

CHAPTER 5

THE EVOLUTION OF BODY, BRAIN, BEHAVIOR, AND MIND FROM BASAL MAMMALS TO PROSIMIANS

The Dawn of Substantive Perception

5.1	General Visceral, Somatic, Behavioral, and Mental Advances in Mammals	240
5.1.1.	The Origin and Radiation of Mammals	240
5.1.2.	Visceral and Somatic Advances in Mammals	241
5.1.3.	Neural and Behavioral Advances in Mammals.....	246
5.1.4.	Affective Advances in Mammals	251
5.1.5.	Perceptual, Mnemonic, and Cognitive Advances in Mammals	255
5.2.	Brain, Behavior, and Mind in Basal Mammals: Insectivores and <i>Tupaia</i> s.....	267
5.2.1.	Generalists and Specialists in Mammalian Evolution	267
5.2.2.	Somatic Traits, Behavior, and Brain Organization of Insectivores.....	270
5.2.3.	Somatic Traits, Behavior, and Brain Organization of <i>Tupaia</i> s	274
5.2.4.	Affect and Cognition in <i>Tupaia</i> s	283
5.3.	Brain, Behavior, and Mind in Basal Primates: The Prosimians	287
5.3.1.	The Origin and Arboreal Adaptations of Primates	287
5.3.2.	Advanced Somatic, Reproductive, and Developmental Traits of Prosimians	288
5.3.3.	Behavioral and Neural Advances in Prosimians	289
5.3.4.	Affective Advances in Prosimians	300
5.3.5.	Cognitive Advances in Prosimians	302
5.3.6.	Our Basal Mammalian and Prosimian Legacies	306

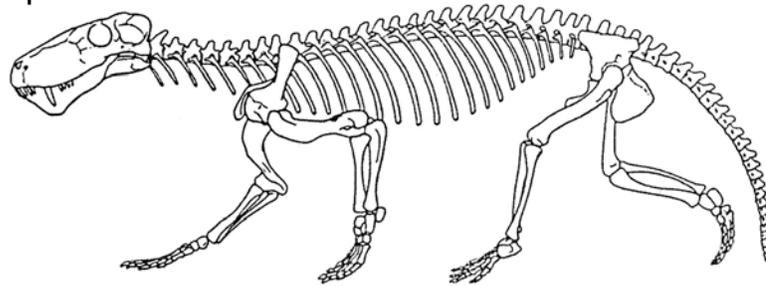
5.1. General Visceral, Somatic, Behavioral, and Mental Advances in Mammals

5.1.1. The Origin and Radiation of Mammals. It is generally believed that the ancestors of mammals were the Therapsids, a line of reptiles that emerged about the middle Permian of the Paleozoic era and diversified greatly during the early Triassic of the Mesozoic about 250 m.y.a. (Strickberger, 2000; Kemp, 2006). There were two major orders of Therapsids, the herbivorous Anomodonts and the carnivorous Theriodonts (Fig. 5-1A). The Therapsids displayed several mammalian traits. Expansion of their brain case indicates growth in brain volume. Possession of heterodont teeth—incisors, canines, and molars—indicates reliance on a greater variety of nutrients and their better preparation for digestion. Strong shoulder and hip girdles and long limbs suggest improved running ability. However, it is not currently known whether the reptilian scales were transformed in Therapsids into insulating hair and made any advances toward internal temperature regulation (homeothermy). Mammals began to evolve in the late Triassic and early Jurassic, about 225-200 m.y.a. It is assumed that the earliest mammals were egg-laying (oviparous) monotremes, like the extant Australian echidnas and platypus. Monotremes have no nipples but ducts that secrete milk onto the fur that the hatched young lick or suck. Live-bearing (viviparous) marsupials that deliver their offspring at an early embryonic stage of development, which then suckle in the mother's pouch, emerged later. Placental mammals, which carry their offspring in the uterus until an advanced stage of fetal development, evolved still later. An early placental mammal recently unearthed in northeastern China, *Eomaia scansoria*, lived about 125 m.y.a. (Ji et al., 2002). It was a small, furry insectivore with small fingers and curved claws adapted for tree climbing (Fig. 5-1B). Shorter rib cage indicates greater trunk flexibility for jumping and perhaps sitting.

It is generally assumed that the early homeothermic mammals with relatively large crania were stealthy and cunning creatures that lived in the shadow of dinosaurs during the Jurassic and Cretaceous. Using their brain against the brawn of the large reptiles, they scavenged and preyed on small invertebrates and vertebrates, preferably perhaps at night when the cold-blooded reptiles were liable to be dormant. The opportunity of these primitive mammals to diversify came at the end of the Cretaceous, about 65 m.y.a., when the dinosaurs became extinct. In time, they succeeded in colonizing virtually all niches of the planet and eventually became its dominant inhabitants. Omnivorous species came to occupy lightly forested regions, feeding voraciously on whatever was available on the ground and in the bushes and trees. Arboreal species evolved that, inhabiting dense forests, specialized on consuming leaves, fruits and berries, and by leaping from tree to tree could avoid descending to the ground where predators lurked. Various herbivores became adapted to life in more open spaces, consuming leaves and plants, grasses and seeds, and digging for tubers and roots. Some specialists, the bats, became airborne, dolphins, seals, and whales returned to the seas. Then, during the middle Cenozoic (about 35-25 m.y.a.) highly specialized, large browsing and grazing mammals came into existence, living off the rich resources of the vast grasslands, and these were joined by powerful carnivores that preyed upon them. The large herbivores and carnivores became the dominant creatures of the planet during the Miocene and Pliocene (about 25-5 m.y.a.), roaming over the land in climatic zones ranging from the tropics to the arctic. Mammals succeeded in accomplishing all that because they acquired many advanced visceral and somatic traits as well

A LATE REPTILE AND AN EARLY MAMMAL

A. Therapsid



B. *Eomaia*

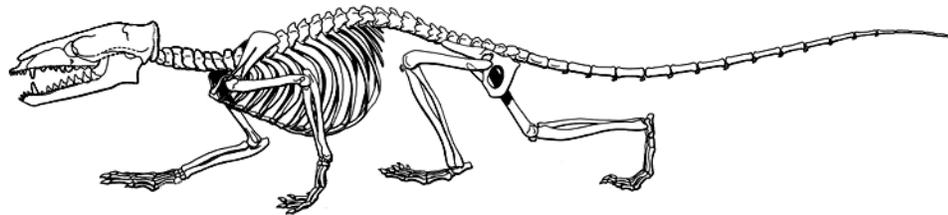


Fig. 5-1. **A.** Skeleton of a carnivorous therapsid (note lower canine tooth), a mammal-like reptile from the late Permian. **B.** Skeleton of *Eomaia*, a furry mammal from about 125 m.y.a. Note shortened rib cage. (A, after Strickberger, 2000. B, after Luo et al., 2002.)

as an expanding and improved brain mechanism that endowed them with improved behavioral abilities and mental powers.

