A 'Handy' Guide to Primate Evolution

The hands of monkeys and apes may hold clues to the riddle of human handedness and brain organization

By BRUCE BOWER

A monkey sits expectantly in psychologist Patricia K. Kuhl's laboratory. The animal wears earphones that keep its head in a fixed, upright position. Its hands rest at its waist near a telegraph key that the monkey can feel but not see. A green light begins to blink and the monkey presses the key to signal readiness. It hears two speech syllables through the earphones, realizes the sounds are different and correctly lifts the key.

Hardly an amazing feat, but Kuhl, of the University of Washington in Seattle, has noticed something remarkable about the exercise. Although either hand could be used to press the telegraph key, every one of 30 monkeys trained in the procedure by Kuhl and her colleagues uses its right hand.

"In 10 years, we have not seen a single animal use the left hand," Kuhl says. "Each animal is tested daily for about two years, and we have never seen an animal reverse this hand preference."

Yet the same animals use either hand in other situations, such as grabbing monkey chow from a feeder and taking apple pieces offered them.

It is generally assumed that a species-wide tendency to favor one hand over the other is characteristic only of humans and is related to the development of brain hemispheres with specialized functions. The right hemisphere guides the left arm and hand, and the left hemisphere controls the right arm and hand. Important mental abilities, such as speaking and understanding language, are largely handled by the left hemisphere in most people, making that side "dominant"; this is thought to have promoted a surplus of right-handers.

However, a growing number of researchers are challenging the long-held notion that nonhuman primates have no hand preferences. These scientists also point to accumulating evidence for specialized brain-hemisphere functions in several primate species. Their argument generates considerable controversy among primate researchers, but if it holds up, the implication is that traits thought to be uniquely human — including handedness, specialized brain hemispheres and language — can be traced back to primates living tens of millions of years ago.

Kuhl is one proponent of the idea that monkeys have hand preferences. Based on laboratory observations such as the one described above, Kuhl suggests monkeys use their right hands to perform well-practiced, precise manipulations, especially when they cannot clearly see what they are handling.

Kuhl's work — as well as recent findings by several other investigators — lends support to a controversial theory devised by three linguists, Peter F. MacNeilage (also a psychologist) and Bjorn Lindblom of the University of Texas at Austin and Michael G. Studdert-Kennedy of Yale University. They contend hand preferences do indeed exist among nonhuman primates and have gone largely unnoticed by researchers. Furthermore, say the linguists, patterns of hand use among prosimians, monkeys and apes hold clues to the evolutionary forces promoting human right- and left-handedness, as well as the functional development of the human brain with its important language abilities regulated in the left hemisphere and critical types of perception handled by the right hemisphere.

MacNeilage and his co-workers dispute the longstanding theory that hand preferences first appeared as evolutionary pressures forced the ancestors of modern humans to manufacture and use stone tools. In the November BEHAVIORAL AND BRAIN SCIENCES, they assert that new evidence from a number of researchers "makes it no longer possible to deny the existence of handedness in nonhuman primates."

In the same journal, for example, psychologist Jeannette P. Ward of Memphis (Tenn.) State University describes a left-hand bias in food-reaching among members of several prosimian species housed in zoos, including black-and-white ruffed lemurs, black lemurs, ring-tailed lemurs and lesser bushbabies. The animals nearly always use their left hands to reach for food floating in a moat, she says, while their hand preferences for reaching during foraging lean only slightly to the left.

The bushbabies Ward studied in the laboratory used a preferred hand more often when standing on two feet rather than clinging to a cage or tree. Furthermore, Ward notes, nine of 10 animals turned their bodies more often in one direction — eight to the left and one to the right. The rigors of maintaining balance and movement when standing on two feet appear to set the stage for biases in turning and hand use, she says.

Psychologists James King and Virginia Landau of the University of Arizona in Tucson report strong left-hand preferences among 18 squirrel monkeys attempting to catch goldfish. In one task, the monkeys caught fish housed in a bowl; in another they caught fish swimming in a wading pool. While moving fish attract the left hand, the monkeys show no overall hand preference in reaching for a stationary piece of food, the researchers say. Their study will appear in a book Ward is preparing.

