Human and animal cognition: Continuity and discontinuity

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Microscopic study of the human brain has revealed neural structures, enhanced wiring, and forms of connectivity among nerve cells not found in any animal, challenging the view that the human brain is simply an enlarged chimpanzee brain. On the other hand, cognitive studies have found animals to have abilities once thought unique to the human. This suggests a disparity between brain and mind. The suggestion is misleading. Cognitive research has not kept pace with neural research. Neural findings are based on microscopic study of the brain and are primarily cellular. Because cognition cannot be studied microscopically, we need to refine the study of cognition by using a different approach. In examining claims of similarity between animals and humans, one must ask: What are the dissimilarities? This approach prevents confusing similarity with equivalence. We follow this approach in examining eight cognitive cases—teaching, short-term memory, causal reasoning, planning, deception, transitive inference, theory of mind, and language-and find, in all cases, that similarities between animal and human abilities are small, dissimilarities large. There is no disparity between brain and mind.

animal/human | Darwin

harles Darwin held that humans were essentially "bigbrained apes" (1). Neuroscientists concurred with Darwin until well into the 1980s, arguing for what they called the "basic uniformity" of the mammalian brain. Not until the 1990s when, aided by new histological techniques, neuroscientists turned to the microscopic study of the human brain did this simple picture change. In 1999, Preuss and Coleman (2) became the first to show microscopic differences in brain organization between apes and humans. In one layer of the human primary visual cortex, nerve cells were organized in a complex meshlike pattern very different from the simpler vertical arrays of cells in other primates. At about the same time, Hof and associates (3) rediscovered a slender tapered neuron, labeled VEN, in both human and ape. Humans, however, have many more VENs than apes; individual VENs are markedly larger; and those in the human are located in only two parts of the brain: the anterior cingulate cortex and the frontoinsular cortex (4). Both of these structures appear to be involved in complex social emotion/cognition such as empathy, feelings of guilt, and embarrassment.

The human reorganization of the brain affected even the minicolumn—80–100 neurons bundled vertically that supports parallel processing—which is the basic unit of information processing in all mammalian brains. Human minicolumns in the left planum temporale, an area involved in language and perhaps music, are organized differently than those of chimpanzees and rhesus monkeys (5). They are far wider, an average of 51 μ m compared with 36 μ m in the chimpanzees and monkeys. The increase is due to an enlarged neuropil space, which contains the axons, dendrites, and synapses that make neural connections (5, 6).

What causes synapses between neurons to form? Barres and associates (7) found, in answering this question, that specialized neuroglial cells called astrocytes (which make up nearly half the cells in the human brain) must be present for synapses to form;

these cells secrete a protein called thrombospondin that triggers synapse formation (8). Preuss and associates (9) then found that human brains produce up to six times as much thrombospondin messenger RNA than do either chimps or macaques. Moreover, the areas found to have enhanced thrombospondin expression have larger neuropil space and thus more room for synaptic connections.

Virtually all the newly discovered human singularities are located in areas associated with either complex social cognition [theory of mind (TOM)] or language. But the reorganization of the human brain has not been without cost. In addition to advancing language and TOM, it brought about neurodegenerative disease: schizophrenia, autism, Alzheimer's, etc. These diseases are as unique to humans as is advanced cognitive function. What cognitive functions make humans susceptible to dementia? Are factors that help humans adjust swiftly to rapidly changing social situations a possibility? A major goal of neuroscience is to find a unified theory that will explain both the positive and negative sides of the reorganization of the brain.

The Cognitive Side

The microscopic study of the human brain, and the reorganization that it discloses, contest Darwin's simple continuity of ape and human brains. What can be said of Darwin's assumption on the cognitive side ["... there is no fundamental difference between man and the higher mammals in their mental faculties" (ref. 1, p. 35)]: Is there a simple continuity between animal and human? Here, there appears to be a disparity between brain and behavior, because virtually every month another cognitive ability, thought to be unique to humans, is reported in an animal. However, the impression of greater cognitive than neural continuity is misleading. The study of cognition has not kept pace with the study of the brain. Cognition is still in the "premicroscopic" phase.

Although a microscopic study of cognition is not possible, we can approximate the function of such a study by a more fine-grained approach to cognition. It is essential, when claiming human-like faculties in animals, to ask this question: Is the animal faculty equivalent to that of the human? The demonstration of a similarity between an animal and a human ability should automatically trigger the next question: What is the dissimilarity? This question will prevent mistaking similarity for equivalence.

We now consider several examples in which animals have shown human-like abilities, in each case searching for the functions of which the ability consists, and weighing the similarity (and dissimilarity) between the animal and human case.

Teaching

Some animals are said to teach. For instance, a cat injures mice, and then brings the injured mice to her kittens, which learn to

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stalk and kill them (10). Teaching takes a different form in meerkats, which do not stalk prey, but eat poisonous food. Adults defang scorpions and kill or disable other prey before giving them to the young. They adjust the frequency with which they disable prey to the age of the young, gradually introducing them to live prey (11).

