subject factor. In each experiment, the Condition X Trial interaction was again significant [Exp. 1: $F(1, 28) = 8.29, P = 0.008$; Exp. 2: $F(2, 42) = 3.68, P = 0.034$], but the Condition X Trial X hollow object interaction was not [Exp. 1: $F(1, 28) < 1$; Exp. 2: $F(2, 42) = 1.27, P = 0.292$], indicating that infants responded similarly whether the can or box served as the hollow object in the test trials. In Exp. 3, the objects used in the test trials could not be counterbalanced because the design called for one furry and one nonfurry object. We therefore conducted an ANCOVA using as the four covariates infants' looking times at the fur-can and box in the familiarization and pretest trials. The Condition X Trial interaction remained significant, $F(1, 28) = 6.48, P = 0.017$, indicating that infants' responses during the test trials did not simply reflect baseline preferences for the fur-can or the box. In Exp. 4, which also used the fur-can and box, we performed a similar ANCOVA using as the two covariates infants' averaged looking times in the fur-can and box familiarization trials (recall that infants received two pairs of familiarization trials and no pretest trials). The Condition X Trial interaction remained significant, $F(2, 43) = 4.10, P = 0.024$, again indicating that infants' responses to the test events did not simply reflect baseline preferences for either test object.

ACKNOWLEDGMENTS. We thank the families who participated in the research, which was supported by National Institute of Child Health and Human Development Grant HD021104 (to R.B.).

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