French investigators Joël Fagot and Jacques Vauclair of the National Scientific Research Center in Marseilles found a significant left-hand preference in six baboons and seven of eight gorillas who had to align a window in a sliding vertical Plexiglas panel with an opening leading to a food reward. Their research will appear soon in NEUROPSYCHOLOGIA.

Such findings raise the question of why years of work failed to detect handedness in nonhuman primates. Many previous studies of reaching among monkeys and apes came up empty-handed, MacNeilage says, because the animals were presented with immobile, easily grasped objects. This approach typically results in an approximately equal number of left- and right-handers, and a varying percentage of animals with no hand preference.

"You really have to make the animals work to see consistent left- and right-hand preferences," he asserts. "A good challenge is hard to come up with, but catching goldfish in a bowl is one good example."

MacNeilage's argument for primate hand preferences receives further support from investigations showing a divvying up of some mental responsibilities in the brain hemispheres of monkeys. Specialized brain hemispheres in humans, with one side being dominant, are associated with handedness.

Two independent studies indicate the left side of the Japanese macaque's brain is critical for the animal to understand the "coo" sounds macaques use for simple communications. Macaques show a significant right-ear advantage in discriminating between two classes of coos, and lose their ability to recognize the communication sounds after surgical removal of a critical portion of the brain's left temporal lobe. If the corresponding area of the right temporal lobe is taken

out, monkeys can still distinguish between the two coos.

The right hemisphere is nevertheless important for processing visual information. When researchers sever a rhesus monkey's corpus callosum — the bundle of nerve fibers connecting the brain hemispheres — only the left eye (controlled by the right hemisphere) effectively discriminates between photographs of monkeys' faces. (To a monkey, and to humans who observe them carefully, monkey facial features can be quite distinctive.)

Humans also have a right-hemisphere advantage in recognizing faces.

The left hemisphere of "split brain" monkeys is better at distinguishing between tilted lines differing in slope, report biologists Charles R. Hamilton and Betty A. Vermeire in the Dec. 23 SCIENCE. In human studies, the right hemisphere is superior on similar visual orientation tasks, note the scientists, both at the California Institute of Technology in Pasadena.

The accumulating evidence leads MacNeilage and his colleagues to propose a theory of brain evolution based on the assumption that early primates preferentially used their right arms and legs, with the left side of the body in a supporting role. Their "postural origins" theory holds that the right side of the body still takes the lead, with some exceptions, in humans.

The researchers' scenario holds that about 60 million years ago the earliest prosimians leaped about in the trees, usually clinging to branches with the help of the right hand and reaching for food with the left hand. This prodded the right side of the prosimian brain toward assuming control of perceptual and motor abilities required for left-handed predation, or food gathering.

At the same time, the theory goes, the brain's left hemisphere gradually assumed control of body posture and positioning. As higher primates began walking on all fours and assuming two-legged stances while foraging, the left-hand preference for grasping food while clinging to trees was modified. The right side of the body led the way in foraging activities and the right hand became favored for manipulation and practiced acts, such as cracking open nuts and holding fruit near the mouth; the left hand was still favored for reaching and pulling in food and other objects.

The left hemisphere's specialization in organizing body posture may also be related to its important role in vocal communication among monkeys and spoken language among humans, maintain MacNeilage and his colleagues. Vocal production involves numerous muscles in the face and throat; a "controller" mechanism on one side of the brain, which does not need to take time to communicate with the other hemisphere, can quickly orchestrate this complex muscular activity, they propose.

The "postural origins" theory does not lay bare the mysteries surrounding hemisphere specializations, handedness and the capacity for language, MacNeilage acknowledges, but it provides a framework for interpreting related findings.