5.1.2. Visceral and Somatic Advances in Mammals. Momentous advances in visceral, somatic, behavioral and neural organization relative to lower vertebrates are distinguishing traits of mammals. Starting with the visceral and somatic advances, we consider below the following. (i) Increased basal metabolism, a property that has greatly enhanced the somatic strength and endurance and the behavioral preparedness of mammals. (ii) Homeothermy (internal temperature control), which enables mammals to survive and prosper in a variety of climatic zones and through all seasons. (iii) Heterodonty and mastication, the possession of specialized teeth for grabbing and tearing prey, grinding tough plants, and cracking bone and hard nuts. (iv) Increased and prolonged care for offspring by the mother. This includes: viviparity (live bearing) based on a period of intrauterine embryonic and fetal development of offspring, which assures them with steady nourishment and protection; and the postpartum secretion of milk by mammary glands (lactation), and the suckling and caring for the young until they become self-sufficient to feed themselves. (v) The transformation of the forelimbs in many genera into organs of object palpation and manipulation.

Increased Basal Metabolism. Basal metabolic rate is defined as the amount of oxygen used by an animal at rest in proportion to its body weight. The basal metabolic rate of mammals is, on the average, ten times higher than that of reptiles of comparable size, and it is largely supported by aerobic metabolism (Carroll, 1988; Armstrong, 1990; Shimizu, 2001). Heightened basal metabolism enables mammals to sustain their visceral and somatic processes, and brain

functions and behavioral activities for extended periods under varied conditions. Among these are a high rate of respiration and blood circulation, prolonged maintenance of postural stability through the contraction of antigravity muscles, prolonged wakefulness mediated by an active brain, and sustained behavioral transaction with the environment.

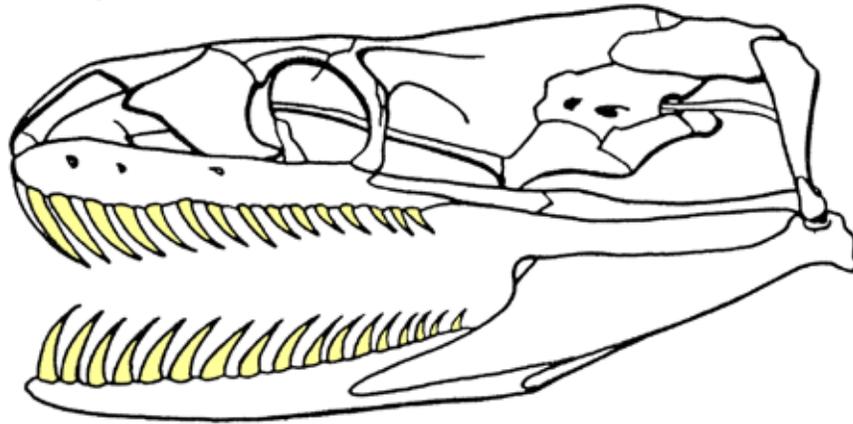
Homeothermy. Because of their low basal metabolism, cold-blooded amphibians and reptiles do not generate enough heat to compensate for heat loss when their habitat gets too cold, and they lack adequate mechanisms to dissipate heat when it gets too warm. Since the thermal range required for the operation of most vital functions is quite narrow, most ectotherms are largely confined to regions with a warm climate. And those ectotherms that live in temperate and cold zones do so by confining their vital behavioral transactions to the season or time of the day when it is warm, or engage in various overt behaviors—such as bask in the sun to warm up, dip into the water to cool off, or bury themselves underground—to survive. In sharp contrast, endotherms, like birds and mammals, possess internal mechanisms to generate, conserve and dissipate heat. Hence, they can effectively engage in behavioral transactions through winter and summer, during cold nights and hot days, and in various climatic zones ranging from the tropics to the arctic.

Since most visceral processes and bodily activities generate heat, the high metabolic rate and sustained motility of mammals necessarily results in temperature gain. And when the heat generated is not sufficient to compensate for heat loss during cold weather, mammals elevate their core temperature by increased nutrient oxidation (burning) and enhanced muscular exertion, such as shivering or running about. Mammals' body covering also plays a role in temperature conservation. Their hairy skin, in contrast to the scaly skin of reptiles, is an excellent insulator, and raising the hair (piloerection) to form an air-filled insulating layer when it gets cold further enhances heat conservation. For added protection, some mammals also grow a heavy fur coat during the winter. Heat dissipation, in turn, is aided by a variety of mechanisms. Some mammals, like ourselves, perspire when their body temperature rises; the evaporation of water secreted by the cutaneous sweat glands effectively cools the body. Another mechanism is hyperventilation (panting), the exhalation of hot air and cooling the body interior by evaporating water present in the lungs, throat, tongue and mouth. Heat dissipation may also be aided by dilation of the capillaries with concomitant increase in blood flow and vaporization through the skin. In summary, endothermy is an advanced evolutionary trait that allows mammals to remain behaviorally active while the external temperature fluctuates widely over its daily and seasonal cycles.

Heterodonty and Mastication. The teeth of most extant reptiles are homogeneous, peg-like, sharp tools suitable to grab a prey and puncture it, and curving inward to ensure that the captured prey does not escape (Fig. 5-2A). Reptiles do not use their teeth for mastication; they swallow large chunks of food, often the entire prey, in one piece. This is not an economical feeding procedure, since much of what is swallowed may be of little nutritional value or indigestible. In contrast, the typical mammalian dentition consists of a series of specialized devices: incisors, canines, premolars, and molars (Fig. 5-2B). Incisors are chisel-shaped cutting tools that help bite off mouthful pieces from a larger source. Canines serve mainly as scissor-like instruments to cut through tough skin. They may also be used as a weapon to