The actions of the cat and meerkat are adaptations and, like all adaptations, have a single target, in this case, eating or stalking. In fact, eating (or stalking) is virtually the only activity that any animals teach. Because most animals eat ordinary diets, they do not teach.

The fact that adaptations have a single target distinguishes teaching by animals from teaching by humans. Human teaching is not an adaptation. It is a domain-general competence with indeterminately many targets. Further, the targets of teaching differ in every culture. Toilet training and table manners are widely taught in the western countries, whereas among the Kalahari San, walking and sitting are the key activities taught to the young (12).

Human teaching consists of three distinct actions: observation, judgement, and modification. A teacher observes the novice, judges his actions or products, and modifies them when they fall short of her standards. The human recognizes that the young are incompetent and therefore need to be taught; has the technology with which to teach; and is motivated to teach by deeply rooted aesthetic standards. Each of these actions has a distinct cognitive source.

The recognition that competence develops with age humans owe to their TOM: It enables them to both differentiate the mental conditions of other individuals, and to analyze the factors, such as age, intelligence, experience, etc., that cause the differences (13–18).

Humans can teach or modify the other one because they are both language-competent and expert in passive guidance (placing other's body in desired positions).

The human motivation to teach is largely aesthetic (19, 20). A parent has a conception of a proper act or product and dislikes the appearance of an improper one. The evidence for such standards is twofold. First, humans "practice," e.g., swing a golf club repeatedly, flip an omelet, sing a song, write a poem, etc., trying to improve their performance of a chosen activity. Second, humans seek to improve their appearance. The mirror is where they begin their day, combing their hair, applying makeup, etc. That humans have mental representations of preferred actions or appearances is suggested not only by the demands they make on themselves but by the corrections they make of children when teaching them. Teaching, the attempt to correct others, is the social side of the attempt to correct self.

It is no coincidence that humans both practice and teach, whereas other species do neither. A species that practices but does not teach—that corrects itself but does not correct otherswill probably never be found. Nor will a species of the opposite kind, one that teaches but does not practice—corrects others but not itself.

Short-Term Memory

Chimpanzee short-term memory is only slightly less than that of humans (21). Both species remember no more than five to seven items. This limitation can adversely affect problem-solving (by limiting the alternatives that can be considered), but does it pose the same danger to both humans and chimpanzees?

Although short-term memory limits the number of units one can remember, it does not define the content of a unit. A language-trained chimpanzee exposed to the numbers 1–9 might remember, for example: 2, 6, 4, 3, 7, whereas humans might remember, for example, 21, 43, 96...; 214, 618, 109...; 1012, 6680, 3456, etc. In language, content of the unit is even more open-ended. A chimpanzee may remember five words; a human may remember five phrases, five sentences, five stories, etc. Humans are able to make these expansions because they are capable of both recursive language and numbers. Thus, despite comparable limitations in short-term memory, animals and humans may differ dramatically in the amount of information they can remember. In addition, humans can, and often do, circumvent short-term memory with written language. Similar limitations in different species may have entirely different consequences depending on the other cognitive resources of the species (22).

Causal Reasoning

In a recent experiment (23), some rats were taught to press a lever that produced a tone, followed by the presentation of food. These rats seek food only when they produce the tone themselves; merely hearing the tone does not lead them to seek food. Other rats were shown a light followed by a tone, followed by the presentation of food. These rats seek food when they hear a tone whether it was preceded by a light or not.

In other words, if you produce food by a goal-directed act, pressing a lever or the like, you will seek food only when you carry out the goal-directed act. Even if the goal-directed act produces not only food but also stimuli—light, tone, etc.—that precede the food, the stimuli will have little effect. If the stimuli occur by themselves, you will not seek food. Conversely, if the goal-directed act does not produce the stimuli, you will nonetheless seek food.

On the other hand, if you do not produce food by a goaldirected act but are presented with food following a sequence of arbitrary stimuli, then any subset of this sequence will lead you to seek food.

The experiment illustrates two basic psychological mechanisms: causal illusion and association.

- 1. Causal illusion: any goal-directed act that is followed by a desired item will cause the illusion that the goal-directed act produced the desired item.
- 2. Association: stimuli that are followed by a desired item will become associated with the item; when the stimuli are presented, the individual will seek the item.

All species (mammal, bird, reptile, etc.) that are capable of goal-directed action, will have both mechanisms: association and causal illusion. Reflexive species that lack goal-directed action, and therefore can respond only when stimulated, will have only one mechanism: association. Not until reflexive creatures evolved into goal-directed ones did causal illusion emerge.

The Perceptual Understanding of Physical Action. Young infants place round objects in round holes, square objects in square holes (chimpanzees are poor at this). Animals suit the dimensions of tools to the task, choosing long ones to reach buried items; some make "tools" that enable them to reach inaccessible objects. Chimpanzees show their understanding of physical action by choosing transformed objects that are appropriate to a tool and, vice versa, tools that are appropriate to a transformed object. When given a sequence consisting of, for example, an intact apple, a knife, and a blank, they choose a cut apple (rather than either a cut orange or an apple with pencil marks). When given a sequence consisting of paper, blank, and marked paper, they choose a pencil (not a knife or container of water) (22, 24).