For instance, according to a report in the September 1988 AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY, the right-arm bones of 150 rhesus monkeys are slightly larger than those on the left in several areas where important muscles are attached. The size differences are statistically significant, say anthropologist Dean Falk of the State University of New York at Albany and her colleagues, although not as pronounced or as widespread as a right-arm size advantage noted by other investigators in human skeletal remains from both right- and left-handers.

The bone measurements indicate the monkeys' right-arm muscles involved in flexing and extending are also larger, the researchers note.

This, they continue, supports the contention of MacNeilage and his colleagues that, although nonhuman primates do not display the across-the-board right-handedness typical of most humans, they have a right-hand preference for fine manipulations, such as grooming.

A preference for right-handed reaching as well as a right-sided orientation of the body shows up early in most humans. In a study conducted several years ago, Patricia Kuhl had 6-month-old human infants watch an experimenter, sitting either to their right or left, playing with toys while a syllable was repeatedly presented from a loudspeaker on the other side. The infants learned to turn their heads toward the loudspeaker when the syllable changed. A correct response caused a toy bear on top of the loudspeaker to bang its drum.

If the loudspeaker was on an infant's right and the experimenter on the left, infants constantly turned toward the right, Kuhl says, although they knew the bear would spring into action only when a syllable sound changed. When the setup was reversed, infants consistently watched the experimenter and turned their heads toward the loudspeaker upon hearing a new syllable.

"Right-postural bias is exhibited very early in human infants, and is quite strong," Kuhl concludes.

Within the first month of life, the vast majority of babies prefer to orient their heads to the right, says psychologist George F. Michel of Children's Hospital Medical Center in Boston. Michel and psychologist Debra A. Harkins of Clark University in Worcester, Mass., find newborns who prefer to turn their heads to the right become right-handers later in childhood, while those who turn to the left become left-handers.

Similar types of preferences in orienting the head and limbs among ancient nonhuman primates may have promoted handedness in later primates, including humans, suggest Michel and Harkins in the June 1987 BEHAVIORAL AND BRAIN SCIENCES — a notion welcomed by MacNeilage and his collaborators.

But Michel and Harkins say reconstructing evolutionary influences from

the behavior of living species is "fraught with pitfalls." Primate handedness in natural conditions must be studied far more carefully before evolutionary theories can be taken seriously, they assert.

No good evolutionary explanation exists, Michel and Harkins add, for the shift from left-handed reaching in monkeys to right-handed reaching in humans.

Canadian psychologist Melvin A. Goodale of the University of Western Ontario in London suggests one possibility. The left side of the brain is particularly important for the timing and sequencing of complex motor behaviors such as throwing objects and articulating speech sounds, he says. Reaching movements made by patients with left-hemisphere damage are markedly disorganized, Goodale points out; reaches made by patients with right-hemisphere lesions are comparable to those of healthy controls, although the former group takes much longer to initiate a reach. This is consistent with a right-hemisphere role in visual and spatial processing.

An increasing demand for accurate, speedy reaching and throwing among early human hunter-gatherers may have emphasized the left hemisphere's strengths and promoted both right-handed reaching and manipulating, Goodale says.

His proposal, and the entire "postural origins" theory, starkly contrasts with a genetic theory of human handedness developed in the 1970s by Marian Annett of Coventry (England) Lanchester Polytechnic. Annett contends population-wide hand preferences are a purely human characteristic. According to her, the majority of individuals inherit a "right-shift" gene weighting the odds in favor of right-handedness and a dominant left hemisphere. Those without the genetic predisposition randomly divide into right- and left-handers, in her view; hemispheric specializations are also randomly distributed in these people.

In practice, there is considerable diversity in hand preferences, Annett says. About 60 percent of humans develop consistent right-handedness and around 10 percent show a strong preference for the left hand; the rest are mainly right-handed but display at least one left-hand preference. For instance, some people write and reach with the right hand but throw a ball with the left.

Yet the relationship of hand use to brain function is more complex than MacNeilage and his colleagues acknowledge, Annett says. For example, the ability to speak usually depends on the left side of the brain, even among left-handers. Furthermore, of the estimated 9 percent of the population who speak mainly with the help of the right hemisphere or both hemispheres, most are right-handers.