REPTILIAN AND MAMMALIAN TEETH

A. Python



B. Early Placental Mammal

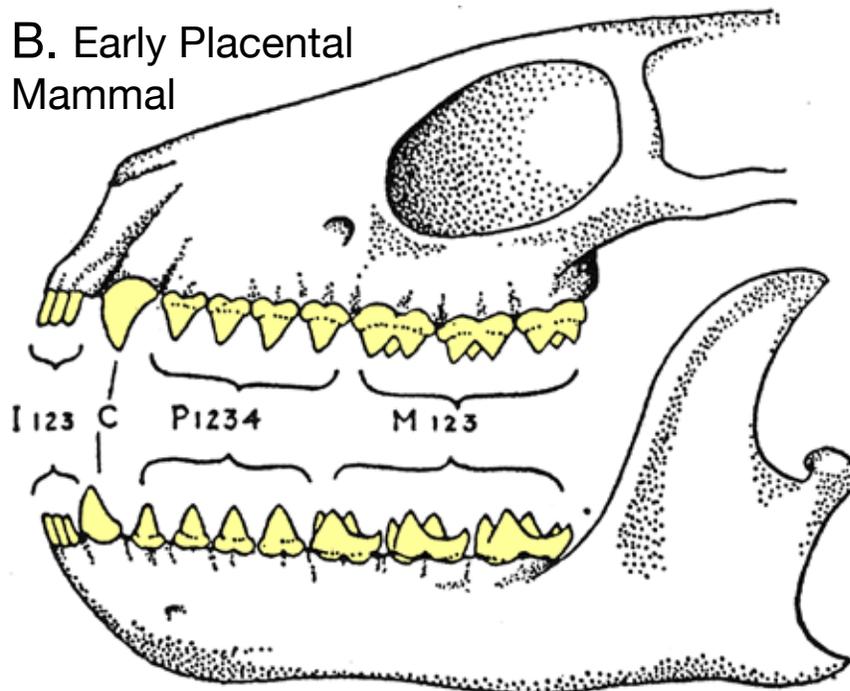


Fig. 5-2. **A.** The skull and undifferentiated teeth (homodonty) of a reptile. **B.** The differentiated teeth (heterodonty) of a Jurassic mammal, with incisors (I), canine (C), premolars (P) and molars (M). (**A.** From Campbell, 1974. **B.** From Le Gros Clark, 1971.)

incapacitate a prey or intimidate an adversary. Premolars aid in cutting larger chunks of food into smaller pieces, and molars have cusp-like surfaces that, by lateral grinding motion, can effectively pulverize organic materials with tough membranes such as grasses, grains and bark. Heterodonty has enabled mammals with high metabolic needs to make use an endless variety of foodstuffs and extract more nutrients from what they consume than reptiles.

Prolonged Care of Offspring: Viviparity and Nursing. Live-bearing and postnatal care of offspring, which enhance offspring survival, have a long evolutionary history in mammals. Monotremes, the most primitive extant mammals, are not viviparous or caring; the egg-laying female leaves its brood behind when she goes foraging, thereby rendering her offspring vulnerable to predation. Offspring protection is more advanced in marsupials in which the oviduct has become transformed into the uterus, an organ in which the embryo develops protected from external hazards. But the gestation period of marsupials is quite short because, lacking a placenta, the growing embryo cannot be adequately nourished by the mother's circulatory system. Marsupials have compensated for this reproductive handicap by having a pouch where the fetus-like offspring suckles until it becomes more mature. It was the evolution of the placenta in more advanced mammals that allowed prolongation of intrauterine fetal development. The placenta, which links the offspring's bloodstream with the mother's circulatory system, provides the developing fetus with oxygen and nourishment, and aids waste disposal.

VARIABILITY IN LITTER SIZE AND LENGTH OF GESTATION. Depending on the number of fetuses carried, the length of gestation period varies in different mammalian species, with birth occurring at different stages of fetal development. In species that carry a large litter, the young are typically delivered early—before their eyes open, before their skin acquires a hairy covering, and before they can walk or run. These helpless infants are called altricial, because they need considerable parental care to survive. In species that carry a small litter, or a single fetus, the young are delivered at a later stage of development—with eyes open, the skin covered with fur, and considerable locomotor ability. These are called precocial infants. Animals that raise their young in a protected nest (like rats) or a den (like dogs) tend to deliver a large litter of altricial offspring. Animals that deliver their young in the open (like goats, sheep, horses) tend to deliver a single precocial newborn that can follow its mother or the herd soon after birth. In animals that deliver large litters of altricial offspring, individual survival assurance is low and the perpetuation of the species is achieved through high fecundity, the large number of offspring carried, delivered and nursed, and more frequent reproductive cycles. In species that carry small litters, or a single young—which includes monkeys, apes and humans—individual survival assurance is enhanced by the prolonged care and protection that the offspring receive.

The following are examples of species differences in the number of offspring carried by a gravid female and the length of gestation period (based on data by Burnie and Wilson, 2001). Small altricial mammals tend to have large litters (shrew, 5; rat, 8; rabbit, 8) and a short gestation period (shrew, 20 days; rat, 22 days; rabbit, 31 days). Midsize altricial mammals have smaller litters (dog, 5; cat, 4) and longer gestation periods (dog, 60 days; cat, 63 days; leopard, 90 days). Large precocial mammals typically carry only a single fetus (yak, cow, horse, camel) and their gestation period tends to be very long (yak, 258 days; cow, 280 days; horse, 330 days; camel, 390 days). Large-bodied mammals require a longer period of embryonic and fetal development than do small ones, and the larger the fetus the fewer can be carried by the mother. But there is an important exception to this generalization. Primates, irrespective of their size, tend to carry a single young (rarely twins) and have a long gestation period. For instance, the gestation period of small marmosets and tamarins is between 140-145 days, the

slender loris, about 169 days, the Western tarsier about 180 days, and of pottos about 200 days. This exception is attributable to the fact that all primates, even the smallest ones, have large brains, and much of their brain development takes place before delivery.

VARIABILITY IN LACTATION AND NURSING LENGTH, AND REPRODUCTIVE MATURATION. All placental mammals lactate and suckle their young. However, the length of lactation and nursing varies in different species in relation to animal size (Burnie and Wilson, 2001). Nursing lasts a few weeks in small mammals: rat, 3 weeks; shrews, 3-6 weeks. It lasts a few months in intermediate size mammals: raccoon, 9 weeks; wolf, 15 weeks. And it endures for a year or longer in large mammals: giraffe, 13 months; camel, 1-2 years; bear, 2 years; rhinoceros, 2 years. Likewise, the length of time before the young reach puberty and become themselves ready to breed, and the length of the reproductive cycle, also varies greatly between small and large mammals. Small mammals, like rats, reach puberty in 2-3 months and may breed several times a year. Intermediate size mammals, like carnivores, do not typically reach puberty until 2 years of age. Larger mammals require several years to reach puberty: the female Bactrian camel, 3-4 years, and the African elephant, 8-12 years. Again, primates are an important exception. For instance, midsize langurs do not reach puberty until 6 years, and capuchin monkeys until 7 years. Since reduced litter size, prolonged gestation and lactation, and delayed puberty—all of which result in reduced fecundity—do not jeopardize species survival, it follows that the longer the gestation period and parental care that the young receive, and the larger their brain, the greater their chance that they will survive as individuals and reach reproductive maturity.