Chimpanzees recognize the reversibility of actions. When given paper, blank, scribbled paper, they choose pencil; but when given scribbled paper, blank, clear paper, they choose eraser. They recognize multiple transformations and differentiate among the tools that do and do not cause them: They place relevant tools in one bin, irrelevant in another. For example, when given the sequence: paper that is cut, blank, paper that is both cut and wet, they place water in the relevant bin, but scissors and pencil in the irrelevant bin. Changing dry cut paper into wet cut paper required water, but not scissors or pencil (22). Evidence of this general kind shows that animals understand the dynamics of physical action.

Causal Reasoning. When adults perceive two events that are temporally and spatially contiguous, they see the first event as having caused the second (25). Young infants have the same reaction (26), suggesting that the reaction is not learned. Although whether animals, too, have the reaction has not been tested, it is reasonable to assume that they do.

Children learn that events can be causally related even though they are not spatially contiguous. A light switch turns on the light although it is far from the light. Children learn to substitute other criteria for judging causal relations. If event A consistently produces event B, and B does not occur without A, A is accepted as the cause of B.

The "Michotte reaction," like "causal illusion," is in all likelihood an automatic reaction. Although a possible precursor of reasoning, it is not itself reasoning. Do animals follow the human course of development: learn about processes such as electricity, adopt new criteria for causality, and equate a consistent relation between two events with temporal/spatial contiguity between events? Do they learn that events in which they play no role, such as the freezing of water, the collapse of a wall, the breaking of a tree in the wind, a spark setting a fire, etc., are examples of cause? Or do animals restrict "cause" to occasions in which their personal action, such as lever pressing for pellets, leads to an effect? The latter is causal illusion, not causal reasoning.

An animal may recognize that a large rock is more likely to break a branch than a small one. But if the animal observes a large rock lying by a crushed plant, will it infer that the rock crushed the plant? There is no evidence that it will. The understanding of physical action is not the equivalent of causal reasoning.

It is of interest to compare the case of teaching with that of causal reasoning. Whereas teaching in animals is almost certainly not an evolutionary precursor of the human competence, the animal version of causality may well be a precursor of the human version. Both humans and animals share causal illusion and arguably the Michotte reaction, mechanisms that can be forerunners of causal reasoning. Although further research may reveal more development than is presently recognized, the cognitive elaboration leading to causal reasoning appears to be lacking in animals.

Planning

Although planning is among those abilities that are said to be unique to humans, a recent experiment with scrub jays calls this into question (27). The demonstration appears to be a triumph of animal cognition, because all previous attempts to show planning in animals (28–30) have been questionable. The scrub-jay test proceeds as follows. The birds were allowed to cache food in the evening and to eat it in the morning. Next, they were shown that kibbles was present in compartment 1, peanuts in compartment 2. When allowed to cache either peanuts or kibbles in the two compartments, the birds cached kibbles in compartment 2, peanuts in compartment 1, thus assuring that, when they ate in the morning, both peanuts and kibbles would be available in both compartments.

A control is lacking. The bird's recognition that "it will eat in the morning" may play no role in its caching. Birds may prefer to cache two different foods, rather than two of the same kind, whether they have a schedule for eating the food or not. For the sake of discussion, however, let us assume that the alleged planning is legitimate, that a control will substantiate the

author's claim, and proceed to the interesting question: How does the bird's planning compare with human planning?

Simple cases of planning, comparable with that of the bird, can be found in the human. In the evening, Donna remembers that she and her husband have dental appointments in the morning but that the drive to the dentist may disturb his bad back; she places pillows by the front door that can be picked up in the morning to cushion his ride.

Cases that are not simple also can be found in humans. Do the complex cases introduce new factors not present in the simple case, or are they merely "large" versions of the simple cases? Consider a family planning the education of its children. The family has attended the same school for generations, making them confident about being able to send both children there. Nevertheless, admission depends on attending the right prep school, getting into the prep school depends on attending the right secondary school, and these days, even the secondary school, on attending the right preschool. Their first discussion, in what will prove to be a long series of discussions over the years, concerns the progress of their preregistration at the preschool and the several individuals they will contact to improve their chances

Complex planning differs from simple planning in these respects. It is social: two or more individuals form the plan, and the beneficiary of the plan is likely to be yet another individual, different from those who form the plan; the plan is not one-shot, but a series of plans; the plan extends not for hours but over years. Neither social nor sequential planning, nor planning that extends over long durations, is likely to be found in animals.

The scrub-jay's episodic memory is centered on caching, and so, in all likelihood, is its planning. Scrub-jays can remember what food they cached, where and when it was cached, even which other birds observed their caching. Does the bird have episodic memory for episodes other than caching, for attracting a mate, avoiding predators, etc.? Can it plan for episodes other than caching? Planning in the scrub-jay may be yet another adaptation, restricted to a single target.