This indicates a relatively weak connection between hand preference and speech control in the brain, says Canadian neuropsychologist Sandra F. Witelson of McMaster University in Hamilton, Ontario. Witelson asserts it is difficult to define hand preference when studying brain function, since, as Annett observes, about one-third of the population uses both the left and the right hand when a variety of tasks are considered.

Thus, hand preferences in nonhuman primates probably did not provide a big push to human hemisphere specialization, Witelson concludes. The reverse is more likely, she suggests. First, the brain hemispheres parceled out responsibility for certain mental skills, such as sequential processing on the left side and spatial orientation on the right; hand preferences developed once the brain changes occurred.

But behavior is, in the words of biologist Ernst Mayr, the "pacemaker of evolutionary change," MacNeilage responds. Witelson does not explain what behaviors led to the mental adaptations in each hemisphere, he argues. The postural origins theory, on the other hand, emphasizes evolutionary consequences of behaviors such as one-handed predation among tree-dwelling prosimians and foraging while standing on two legs.

The postural origins theory also accounts for many left-handers with left-hemisphere language control, MacNeilage says, but only when an additional part of the body is considered: the foot.

Foot preference, usually determined by observing the foot used for kicking, provides a good measure of whether an individual's posture is biased toward the right or left, MacNeilage asserts. In fact, foot preference may be more closely aligned with brain function than is hand preference, he says.

People tend to favor one foot over the other, MacNeilage points out, but foot preferences often do not align with hand preferences. In a recent survey of footedness studies, Canadian psychologist Michael Peters of the University of Guelph, Ontario, finds about one-half of left-handers are right-footed. Virtually all right-footed left-handers tested so far display a right-ear advantage in discriminating between sounds played through headphones. The evidence suggests the left hemisphere is dominant in right-footed people, even if they are left-handed.

Footedness tests have not been conducted on nonhuman primates, MacNeilage notes, because there is not yet an established way to elicit foot preferences in monkeys and apes.

MacNeilage and his colleagues conclude that language and body posture are critically controlled by the left hemisphere in more than 90 percent of the human population, including left-handers who are right-footed. This is consistent with the postural origins theory, they say, although exceptions to the left-brain specializations turn up in about 1 person out of 10.

"Lurking in the background," MacNeilage adds, is the theory of the late Harvard University neurologist Norman Geschwind (SN: 4/27/85, p.263). He believed that if a human fetus is highly sensitive to the male hormone testosterone, or if it is exposed to high levels of testosterone, left-brain development is stunted and the right side grows larger. The consequence is left-handedness.

The postural origins theory is "interesting, even appealing," remarks psychologist Michael Tomasello of Emory University in Atlanta. Still, he notes, more and better studies of nonhuman primates — particularly chimpanzees and orangutans — are essential before it can be properly judged.

Taking a narrower view than that of MacNeilage and his colleagues, Tomasello says specialized speech mechanisms, not language in general, are all that have been located in the left hemisphere. But the notion of evolutionary forces playing a role in human speaking ability mirrors the position of linguist Philip Lieberman of Brown University in Providence, R.I. Lieberman argues that Broca's area, a left-hemisphere structure involved in speech production and the comprehension of complex sentences, has a primitive counterpart in the ape brain and a long evolutionary history.

Lieberman's view, as well as that of MacNeilage and his co-workers, contradicts an influential theory of language developed by linguist Noam Chomsky of the Massachusetts Institute of Technology. Chomsky contends the brain structures governing human language have no biological precedent. An innate set of grammatical rules, or "deep structures," is generated by the human brain, enabling people to speak and understand strings of words and sentences, according to Chomsky.

The laws of scientific skepticism, perhaps embedded more firmly in the brain than Chomsky's deep structures, ensure continued debate over the postural origins theory. But from now on, many researchers will look at the hands and feet of nonhuman primates with a renewed curiosity. □