Transformation of the Forelimbs into Skilled Manipulatory Organs. The principal function of the extremities of lower vertebrates is locomotion. But even in that original function there are some differences in the role played by the forelimbs and the hind limbs. The forelimbs pull the body forward and are used for turning; hence, they tend to be more flexible than the hind limbs that push the body forward. The more powerful hind limbs provide much of the force used for jumping and they support body weight during climbing. However, reptiles rarely employ their short forelimbs to reach for and grasp objects in front of them. That may partly be due to the circumstance that their short forelimbs are situated behind their head and under their trunk and they cannot readily use their eyes to guide their arms and digits to manipulate things. To turn the forelimbs into manipulatory instruments requires hand-eye coordination and that necessitates that the reaching arms and the grasping arms can be thrust forward so that the eyes can monitor what the hands are doing. This occurred in many lines of mammals, and that, in combination with some added morphological changes, imparted many behavioral advantages to them. One of these changes was the shifting of the eyes from a lateral to a medial position to provide binocular stereoscopic vision for improved hand-eye coordination. Another change was the development of more flexible vertebrae, enabling mammals to rotate their heads and bend their trunk at the sacroiliac articulation (Gans et al., 1997). Unlike reptiles with limited dorsoventral torso flexibility, various mammals can raise their trunk with forelimb support to an angle of about 45°-90°, shift their center of gravity to their hindquarters, and sit upright (Fig. 5-1). Sitting upright frees one or both forelimbs from the need for postural support, allowing the animal to use its paws to reach for and grab insects, pick berries or fruits, groom oneself or a companion, and, above all, to palpate and manipulate objects that are seen or smelled. Still

another required change was the evolution of digital dexterity, the ability to move individual fingers separately rather than in unison, the change from holokinetic to ideokinetic motor control for manipulatory precision.

The intermittent use of the forelimbs as manipulatory organs is probably an early mammalian adaptation. Extant marsupials—like opossums, koalas, and wallabies—use their paws during feeding, and primitive placental mammals, like shrews, mice, rats, and squirrels regularly grab food items with their paws and carry them to their mouth. Squirrels typically hold a nut between their paws, much as in a vice, turn it around under visual guidance, and use their sharp teeth to crack the shell and extract the highly nutritious kernel. Squirrels also use their paws to dig a hole in the ground to bury nuts and then cover them with dirt or leaves. The fingers of raccoons are far more dexterous than of squirrels, and they are very skillful in tearing things apart. Among large mammals, bears use their paws to dig for insects and worms, splinter old logs to get at ants or termites, or remove honey from bees' nests. Bears may also sit when munching on leaves, fruits or berries, and use both hands when mock fighting with one another or engaging in a territorial battle. Significantly from the perspective of human evolution, manual dexterity is best developed among primates. Monkeys use their elongated padded fingers to hold on to branches as they climb trees or jump from one tree to the next. Then, sitting on their haunches on a tree branch, they use their free hands to gingerly pick fruits, sometimes with a finger and the thumb serving as pincers, and peel them or break them open before carrying the edible parts to their mouth. Primates can use their hands for both power grip and precision grip, holding fast to a branch or picking a berry, hitting an adversary or caressing an infant, grooming oneself or a friend, and many other useful functions. These abilities, of course, require delicate sensorimotor coordination, that is, neural mechanisms specifically dedicated to the task of handling and manipulating objects purposively and skillfully.

5.1.3. Neural and Behavioral Advances in Mammals. The most important of all the mammalian advances relative to reptiles was the evolution of a novel neural control system, the neencephalon, a component of the CNS consisting of the cerebral neocortex and several ancillary subcortical and limbic structures. The neencephalon, superimposed upon the ancient paleocephalon, provides mammals with enhanced learning ability and cognitive powers and that, in combination with their prolonged infantile and juvenile apprenticeship, has greatly contributed to their becoming the dominant inhabitants of all terrestrial niches.

Progressive Encephalization and Evolution of the Neencephalon. The visceral, somatic and behavioral advances occurring in several mammalian lines were coupled with the great expansion and elaboration of their brains. To appreciate brain size as a factor in behavioral and mental advancement, we must remember that brain size is also a function of body size. An animal with a larger body must have a bigger brain than an animal with a smaller body because it needs more and bigger neurons to innervate a more extensive skin surface, larger internal organs, and a larger skeletomuscular apparatus. Conversely, a big brain needs a sufficiently large body to furnish it with its high energy and substrate requirements because the maintenance of neuronal activity is a very expensive metabolic process. For instance, the mammalian brain uses as much as 20 per cent of the body's glucose supply, and that level of energy consumption is sustained even when the body's glucose content drops precipitously (Kety, 1957). It is for this

reason that when considering brain size as an index of evolutionary advance (encephalization) in a particular species, that measure must be corrected for differences in their body size. This is called the allometric method (Stephan and Andy, 1969; Jerison, 1973; Martin, 1982).

PROGRESSIVE ENCEPHALIZATION. Jerison (2001) plotted the brain-body ratio of 1027 species of extant bony fishes, 41 amphibians, 180 birds, and 647 mammals. He found that the brains of bony fishes, amphibians and reptiles form a cluster with low brain-body ratios, and the brains of birds and mammals form another cluster with high brain-body ratios (Fig. 5-3). That is, allometric comparisons indicate that fishes, amphibians and reptiles are collectively small-brained (oligocephalic) vertebrates, whereas birds and mammals are large-brained (macrocephalic) vertebrates. These results are consistent with his earlier paleontological plots of fossilized endocasts (Jerison, 1973).