Although adaptations are inflexible in being restricted to a single goal, they are not inflexible in the behavior that can potentiate or bring them about. Do scrub-jays encounter foods in the wild separated from one another as the kibbles and peanuts were separated in the experiment? If not, then the bird's behavior in the laboratory is a nice extension on its behavior in the wild. The cat's teaching of its kittens is an adaptation in which the same flexibility can be seen. If the kittens were made inaccessible by placing them in a loft, a cat would learn which button to press to make them accessible. Adaptations are inflexible in only one respect. The cat can teach stalking, nothing else. The scrub-jay may resemble the cat in being able to plan about caching food, but nothing else.

Deception

Deception comes in two flavors: false positives and false negatives. A signal that indicates food or a predator, when in fact there is no food or predator, is a false positive (the famous negative version of a false positive is "crying wolf"). Conversely, the failure to give a signal when in fact food or predator is present is a false negative. In nature, false negatives greatly outnumber false positives. For example, unobserved monkeys sometimes fail to signal the presence of food, and when caught are punished by other monkeys (31). There are, however, virtually no reports that monkeys, or any other species, falsely signal the presence of food or predators.

We gave four young chimpanzees the opportunity to engage in deception in the laboratory (32). The experiment proceeded as follows. We showed the chimpanzees which of two containers held food but placed the containers out of the animals' reach. Two trainers were in the opposite predicament: They had access to the containers but did not know which container held the food. To find the food, the trainers were forced to rely on signals from the animals.

One of the trainers was a "good guy," the other a "bad guy." Whenever the good guy found food, he shared it with the animals, whereas whenever the "bad guy" found food, he kept it for himself (the trainers were distinguished by different face

The trainers were held to one rule: They could not choose a container on the basis of an inference, but had to extract an actual signal from the animal. The chimpanzees signaled the trainers in two ways, by glancing in the direction of the container that held the food and, surprisingly, by pointing, which the animals developed on their own in the course of the experiment.

When dealing with the good guy, all four chimpanzees quickly learned to both point and glance at the baited container. By contrast, when dealing with the bad guy, they no longer either pointed or glanced at the baited container. They used false negatives, or rather, they tried to use them, but only the oldest of the four animals succeeded.

The bad guy could recognize the baited container, without any signal from the animal, from the fact that all the animals tried not to look at it. So he did everything he could to catch their gaze and lead them into looking at the baited container. The oldest animal held him off, staring steadfastly into space, refusing to

The three young animals were unable to resist his gaze. Although they "knew" they should not communicate with the bad guy, he always caught their gaze and led them into "giving" away the baited container. At the end of the experiment, which lasted over a year and involved hundreds of trials, they still fell victim to the bad guy, revealing the food by glancing at it. The bad guy remained true to his role, always gloating over the food as he ate it alone.

As the experiment progressed, the oldest animal began to both glance and point at the wrong container. Rather than merely withholding information from him, she began giving him false information: a false positive! The moment she "fooled" the bad trainer into choosing the wrong container, her head snapped, and her gaze darted from the wrong to the right container. The abruptness of her transition from wrong to right container made it clear how major a role suppression had played in her action. It became evident, too, why false positives are rarely seen in animals. To fool a recipient by looking at the wrong place, one must be able to resist the almost overpowering impulse to look at the right place.

Chimpanzees do not confine false positives to the laboratory, however. On one occasion, an adult chimpanzee pretended that she could not reach her food; when the deceived person pushed the food toward her, she bit the person's finger to the bone. Why? What led to the sudden deception? When two people, who had given the chimpanzee their undivided attention, were joined by a third person, the people began talking among themselves, denying the chimpanzee full attention.

The plover is famous for leading intruders away from its nest by feigning a broken wing and then, when the intruder is beyond the nest, flying normally. This deception is a perfect example of an adaptation because the plover cannot use it for any other purpose than protecting its nest.

The bird's deception is said to be like human deception because the bird can be taught to restrict its broken-wing display to "serious" intruders, not wasting it on nonserious ones (33). It is also argued that the plover's display is "intentional" and therefore equivalent to human deception.

Although there is no clear demonstration of intentionality in the plover, whether, in general, an act is intentional is not difficult to determine. Consider raising the same question for a vervet monkey. When the monkey gives the cry for, say, leopard, is its cry intentional? Suppose the animal that receives the call mistakenly takes countermeasures for snake rather than leopard, does the sender take steps to correct it? If it does nothing to correct its recipient, then the call is merely a reflex. On the other hand, if the sender acts to correct the recipient, e.g., by calling again (putting itself at risk), then the sender's call was intentional: Its goal in calling was to protect its recipient.

