gather visual information from the retina and propagate it through a series of visual and ultimately motor areas. However, the delays involved in this pathway could lead to serious instability in the control of movement (*7*). An alternative possibility, suggested by computational models, is that the brain uses a "forward model" that generates a much faster prediction of the consequences of a given motor command (*7*). The forward model contains an estimate of the arm's musculoskeletal properties and of external forces such as friction. The model combines these estimates with a copy of the motor command being sent to the arm from M1 (see the figure) and predicts, with minimal delay, the actual arm trajectory expected to result from that motor command. In the task set by Schwartz *et al.*, the output of the forward model could be represented by the PMv activity that lags M1 activity and encodes the visible (predicted) path of the cursor. By comparing the predicted movement with the required movement (the target contour) the brain can then make rapid corrections to the ongoing arm trajectory.

The likely contribution of PMv neurons to motor control does not, of course, preclude the possibility that this area also influences perception. Several important questions remain to be answered in this regard. First, it is necessary to determine whether the visual signals encoded in the PMv correlate with visual perception within an individual subject (a macaque monkey). Second, it must be established whether and how inactivation, lesioning, or other manipulations of premotor areas affect perception. Finally, it must be determined whether different populations of neurons within a single premotor structure contribute differentially to action and perception.

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PSYCHOLOGY

Is Language the Key to Human Intelligence?

David Premack

Humans have acquired six symbol systems: two that evolved—the genetic code and spoken language—and four that we invented: written language, arabic numerals, music notation, and labanotation (a system for coding choreography). Dobzhansky's quip "All species are unique, but humans are uniquest" raises the question: Is it language, the symbol system that evolved only in humans, that makes humans the "uniquest"? Dobzhansky's quip raises a more fundamental question: What exactly is the nature of human uniqueness?

The grammar or syntax of human language is certainly unique. Like an onion or Russian doll, it is recursive: One instance of an item is embedded in another instance of the same item. Recursion makes it possible for the words in a sentence to be widely separated and yet dependent on one another. "If-then" is a classic example. In the sentence "If Jack does not turn up the thermostat in his house this winter, then Madge and I are not coming over," "if" and "then" are dependent on each other even though they are separated by a variable number of words (*1*–*3*). Are animals capable of such recursion? In a paper on page 377 of this issue, Fitch and Hauser (*4*) report that tamarin monkeys are not capable of recursion. Although the monkeys learned a nonrecursive grammar, they failed to learn a grammar that is recursive. Humans readily learn both. The lack of recursion in tamarins may help to explain why animals did not evolve recursive language, but it leaves open the question of why they did not evolve nonrecursive language. Recursion is not, of course, the only preexisting faculty on which the evolution of language depends, and when we examine some of the other factors (listed in the table), we can see why animals did not evolve language of any kind.

Voluntary Control of Sensory-Motor Systems

A laboratory chimpanzee does not call to attract the attention of its trainer; instead, it pounds on a resonant surface. Similarly, when chimpanzees become separated in the compound, they do not call to one another, as humans would, but search silently until they see one another and then rush together. If, as the evidence suggests, vocalization in the chimpanzee is largely nonvoluntary (reflexive), speech could not have evolved. But then why don't chimpanzees sign to each other? The chimpanzee has voluntary control of its hands. However, sign language depends on the face as well as the hands, and facial expression in the chimpanzee is evidently as reflexive as vocalization. Facial expressions play linguistic roles in signing, such as denoting the boundaries of clauses. A signer processes emotional facial expression in the right hemisphere, but linguistic facial expression in the left hemisphere (*5*). This does not mean, of course, that chimpanzees could not have evolved a language based on pounding on resonant surfaces, arranging stones on the ground, and so on. But it does suggest that they could not have evolved one that is like either speech or sign. (Of course, speech and sign "travel" with the speaker in a way that stones and resonant surfaces do not.)