ALLOMETRY AND ENCEPHALIZATION

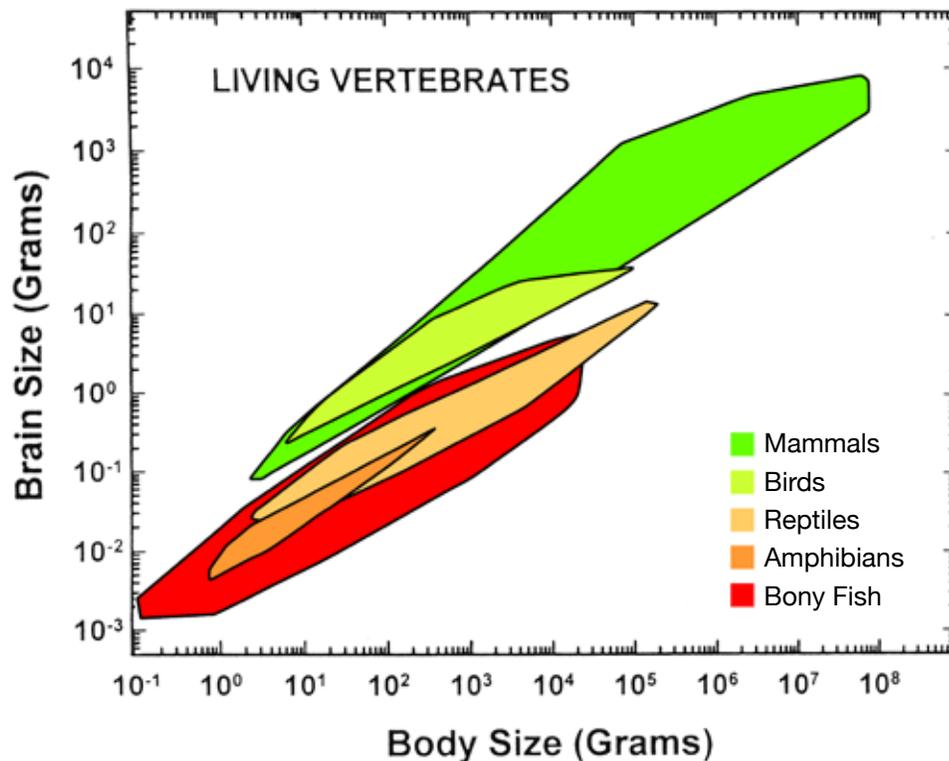


Fig. 5-3. Brain-body ratios of extant vertebrates, enclosed in minimum convex polygons. Bony fish and reptiles have relatively smaller brains than birds and mammals. Large-bodied mammals have the biggest brains among all vertebrates. (Modified, from Jerison, 2001.)

A few examples from the compilation of Blinkov and Glezer (1968) illustrate this evidence for brain weight increase (encephalization), independent of body weight change, as we pass from lower to higher vertebrates. The small lizard has a miniscule brain (0.12 g) when compared with the brain of the large crocodile (15.60 g), and the small house mouse has a much smaller brain (0.43 g) than the large black rat (1.59 g). The Indian elephant that weighs over 3,000 kg has a brain of 4,717 g, which is almost 3 times the weight of the human brain. But after body size is taken into consideration, mammals stand out as a unique group with

large brains. For instance, the crocodile that weighs 134 kg has a 15.6 g brain; the porpoise that weighs 142 kg has a 1,735 g brain. The difference in encephalization between the aquatic reptile and the aquatic mammal is over a hundred-fold. The dramatic spurt in encephalization both in birds and in mammals suggests that a prerequisite for that expansion is a shared property of the two: high basal metabolic rate and homeothermy. Importantly, the lesser increase in the brain weight of birds relative to lower vertebrates is correlated with the expansion of the basal ganglia, whereas the greater increase in the brain weight of mammals is correlated with the expansion of the cerebral cortex (neencephalon).

EVOLUTION OF THE NEENCEPHALON. The mammalian neencephalon consists of two novel components: (i) the neocortex and (ii) a series of subcortical structures that have evolved in parallel with the neocortex,

The neocortex, characterized as the six-layered isocortex, is composed of topographically organized primary sensory and primary motor “projection” areas, shared alike by all mammals, and several “association” areas that increase in number, complexity and interconnections in several mammalian taxa, especially in primates. The primary sensory projection areas are involved in the unimodal processing of visual, tactile and auditory information; the primary motor area is responsible for the voluntary control of skilled activities. The neocortical association areas are mechanisms for the multimodal integration of sensory information, their long-term mnemonic storage and retrieval, and the patterning, sequencing and monitoring of ever-more complex, skilled motor actions and reactions. The evolutionary expansion and elaboration of the neocortical association areas is reflected in the transformation of the smooth-surfaced neocortex of small basal mammals, like insectivores and rodents, to the bigger and more convoluted neocortex of large herbivores and carnivores. The progressive expansion of the neocortex is particularly pronounced in primates (Stephan and Andy, 1969, 1970; Stephan et al., 1981, 1984). Considering the size of the neocortex of insectivores as 1, the neocortex of tupaia is 8 (8 times larger than the neocortex of insectivores), that of prosimians 17-23, of monkeys 30-50, the chimpanzee 60, and man 156 (Fig. 5-4).

In tandem with neocortical enlargement, several subcortical structures have expanded in the mammalian CNS. The mammalian spinal cord contains a large afferent system, the ascending dorsal funiculus, which conveys somatosensory information to the neocortex, and a massive efferent system, the descending corticospinal tract, which provides voluntary control of the spinal motor neurons. The latter two systems may be considered the neospinal components of the mammalian CNS (Altman and Bayer, 2001). The ascending neospinal somatosensory input passes through two relays before it reaches the neocortex, the dorsal column nuclei of the medulla and a set of somatosensory thalamic nuclei. Hence, these structures may be looked upon as neomedullary and neothalamic constituents of the CNS. The mammalian thalamus also contains large auditory and visual relay stations (the medial geniculate nucleus and the lateral geniculate nuclei) that convey auditory and visual information to the neocortex. In the mammalian pons, there is a large nucleus (the pontine gray) that serves as a recurrent loop from the cerebral cortex to the cerebellum, in particular to the neocerebellar lateral hemispheres, which expands in parallel with the neocortex. Finally, the basal ganglia have components—the neostriatal caudate nucleus and the putamen—that provide another feedback loop to the