Whether the plover's act is goal-directed could be determined by arranging two cases, one in which its display leads intruders away and another in which its displays do not succeed in leading intruders away. If, when the displays fail, the bird ceases to make them, the act is intentional. For intentional acts that fail to realize their goal extinguish. However, neither the potential intentionality of the plover's display nor the fact that the plover can discriminate real intruders from fake ones changes the status of the display. It is an adaptation that serves only one goal. It is not comparable with human deception, a domain-general competence that can serve indeterminately many goals.

Transitive Inference

Many animals, including chimpanzees, monkeys, and birds, are capable of transitive inference (34–39). When they find that A leads to a larger reward than B, B a larger reward than C, C a larger reward than D, D a larger reward than E, and are given a choice between A and E, they choose A.

Fish are the latest addition to the list of animals capable of transitive inference (40). The demonstration is based on observations by male fish. As a bystander, the fish observes pairwise fights between size-matched rivals in a competition for territory. The bystander sees that fish A defeats fish B, fish B defeats fish C, C defeats D, and D defeats E. The bystanders are then tested by being given an opportunity to swim freely between the pairs A and E, and B and D. Like other aggressive fish, A. Burtoni prefer losers to winners and spends more time swimming with them. All of the bystanders followed this pattern, proving their capacity for transitive inference.

Transitive inference is taken as unequivocal evidence of reasoning in humans. However, behavior found in children but lacking in animals suggests that, in animals, transitive inference may not be based on reasoning. Children understand the concept of monotonic order. When given dolls that vary in size, children both copy a model and spontaneously place the dolls in a monotonic order. Moreover, when copying a model, they do not use the model's physical arrangement, but invent their own arrangements. When "copying" a model's horizontal arrangement of the dolls, 3-year-old children made 13 different arrangements, all of them monotonic (24). In other words, children copy the concept of monotonic order but invent their own instantiations. The child's understanding of monotonic order assures that he can recognize the consistent order of the A to E sequence used in testing transitive inference.

Chimpanzees, when given the dolls, neither spontaneously placed them in a monotonic order nor copied the model's monotonic order (24), suggesting that they lack the concept of monotonicity. Other species have not been tested, but if the chimpanzee lacks the concept, prospects for other species seem

How is it possible for species that lack the concept of monotonicity to do transitive inference? They probably use a hardwired mechanism and do not do it as humans do. Earlier, we suggested that animals are not capable of causal reasoning. How can they have a hard-wired mechanism for one kind of reasoning but not the other? Causal reasoning is more complex than transitive inference, involving not one simple inference, like transitive inference, but many inferences. Evolving a simple hard-wired mechanism is therefore less likely.

TOM

The advanced function most clearly associated with the reorganization of the human brain is complex social cognition. No less than language, it distinguishes humans from animals. The function is precocious, one of its earliest signs being empathy, which is found in 18-month-old infants. When an infant sees an individual in distress, for example, a child who cries when her teddy bear breaks, the infant consoles her, pats her, speaks softly to her, and may even try to fix the teddy bear (41).

Do either of the two basic evolutionary models for altruism kin selection (42) and reciprocal altruism (43)—explain empathy? In fact, empathy is not confined either to kin or to individuals who have been helpful in the past; it has only one triggering condition: an individual in distress. Nevertheless, the evolutionary factors may have contributed to the evolution of empathy. The kinship level was high in hunter-gatherer bands, not only among the men, but also among the women (who were often sisters or cousins, having been brought in as wives from the same village). Empathy is one of three principles of which human morality may consist: (i) do not harm others; (ii) deal fairly with others; and (iii) help those in distress. The power of these simple princples lies in their fecundity. "Harm" may consist of either physical or mental injury: hitting another or telling lies about him. "Fairly" is equally prolix and may take innumerable forms, such as paying proper wages or sharing goods. "Distress," too, includes innumerable examples ranging from a minor accident to the loss of a loved one. It is because humans can recognize all the forms that fecundity is effective.

Further evidence of precocious social cognition lies in the 6-month-old infant's division of the world into physical and psychological objects. Physical objects move only when acted on by another objects; whereas psychological objects are self-propelled (44). Psychological objects interact with one another, and infants—using the intention or social motive they attribute to the actor—assign valence to the interactions.

When one object hits, bites, etc., another, the infant assigns negative valence; when one objects caresses, strokes, etc., another, the infant assigns positive valence. Similarly, when one object seeks to achieve a goal, and a second object helps, they assign a positive value. When one object seeks to achieve a goal, and a second object interferes, they assign a negative valence (45).

Does the infant assume that the recipient of the action recognizes the intention of the actor? Does it expect the recipient to reciprocate? For instance, if object A was hit by object B, does the infant expect A either to interfere with the goal-seeking of B, or hit B? Although these questions remain to be answered, the fact that it is sensible to raise them in the case of 10-month-old infants testifies to the magnitude of the early social competence of the human.

Looking time tests show that infants assign higher priority to similarity in valence than to similarity in physical form. If, for example, an infant is shown one object hit another until it habituates and ceases to look and is then shown one object interfere with another, despite the physical difference between the two actions, the infant does not recover. If, however, following habituation on hitting, the infant is shown one object help another, it recovers and looks again. In another words, a change in valence restores the infant's interest, whereas a change in physical form does not (45).