Imitation

Many species can copy the object (or location) chosen by a role model. This is the first level of imitation. There is, however, a second level of imitation when the individual copies not the model's choice of object, but rather the model's motor action. Quite a different kettle of fish. Now the individual must form a mental representation of the visually perceived action and produce an action conforming to the representation (*6*). Although humans, even as infants, can do this (*7*), most species cannot, the exception being chimpanzees but they require human training (*8*–*10*). Could language evolve in a species in which the young cannot imitate the action of the speaker?

Teaching

Teaching, which is strictly human, reverses the flow of information found in imitation. Unlike imitation, in which the novice observes the expert, the teacher observes the novice—and not only observes, but also judges and modifies (*6*). Imitation and teaching pair efficiently in humans. Imitation produces a rough copy; teaching smoothens it. A chimpanzee mother could not teach her infant anything because, although the infant watches her problem-solving intently, she never returns the infant's observation (*11*). If we asked a chimpanzee mother whose infant was learning to crack nuts with a rock (the chimpanzee's most complex technology), "Where is he

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now? Is he finally putting the nut on the anvil [root of a tree] or is he still leaving it on the ground? Is he hitting it with a rock or with his hand?" she could not answer, for she never looks. This helps to explain why it takes 10 years for the animal to acquire a technology that humans could probably teach it in a matter of days or weeks. Now, a human mother does not (arguably could not) teach her child grammar (*12, 13*), but she definitely teaches her child words (*3*). Could a species that does not teach evolve language?

Theory of mind

Human communication is intentional: A speaker's goal is to inform the listener. If the speaker says "Turn right" and the listener turns left, the speaker will correct the listener (because the listener's error violates the speaker's goal). If a vervet monkey signals "leopard" and its recipient takes countermeasures for python, will the monkey correct its recipient? There is no evidence that monkeys correct errant listeners or that their communication is intentional (*14*).

Recursion is so observable in human social behavior that it need not be inferred. In a classroom, we may observe child A watch child B watch child C watch the teacher, whereas among chimpanzees we may observe animal A watch its mother, animal B watch its mother, animal C … —an iteration of acts all on the same level, as opposed to the child's recursive embedding of acts. On the other hand, recursion (although a prominent feature of human social cognition) is not a necessary condition for theory of mind, that is, the attribution of mental states. Chimpanzees, we know from two sources, are capable of attributing goals. When properly pretrained, chimpanzees are capable of analogies—not only perceptual analogies, such as "small square is to large square as small circle is to large circle," but also functional ones, such as "can opener is to can as key is to padlock" (*15*). Turning a key and operating a can opener are not similar actions, nor are the types of objects in this analogy similar. The equivalence lies in the goal that the two actions share—the goal of opening (*6*). The chimpanzee's attribution of goal is corroborated by tests of a different kind. When shown videotapes that, in human eyes, depict a person "trying" to solve a problem, chimpanzees choose photographs showing the person carrying out an act that fulfills a goal (solves the problem) (*16*). The thought, "John thinks that Henry thinks that Donna thinks Bill's goal is to beat John," common enough in humans, is quite beyond chimpanzees. There is no evidence for recursion in chimpanzees. But there is evidence for the attribution of goals. This is a rare case: a nonrecursive competence that is nonetheless decidedly humanlike. It is as though chimpanzees had evolved a nonrecursive language.

FACULTIES THAT UNDERLIE THE EVOLUTION OF LANGUAGE

Faculties	Human	Chimpanzee	Monkey
Voluntary control of the voice, face, hands	+	Hands	Hands
Imitation, level 2	+	Only with human training	–
Teaching	+	–	–
Theory of mind recursive/nonrecursive	Recursive	Nonrecursive	–
Capacity to acquire recursive and/or nonrecursive grammar	Both	Nonrecursive*	Nonrecursive

*Fitch-Hauser test needs to be repeated with chimpanzees (*4*).