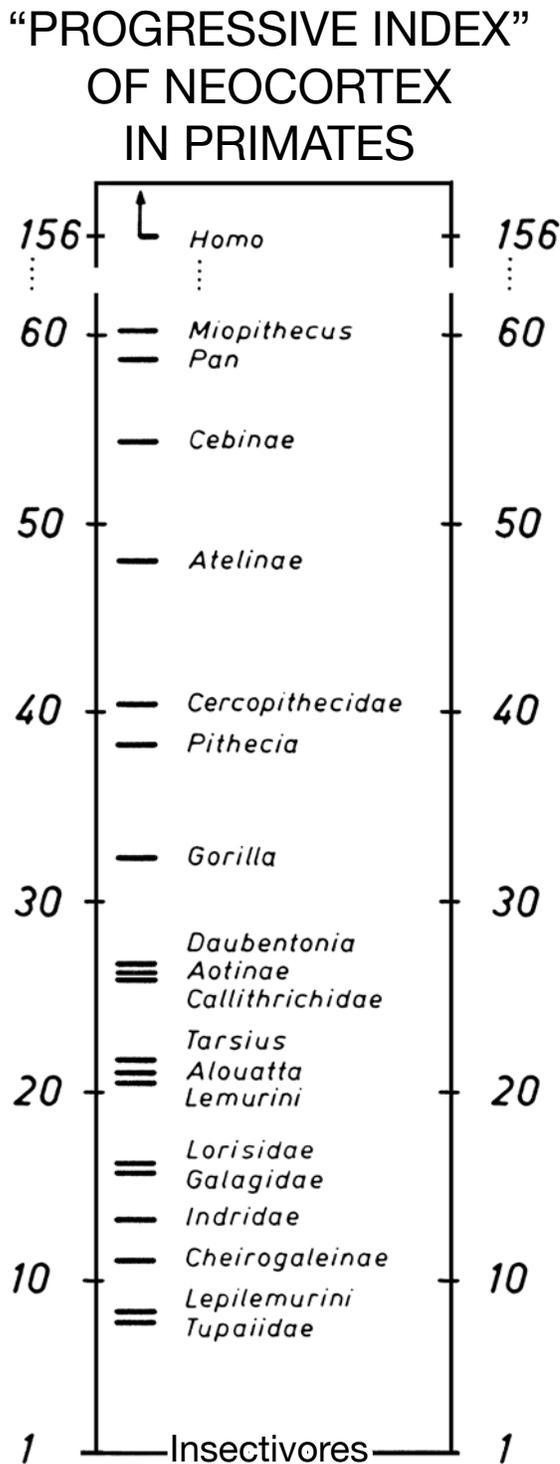


Fig. 5-4. The number of times the neocortex is larger in a large series of primates than in basal insectivores of equal body weight (“progressive index”). (Modified, from Stephan and Andy, 1969.)

neocortex and expand in parallel with it. Therefore, the great increase in the size of the mammalian brain relative to lower vertebrates may be considered to be primarily due to the expansion of the cortical and subcortical components of the neencephalon. This expansion, in turn, is correlated with some notable advances in the behavioral and mental dispositions and abilities of mammals.

Behavioral Advances: Family Bonding, Gregariousness, and Social Organization. Lower vertebrates are not social animals in the same way as certain invertebrates, such as ants are. Ants form large colonies consisting of morphologically and behaviorally distinct caste members—a large fertile female (the queen); some fertile males (drones); and a large population of infertile soldiers and workers with different functions. Individual members of these castes do not labor for their own gain but in the interest of the colony. Lower vertebrates aggregate in larger groups but members of the group are much alike and each individual is preoccupied with its own survival and welfare. For instance, fishes form shoals when foraging and schools when migrating but they do so not because the group benefits from the cooperation of the joining individual but because the individual derives benefit from joining the group. As we described it earlier (Section 3.2.3), isolated fish become fearful and depressed, hiding and abstaining from feeding, but relax when surrounded by others of their own kind. Let us call this *egosocial* behavior, and distinguish it from the *allosocial* behavior of the gravid and lactating mammalian mother who builds a nest before parturition, nurses the young after delivery, licking them and keeping them warm, and protecting them until

they can take care of themselves. The gravid female of lower vertebrates makes considerable investment in the propagation of the species by producing a large batch of ova (roe), migrating to a breeding site, and depositing the fertilized eggs in a way that assures some degree of protection. But her behavior toward the hatched young, which whom she may never interact, is not a social one like the mammalian mother's establishment of an intimate relationship with her young.

Viewed from the perspective of the young, all mammalian infants begin their life in a social setting, minimally in the company of the mother, more typically as members of a nuclear family, the pack, troop or herd. However, unlike the mother's behavior, the infant's behavior is not allosocial but egosocial. The infant takes as much as it can from the mother—demanding nourishment, contact, care and protection—but does not (and cannot) reciprocate. Materially, the infant's sociality is similar to that of the isolated fish's that seeks and joins the school of its peers in order to promote its own satisfaction, imparting little or no gain to the school. As they mature and become independent, some mammals become solitary, while others keep the company they grew up with. Solitary mammals—which includes most basal mammals, like insectivores—establish a territory for themselves, forage and rest by themselves, and, in some cases, display outright hostility towards conspecifics. But even in those species in which group living has become the norm, the interrelation of the individuals is an ambivalent one, cooperating or competing with one another as living conditions dictate. Both phylogenetically and ontogenetically mammalian sociality is superimposed upon a fundamentally self-centered individualism, a disposition that is our enduring vertebrate legacy. Of course, social cooperation imparts great advantages to both the individual and the species, and there has been evolutionary pressure to form enduring groups through mutualism and cooperation. Starting out with the establishment of an enduring bond between mother and her offspring, and where pair-bonding has evolved, between female and male parents, most higher mammals form a nuclear or extended family, and some more complex groups in which social relations are governed by acquired customs and rules. In all instances, the foundation of this trend is a biopsychological one, the mother's selfless care for her young and their selfish demand for that care.

MATERNAL AND FILIAL BONDING. The mammalian mother has an emotional disposition to care for her young; the helpless young display emotional expressions of distress when isolated, to which the mother promptly and unfailingly responds (Gubernick, 1981; Guyot, 1998). Rosenblatt (1988) distinguished three patterns of mammalian care giving and bonding: (i) nesting together, (ii) leading-following, and (iii) clinging-carrying. In altricial mammals, like rodents and many carnivores, the mother either builds a nest before parturition or deposits its litter in a burrow or den. At various intervals between her foraging and hunting excursions, she returns to the nest to nurse the young. She may also groom them, warming them by huddling over them, and retrieving them when they stray from the nest. In precocial rats, the bond between mother and offspring may not be very discriminating; typically, the mother will nurse young that are not her own if the bond is established early enough. In altricial mammals, like most browsing or grazing mammals, the intimate bond that develops between the mother and her offspring is based on olfactory and gustatory imprinting (see below), and she may refuse to nurse a young that is not her own. In turn, the single young follows its mother as she moves about and nurses at intervals when she stops moving with the herd. In arboreal

primates, the mother tends to carry her infant as she runs up and down a tree or leaps from one tree to another, and the infant clings to her tenaciously. The maturing young may return to the mother when threatened or stressed, and in many species several generations of females may permanently stay together, forming a cooperating extended family.

Elective Affinity, and Social Organization. Among social mammals, a close relationship is not limited to the nexus between mother and young. Animals that grow up together, whether close kin or not, seek and maintain close relationships which are overtly manifested as the seeking of physical contact with each other. In lower vertebrates, physical contact tends to be a negative stimulus, since being touched is tantamount to being captured (Tinbergen, 1951). Schooling fish, for instance, maintain a certain distance from one another when they swim together, and among amphibians and reptiles, physical contact is usually limited to the short period during the breeding season when they copulate. In contrast, mammals regularly huddle together, lick one another, rub noses, or engage in mutual grooming bouts. The seeking of physical contact may start as a utilitarian step among many social mammals. Huddling aids heat preservation and grooming helps to get rid of parasites and keeps the fur clean. Grooming is often directed towards part of a companion's body that it cannot itself reach, such as behind the ears or under the chin (Ewer, 1968). Reciprocity in huddling and grooming leads to the development of mutualism between particular individuals within the group, not unlike that between the mother and her young. Mutual grooming is particularly prominent among primates, and the grooming partners often establish cooperative relationships within the group, such as sharing food or defending one another when conflicts develop. Considering the strong emotional element in the interrelations between mother and young, and the gregariousness that develops among companions, we now turn to a consideration of the nature and evolution of mammalian affectivity.