Human adults explain the actions of others by attributing states of mind to them, such as want, belief, hope, trust, promise, etc. Chimpanzees and monkeys do the same, albeit in a highly circumscribed way. The animals attribute only two mental states, goal-seeking and perception. For instance, if a monkey sees food close to its trainer, and the trainer happens to be looking to the right, it will attempt to steal food from the left, suggesting that

the monkey attributes perception to the trainer, as well as the goal of preventing the monkey from taking food.

Competition has been hailed as the magic key for bringing out the animal's motivation to use TOM (46). The individual must, indeed, be motivated to use TOM, and competitive motivation is often easy to arrange; however, cooperative motivation, once arranged, is as effective as competitive.

When home-reared chimpanzees were tested in the laboratory, animals and trainers often had an amiable relation, and tests were based on cooperation. For instance, juvenile chimpanzees were required to choose between two containers. But they hesitated to choose. A barrier blocked their view, preventing them from seeing which container had been baited. We added two trainers, stationing both of them behind the barrier. One of the trainers, as the chimpanzees could see, was in a position to observe the baiting; the other was not. Before making their choice, the chimpanzees were allowed to request help from the trainers. Whichever trainer they chose then pointed to one of the containers. Three of the four animals choose, from the first trial, the trainer who could observe the baiting. These animals not only attributed perception to the trainer, they inferred that the trainer's directions would be honest not deceptive (47).

Chimpanzee mothers do not recognize that their infants lack knowledge and cannot therefore, for example, crack nuts with rocks. Therefore, they do not teach them. Chimpanzees do not have the concept of knowledge, do not distinguish a knowing individual from an ignorant one, and do not attribute the mental state of knowing, perception, and intention being the only mental states they attribute (22).

Humans attribute embedded mental states, such as, John thinks that Bill thinks that Henry believes that John should put his kids in Sunday school. Women think that men think that they think that men think that women's orgasm is different. There is a behavioral counterpart to embedded mental states in human social behavior. One individual watches another individual watch yet another individual engage in some act. In the classroom, for instance, we may observe child A watch child B watch child C look at the teacher. In animals there is nothing comparable. In the wild, we sometimes see one chimpanzee infant watch its mother, another infant watch its mother, etc., but this is a string of independent acts, not a sequence in which each act is embedded in the preceding one. Animals neither attribute embedded mental states nor have embedded social behavior (22).

Humans are tied together in a tight social web. The human sense of self, for instance, is based on this web. Personal achievements, which give a human his sense of self, do not have an intrinsic value. The quality of a book, a scientific discovery, etc., is evaluated socially. How highly an individual regards himself depends on his judgment of how others regard him.

Language

The faculty of recursion has two expressions in humans: number and language [the recursion reported in birds (48) represents a weak degree of recursion, comparable with the double alternation (AABB) of raccoons, far below the minimum requirements for human language, number, etc.]. Digital numbers are infinite because every number has a successor based on adding one. Sentences in a recursive language can, in principle, be infinitely long. Recursion permits dependence among words that are physically remote. In the sentence, "If she uses lilac-scented soap, then Madge and I will blow bubbles with her," "if" and "then" are dependent on each other even though they are separated by a variable number of words. Recursion also permits phrases of like kind to be embedded in one another. One can talk of "Ida the red-haired women who left her hat in the theater, the old one that burned down, because arguing with Henry, her husband of forty years, who still has all his hair, wears a maroon smoking jacket in the evenings and is as broke as ever, had rattled her." The grammar of a recursive language permits an endless compacting of information limited only by human memory.

The hierarchical organization of information is a related case. Humans divide biological objects into plants and animals, plants into fruit and vegetables, fruit into..., etc. Whereas chimpanzees sort, for example, apple, grape, etc., into one bin, bread, cupcake, etc., into another, thus recognizing categories (24), and category is a precursor of hierarchical information, there is no evidence that they recognize class-inclusion, which is another precursor of the hierarchical organization of information. Class-inclusion requires that the chimpanzee recognize, for instance, that although apple is included in fruit, fruit is not included in apple. Children apparently do not acquire class-inclusion until ≈5 years of age, suggesting that chimpanzees will not acquire it. A good rule of thumb is this: Concepts acquired by children after 3 years of age are never acquired by chimpanzees (49).

When researchers examine the brain to find the location of the recursive function, will they find one recursive faculty, "shared" by number, language, and hierarchically organized information or three independent recursive faculties, each tied to its own system?

Is recursion an automatic part of human language, number, and organization of information, such that these systems have only a recursive form? Or do they occur in both recursive and nonrecursive forms, being recursive only under appropriate cultural pressure? Perhaps the answer is different for the three systems. Number is likely to differ from the other two cases because humans have an innate system (located in the left and right intraparietal sulci) for representing analogue quantities, a system they share with animals, as well as a second system for representing digital quantities, which they do not share with animals (50). Hunter-gatherers, unlike people today, often distinguished only two quantities, "few" and "many," having no need for digital numbers.