Grammar

Humans have the capacity to acquire a recursive grammar, whereas the available evidence indicates that animals do not. Do the words of the language-trained chimpanzee resemble those of the human? Although this question is easily answered in the case of sentences, it is not so easily answered in the case of individual words. What is a word? There is no science of words; linguistics is a science of sentences (*17*). If we fall back on operationalism, we find a fundamental property that chimpanzee words share with human words. The information a chimpanzee can retrieve with the name of an object approximately equals the information it perceives by looking at the object (*6, 18*). Chimpanzees, therefore, can do what humans do, engage in displacement—"talk" about things that are not present. But chimpanzees have only a few hundred words at most, compared to the thousands that humans have. The acquisition of words, like language use itself, becomes autonomous in the child but not in the chimpanzee. Hence, when Mary graduates from college with her 60,000 words, she will have engaged in language for about 75,000 hours, versus about 600 hours for a language-trained chimpanzee. There is a corresponding difference in storage capacity: 1350 cc versus 450 cc of brain. But does this difference make chimpanzee and human words qualitatively different (*3, 6*)?

Metaphors may be the principal verbal difference between the two species. Arguably, many human words are metaphors—words based on analogies, not sensory properties (*19*). Time, a classic example, is a spatial metaphor; that is, space has normal sensory properties—we can both see and feel it—but we can neither see nor feel time. English speakers represent time on the horizontal, placing earlier events to the left of later ones; Mandarin speakers use the vertical, placing earlier events above later ones (*20*). Chimpanzees, even when taught analogies, could not use them to form words. All their words are based on sensory experience.

Intelligence

What are the factors that distinguish human intelligence? A major distinctive feature of human intelligence is flexibility. Animals, by contrast, are specialists. Bees are adept at sending messages through their dances, beavers at building dams, the nuthatch at remembering the location of thousands of caches of acorns it has buried. But each of these species is imprisoned by its adaptation; none can duplicate the achievement of the other. The nuthatch cannot build dams; bees do not have an uncanny memory for hidden caches of food; beavers cannot send messages. Humans, by contrast, could duplicate all these achievements and endlessly more. Why? Is recursive language the key to human flexibility?

To understand human flexibility, let us return to the sensory-motor system, this time to the size and number of elements in the motor repertoire. The motor flexibility of a species, its play, even the technologies it develops, are all reflected in the composition of its motor repertoire. A contrast between chimpanzees and monkeys illustrates this point. A group of resting hamadryas baboons looks regal, all sitting in the same posture; a group of chimpanzees looks slovenly, all reclining in different postures (*21*). Not only motor plasticity but also play is highly limited in most monkeys. Technology follows suit. A form of play in chimpanzees, inserting sticks into holes, reappears in the straws they insert into orifices in termite mounds (*22*). Baboons, despite protracted observation of chimpanzees, never develop any technology for obtaining termites; they scrape up termites from the ground that have been left behind by the chimpanzees.

Not only can chimpanzees reproduce playful acts, they can simulate or image the actions, using mental representations to guide their problem-solving (*23*). When shown fruit overhead, a chimpanzee can picture placing two sticks together (a form of play), obtain the sticks, and use them to knock down the fruit (the match between play and technology is imperfect: Although needing sticks that form a vertical extension, the chimpanzee may attach the sticks at a 90° angle) (*24*).

The chimpanzee's simulation of motor acts, although limited, represents a preexisting capacity for a final development that appears only in humans. The human can recombine mental elements—mixing the features of one object with another—producing such things as ghosts (objects to which the transcendent properties of thought have been given, so that they can pass through walls), plants whose flowers have faces, humans who can fly, and so on. In other words, chimpanzees can represent what they perceive, whereas humans can represent what they imagine. The recombining of mental elements makes the counterfactual a natural step, and leads to science (as well as art) (*25*). Galileo's world without friction, where objects set in motion remain in motion, is clearly an imagined world and not a perceived one.