5.1.4. Affective Advances in Mammals. Mammals display all the basic affects that we have identified in lower vertebrates—pain, hunger, thirst, fear, anger, and amorousness. As we noted earlier, these basic affects are mediated in fish and reptiles by mesencephalic and diencephalic mechanisms, such as the reticular formation, periaqueductal gray, hypothalamus, and preoptic area, and are supported by telencephalic limbic structures, such as the amygdala, septum, and nucleus accumbens. These basic emotions and their neural mediating mechanisms have been preserved in mammals. But mammals also manifest additional affects that are absent or poorly developed in lower vertebrates. Most notable of these are the following. *Parental/filial affection*: the mother's solicitous love for her young and the infant's pining when the mother is absent. *Cordiality*: fondness for siblings, close kin, and playmates, and amicable relations among peers and group members. *Curiosity*: the delight in coming across new things, toying with them, and exploring new places. *Exuberance*: delight in running, chasing, and engaging in playful activities with others.

Parental-Filial Affection. Before delivery, the mammalian mother, much like a reptile, undergoes hormonal changes, including an increase in the concentration of estrogen (Bridges et al., 1990) and oxytocin (Fahrbach et al., 1984; van Leengoed et al., 1987; Kendrick et al., 1987). Associated with that change, she engages in preparatory activities, such as building a nest. Following parturition, a selective bond forms between the lactating mother and her

young that is rare in lower vertebrates. The formation of this selective bond begins with the mother consuming the birth fluids, and licking and sniffing the newborn (Poindron et al., 1988; Malenfant et al., 1991; Morgan et al., 1992; Lévy et al., 1996). This behavior establishes an acquired bond between mother and her own young. Initially, the mother takes the initiative in care giving, she solicits suckling in the newborn by hovering over it. As the infant matures, the relationship becomes more interactive. The mother may emit an alarm call when she perceives some danger, and the young responds by running to her for cover. Or the frightened young may emit distress calls, and the mother responds by grabbing the infant's nape of the neck with her teeth and carrying it to safety. In both altricial and precocial mammals, the mother's solicitous behavior—grooming, retrieving, and protecting the young—continues for some time, and the juvenile is not fully weaned until it can fend for itself. When canine or feline cubs start to consume solid food, but are not yet able to join the hunt, the mother often supplies them with meat by regurgitating part of the meal she has earlier consumed. There are also reports of cats bringing back an injured mouse or a rat, which the kittens then try to kill (Ewer, 1968). When they get older, the young may join their mother on a hunt and she may immobilize or injure the prey, standing by as the cubs kill and consume it. As the offspring mature, their attachment becomes episodic, moving around and playing with peers but returning to the mother when resting or sleeping.

Gubernick (1981) identified the following emotional features of infantile attachment in mammals: (i) seeking to maintain close proximity with the mother (or other attachment figure); (ii) protesting when she leaves and expressing relief when reunited; (iii) expressing dejection and despair following prolonged separation; and (iv) use of the mother as a secure base during exploration. Not all these features are evident in the attachment of lower mammals. Rat pups become aroused and emit ultrasound distress vocalization when separated from their mother (Conely and Bell, 1978). However, they do not discriminate between their own mother and another dam that has been fed on the same diet (Leon, 1975). Dog pups become distressed when separated from their mother or siblings but the presence of a human caretaker can reduce that distress (Scott, 1971). Isolated kittens may develop normally when reared by animate or even inanimate surrogates (Guyot, 1998).

Curiosity and Exuberance. The daily behavior of lower vertebrates is limited to the imperatives of individual and species survival. These include finding feeding grounds and selecting nutrients; shunning inhospitable and toxic sites; fleeing from predators or other sources of danger; establishing and protecting territories that serve as shelters or breeding sites; intimidating, fighting or subordinating competitors and adversaries; gathering with peers for protection; and ensuring the survival of the species by pursuing and competing for mating partners. However, fishes, amphibians and reptiles display little or no curiosity about the properties of objects that are not directly related to their vital needs, and they do not manipulate objects. Well-fed and secure mammals, particularly juveniles, behave quite differently. They spend much time and exert much effort to explore their habitats, examining novel objects they encounter, chasing whatever moves about, and challenging parents, siblings and peers to play.

Mammalian young are distinguished by a prolonged period of dependency when, aided by parents and older members of the group, they learn how to cope with the challenges of

their particular habitat. Trailing parents or other adults, the young learn what to nibble on and what to avoid consuming; where to roam freely and where to tread cautiously; whom to avoid and whom to befriend; how to track, hunt and subdue a prey. As the young mature, they take progressively longer forays from the nest or den and thus become familiar with every nook and cranny of their home range. Coming across different inanimate and animate objects as they move about, they sniff, chew, paw, pull, shove, turn over, and pounce upon these objects, thereby becoming familiar with their features and properties. Playing with siblings and peers, the young learn about their strength, skills and disposition, and thus acquire a particular status in the social order.

CURIOSITY AND EXPLORATION. Virtually all mammals display curiosity. When a rat is placed in an arena containing different objects, it spends more time examining novel objects than familiar ones (Berlyne, 1950, 1955). When it is placed at the starting alley of an unfamiliar T-maze for the first time, it will randomly enter and explore either the right or the left arm. But given a second trial, it will, with a high degree of probability, choose the arm that it had not previously explored (Dember, 1956; Fowler, 1965). This phenomenon, known as spontaneous alternation, suggests two notable features of rat behavior: first, a tendency to explore unfamiliar spaces and, second, a good memory, i.e., recollection for what was done previously. When a hungry rat is placed in an eight-arm maze, in which every arm is baited with food, it will enter all the arms in rapid succession, rarely visiting twice an arm that has already been explored, confirming their excellent short-term memory (Olton and Samuelson, 1976). In fact, a rat will systematically explore all eight arms even if it is not rewarded with food (Timberlake and White, 1990).