The shift from foraging to agriculture is an example of a cultural pressure that will bring a need for exact numbers. If a human stores eight bins of grain, he will want to receive eight bins when he collects it. Since the advent of agriculture (\approx 10,000 years ago), there have been no human groups (except for remnants of hunter–gatherers) that lack digital (recursive) numbers.

Humans do not have a second system for language or the storage of information, hence these systems may take only a recursive form. Although there are preliminary claims of hunter-gatherer groups with nonrecursive language; all investigated human languages are recursive. Is all human information storage hierarchical? One cannot say, because there has been no broad study of human information storage.

Because animals lack recursion (and human language is recursive), the animals' lack of language is attributed to this factor. But recursion is not the only factor animals lack. If a species lacked language, even a nonrecursive language would be an enormous boon. Yet, chimpanzees have no language of any kind, recursive or nonrecursive.

A number of factors stand between animals and language. For instance, chimpanzees lack voluntary control of their voice. When a chimpanzee wants the attention of its trainer, it does not call; instead, it pounds on a resonant surface. Chimpanzees, therefore, could not have speech. But sign language is a possibility, for they do have voluntary control of their hands.

Chimpanzee sign language, however, could not be comparable with human sign language, because chimpanzees also lack voluntary control of their face, and in human sign language, facial expression plays grammatical roles, such as denoting the boundary of clauses (51).

A weaker form of sign that dropped facial expression and relied exclusively on hand signs would still pose a problem for the chimpanzee. The young animal could not imitate the hand signs of its mother. Most species can imitate the object or location that a model chooses, but there is a second level of imitation in which the novice must copy the motor act of the model (this would be the requirement in the case of sign language). Motor acts are more difficult to copy than objects or locations, because motor acts are ephemeral, and one must form a mental representation of the motor act and then copy the representation (52). Only humans imitate motor acts, although chimpanzees, when taught by humans, can do so. But the untrained chimpanzee cannot, so if a mutant chimpanzee with a simplified sign language were to appear, the other chimpanzees could not copy it.

Teaching is essential for language. Not for grammar, which arguably cannot be taught, but for words. Children are taught their initial words by their mother, and only later do they acquire words more or less on their own. Inasmuch as chimpanzees do not teach, even if they possessed all the other factors mentioned above, they could not have evolved language. In humans, the evolution of teaching evidently preceded that of language.

Conclusion

Animal competencies are mainly adaptations restricted to a single goal. Human competencies are domain-general and serve numerous goals. For instance "planning" may be tied to episodic memory, suggesting a broad competence. However, if episodic memory is confined to one (or only a few) activities, planning itself will be a narrow competence. Differences in the evolutionary origins of animal and human abilities help explain why the one is tied to a single goal, and the other to indeterminately many goals.

In humans, teaching did not evolve in the context of food seeking (by stalking or coping with toxic food) as it apparently did in animals; but in a far broader context arguably involving TOM, language, and aesthetics. In causal reasoning, animal limitations are of a different kind: The sense of cause may originate in personal actions that result in a desirable or undesirable outcome. In the human, the sense graduates to impersonal actions: a rock that falls on a plant crushing it, a wind that blows out a flame, etc., to events that humans recognize as causal. Does the animal make the human transition, or does its sense of cause remain tied to personal action? This question awaits decisive evidence. Further, because animals have no concept of monotonic order, although "transitive inference" is widely found in animals, it cannot be based on logic or reasoning.

The broad range of cognitive cases, which includes teaching, causal reasoning, short-term memory, planning, TOM, etc., consistently shows fundamental limitations in the animal version of the human competence. There is no anomaly in the disparity—the disparity between human and animal cognition is compatible with the disparity between human and animal brain. The coming challenge is to understand the function of the cellular-level differences between human and animal brain. Work linking these neural changes to cognitive processes can now move forward.

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- 1. Darwin C (1871) Descent of Man (J Murray, London).
- 2. Preuss TM, Coleman GQ (2002) Cereb Cortex 12:671-691.
- 3. Nimchimsky EA, Gilissen E, Allman JM, Perl DP, Erwin JM, Hof P (1999) Proc Natl Acad Sci USA 96:5268-5273.
- 4. Semmendeferi K, Armstrong E, Schlecher A, Zilles K, Van Hoesen CW (2001) Am J Phys Anthropol 114:224-241.
- 5. Buxhoeveden D, Casanova MF (2002) Brain Behav Evol 60:125-151.
- 6. Sherwood CC, Rilling JK, Holloway RL, Hof PR (2008) in Encyclopedia of Neuroscience, eds Binder MD, HirokawaN, Windhorst V, Hirsch MC (Springer, New York)
- 7. Ullian EM, Sapperstein SK, Christopherson KS, Barres B (2001) Science 291:569-570.