Human intelligence and evolution are the only flexible processes on Earth capable of producing endless solutions to the problems confronted by living creatures. Did evolution, in producing human intelligence, outstrip itself? Apparently so, for although evolution can do "engineering," changing actual structures and producing new devices, it cannot do science, changing imaginary structures and producing new theories or explanations of the world. Clearly, language and recursion are not the sole contributors to human uniqueness.

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STRUCTURAL BIOLOGY

Surprising News from the PCC

Bernhard Dobberstein and Irmgard Sinning

Proteins destined for secretion are targeted by signal sequences to the inner membrane of bacteria or to the endoplasmic reticulum (ER) of eukaryotic cells. At the membrane, these signal sequences initiate the translocation of newly synthesized (nascent) polypeptides across the lipid bilayer. Translocation is envisaged as the threading of the nascent linear polypeptide chain through a protein-conducting channel (PCC)—the SecY complex in bacteria and the evolutionarily conserved Sec61 complex in eukaryotes (*1, 2*). Newly synthesized membrane proteins are also inserted into these channels, but in contrast to secretory proteins, parts of these proteins—the transmembrane (TM) segments—are not completely translocated across the membrane but are released into the lipid bilayer. The PCC is thought of as a two-way gate with an aqueous pore for transport of a polypeptide across the membrane and a lateral gate for entry of TMs into the lipid bilayer. Much has been learned about the structure and function of the SecY/Sec61 channel [reviewed in (*2, 3*)]. It is widely accepted—and even reported in textbooks—that the actual pore of the channel is assembled from several SecY/Sec61 complexes. However, the first crystal structure of the PCC from the archaeon *Methanococcus jannaschii*, recently published by van den Berg *et al*. in *Nature* (*4*), provides strong evidence that a monomeric, not polymeric, SecY complex forms the pore through which proteins are translocated.

The SecY/Sec61 complex is a heterotrimeric membrane protein consisting of an α subunit (SecY in bacteria and Sec61α in mammals), a β subunit (SecG in bacteria and Sec61β in mammals), and a γ subunit (SecE in bacteria and Sec61γ in mammals). The α subunit is thought to span the membrane 10 times, whereas the smaller β and γ subunits each span the membrane once or twice. Site-specific cross-linking of different parts of newly synthesized polypeptides reveals that the hydrophilic pore of the PCC is formed by α subunits. These experiments also show that the hydrophobic segments of signal sequences and TM sequences of the polypeptide move during their insertion from the α subunit of the channel, via an interface, into the lipid bilayer (*5–7*).

Low-resolution structures of isolated SecY and Sec61 complexes or of the Sec61 complex bound to a ribosome, obtained by cryo-electron microscopy (cryo-EM), revealed ringlike structures with an outer diameter of about 100 Å, a pore size of 15 to 20 Å, and a calculated mass equivalent to three or four SecY/Sec61 complexes (*8, 9*). Furthermore, the central cavity in the Sec61 complex was found to align with the exit site of the tunnel in the large ribosomal subunit through which nascent polypeptides are extruded during their synthesis. The observation that large, reactive molecules (20 to 50 Å in size) could gain access to the nascent polypeptide in the channel also provided support for the presence of a large aqueous pore across the membrane (*3*). The ribosome and chaperone proteins were suggested to seal the pore on the cytoplasmic and lumenal side of the ER membrane, respectively. More recently, the structure of a SecY complex was determined at 8 Å resolution by cryo-EM from two-dimensional crystals (*10*). The SecY complex appeared to be a dimer with a central cavity measuring 16 Å by 25 Å that was closed on the periplasmic side; a pore was proposed to form between the two monomers (*10*). These data suggested that the PCC is formed by SecY/Sec61 complex oligomers. However, the results of a biochemical analysis of the oligomeric state of SecY complexes by Yahr and Wickner (*11*) strongly challenged this view. They concluded that the active form of the PCC associated with its translocation motor SecA is a monomeric SecY complex because (i) formaldehyde cross-link-

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