- 8. Christopherson K, Ullian E, Stokes C, Mullowney C, Hill J, Agah A, Lawler J, Mosher D, Brownstein P, Barres B (2005) *Cell* 120:421–433.
- Caceres M, Suwyn C, Maddox M, Thomas JW, Preuss TM (2006) Cereb Cortex, 10.1093/cercor/bhl140.
- 10. Leyhausen P (1979) Cat Behavior: The Predator and Social Behavior of Domestic and Wild Cats (Garland, London).
- 11. Thornton A, McAuliffe K (2006) Science 313:227-229.
- Konner MJ (1976) in Kalahari Hunter-Gatherers. Studies of the !Kung San and Their Neighbors, eds Lee RB, Devore I (Harvard Univ Press, Cambridge, MA), pp 219–246.
- 13. Premack D, Woodruff G (1978) Behav Brain Sci 4:515-526.
- 14. Dennett DC (1978) Behav Brain Sci 1:568-570.
- 15. Leslie AM (1987) Psychol Rev 94:412-426.
- 16. Wellman HM (1990) The Child's Theory of Mind (MIT Press, Cambridge, MA).
- Perner J (1991) Understanding the Representational Mind (MIT Press, Cambridge, MA).
- Baron-Cohen S (1995) Mindblindness: An Essay on Autism (MIT Press, Cambridge, MA).
- Premack D (1984) in Handbook of Cognitive Neuroscience, ed Gazzaniga M (Plenum, New York), pp 15–35.
- Premack D (1991) in Cognition and the Symbolic Processes, eds Hoffman RR, Palermo DS (Erlbaum, Hillsdale, NJ), pp 303–325.
- 21. Premack D, Premack A (2003) Original Intelligence: Unlocking the Mystery of Who We Are (McGraw-Hill, New York).
- 22. Kawai N, Matsuzawa T (2000) Nature 403:39-40.
- 23. Blaisdell AP, Sawa K, Leising KJ, Waldman MR (2006) Science 311:1020-1022.
- 24. Premack D (1976) Intelligence in Ape and Man (Erlbaum, Hillsdale, NJ).
- 25. Michotte A (1963) The Perception of Causality (Methuen, Andover, MA).
- 26. Leslie AM, Keeble S (1987) Cognition, 25:265-288.
- 27. Raby CR, Alexis DM, Dickenson A, Clayton NS (2007) Nature 445:919 921.
- 28. Suddendorf T, Corballis MC (1997) Genr Psych Monogr 123:133–167.
- 29. Naqshandi M, Roberts WA (2006) J Comp Psych 120:345-357.
- 30. Mulcahy NJ, Call J (2006) Science 312:1038-1040.

- 31. Hauser MD (1992) Proc Natl Acad Sci USA 89:12137-12139.
- 32. Woodruff G, Premack D (1979) Cognition 7:333-362.
- Ristau CA (1991) in Natural Theories of Mind: Evolution, Development and Simulation of Everyday Mindreading, ed Whiten A (Basil Blackwell, Oxford), pp 209–222
- 34. McGongle BO, Chalmers M (1977) Nature 267:694-696.
- 35. Von Fresen L, Wynne CD, Delius JD, Staddon JE (1991) J Exp Psychol Anim Behav Process 17:334–341
- 36. Davis H (1992) J Comp Psychol 106:342-349.
- 37. Roberts WA, Phelps MT (1994) Psychol Sci 5:368-374.
- 38. Stein JN, Weaver JE, Zentall, TR (1995) Anim Learn Behav 23:76-82.
- 39. Bond AB, Kamil AC, Balda RP (2003) Anim Behav 65:479-487.
- 40. Grosenick NJ, Clement TS, Fernald RD (2007) Nature 445:429-432.
- Bischof-Kohler D (1991) in *Infant Development: Perspectives from German-Speaking Countries*, eds Lamb ME, Keller H (Oxford Univ Press, Oxford), pp 245–273.
- 42. Hamilton WD (1964) J Theor Biol 7:1-52.
- 43. Trivers RL (1971) Q Rev Biol 46:35-57.
- 44. Premack D (1990) Cognition 36:1-16.
- 45. Premack D, Premack A (1997) J Cognit Neurosci 9:848-856.
- 46. Lyons DE, Santos LR (2006) Philos Compass 1:481-492.
- Premack D (1988) in Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes and Humans, eds Byrne W, Whiten A (Oxford Univ Press, New York), pp 286–322.
- 48. Gentner TQ, Kenn KM, Margolash D, Nusbaum HC (2006) Nature 440:1204–1207
- Premack, D. (1986) Gavagai! Or The Future History of the Animal Language Controversy (MIT Press, Cambridge, MA).
- Dehaene S, Dehaene-Lambretz G, Cohen L (1998) Trends Neurosci 21:355–361.
- 51. Newport EL, Suppalla T (1999) in *The MIT Encyclopdia of the Cognitive Sciences*, eds Wilson R, Keil F (MIT Press, Cambridge, MA), pp 758–760.
- 52. Premack D (2004) Science 303:318-320.