Exploratory behavior is a mammalian trait and there is some evidence for its intensification in higher mammals (Fig. 5-5). Reptiles show virtually no interest in novel objects, marsupials and insectivores some, rodents much more, and carnivores and primates are extremely curious (Glickman and Scroggs, 1966). Berlyne (1963) has argued for the knowledge-building (“epistemic”) function of the disposition of a rat to explore its environment and its tendency to examine the features and properties of novel objects. While the promotion of knowledge is the long-term outcome (“final cause”) of curiosity, its motivating force (“proximate cause”) is more likely affective in nature: the pleasure in encountering and examining new things. We assume that the proximate motive of the inquisitiveness of a rat, cat or dog is similar to the joy and thrill we experience when we explore a new environment or examine novel objects that we encounter or discover. The long-term benefit of these activities is that we become familiar with the world we live in and how to cope with its contingencies. Since exploration does not directly gratify a visceral need (like eating reduces hunger pangs), what motivating mechanism instigates it? We postulate that curiosity is a neurogenic drive. Brain mechanisms have evolved in mammals (we shall identify later the crucial role of the hippocampal formation) that make new experiences and discoveries emotionally rewarding.

Exuberance and Play. Play, like curiosity, is another affectively motivated mammalian activity that does not directly gratify any visceral need. But unlike curiosity, which tends to wane after a shorter or longer encounter (Fig. 5-5), play tends to be more enduring, often not ending until the animal has become completely exhausted. Mammals typically play when they

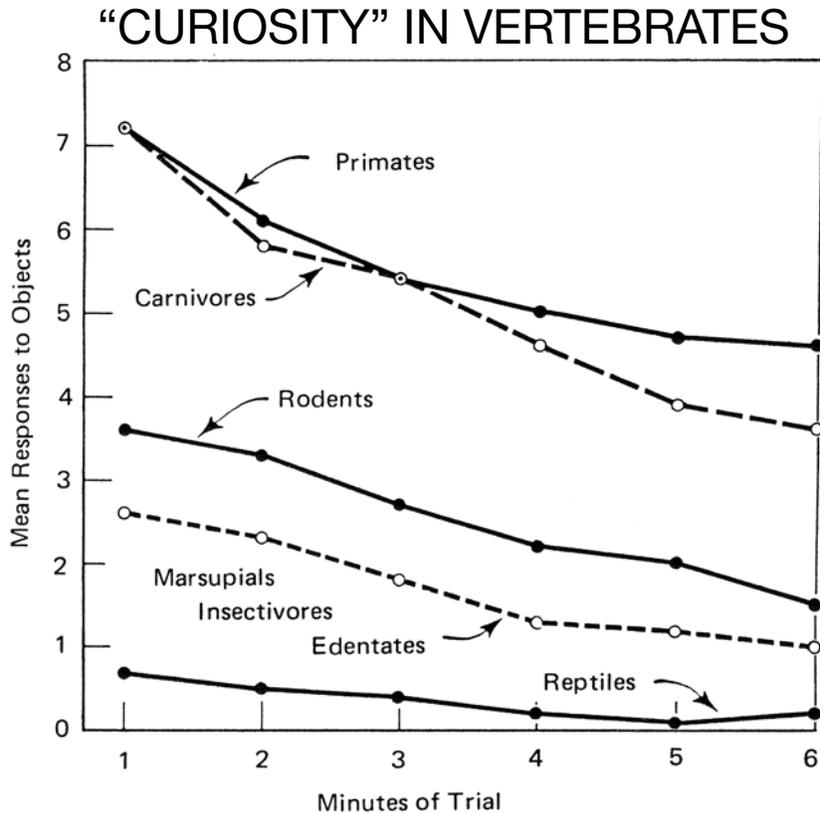


Fig. 5-5. Average exploratory responses to novel inanimate test objects in reptiles and mammals. Reptiles display virtually no interest in them. In mammals there is a correlation between the number of responses emitted and phylogenetic status. (From Glickmann and Scroggs, 1966.)

are sated, feel secure and have nothing serious to occupy them (Eimon, 1983). They may be playing either by themselves or with others (Aldis, 1975). In solo play, the animal may carry around an object, run around in a circle, jump across gaps, or somersault. In social play, a sibling or peer may be chased, tagged or wrestled with. An animal in a playful mood will often invite a peer to join it. The invitation begins with signaling, such as bowing by dogs or monkeys displaying a play-face, followed by running in front of the other animal, climbing on top of it, mock-attacking it with retracted claws, or biting it gently without drawing blood. Quite often, a smaller animal will tag or attack a larger and stronger one with impunity. Generally, play participants do not get hurt. Mammals share some basic forms of play, but some are species-specific. Rough-and-tumble mock fighting is widespread among all. More species-typical plays are the fleeing maneuvers of galloping colts, the stalking and pouncing of kittens, and the acrobatics and tree-swinging of monkeys and apes (Aldis, 1975; Fagen, 1981). There is a correlation between the kind of play in different mammalian species and the complexity of their behavioral repertoire. The play of precocial herbivores (sheep, cattle, horses) tends to be simple, those of altricial omnivores and carnivores (rats, cats, dogs, monkeys) more complex. Groos (1898) suggested that play has an important function, it provides the naïve young with the opportunity to learn through practice, turning the helpless mammalian juvenile into a competent adolescent and adult.

In contrast to mammals, there is little evidence for play in lower vertebrates, such as fishes and reptiles. One factor may be their metabolism, which makes them less exuberant than warm-blooded mammals (Barber, 1991). Another likely factor is that since most of their

behavior is coordinated by inborn neural mechanisms, they do not need to learn and practice to build a repertoire of learned skills (Byers and Walker, 1995). Like curiosity, the proximate instigator of play is affective gratification. But they differ in their ultimate functions. Curiosity promotes knowledge acquisition through sensory exploration; play promotes skill acquisition through motor exercise. The young animal that has not learned how to maneuver to avoid being caught when pursued by another, how to pursue and catch the other as it tries to escape, and how to subdue the other in a fight, will be handicapped when it has to catch prey to feed, run to avoid predators and, when necessary, fight for its life.

5.1.5. Perceptual, Mnemonic, and Cognitive Advances in Mammals. In association with the evolution of a new neural system, the neencephalon, the mental life of mammals exhibits properties that are absent in lower vertebrates. Paramount among these are: (i) the advance from phenomenal to substantive perception, (ii) increased use of memory images in the guidance of behavior, and (iii) limited ability to think and reason by utilizing imagery. We begin with the perceptual advances of mammals.

From Phenomenal to Substantive Perception. The partial transformation of the vertebrate locomotor forelimbs in basal mammals—as in shrews, rodents and prosimians—into palpating and manipulatory organs had a profound effect on how they perceive what transpires in their environment. As we have argued earlier (Section 3.4.2), fish with topographically organized eyes but without palpating fingers, perceive external objects as pictures, not as substantive entities. Of course, they do not bump into solid objects, thanks to their lateral line system that detects changes in water pressure and wave action. However, without active exploration of what is perceived by touching, palpating and lifting it—without a haptic sense—the sight of something does not become a concrete entity with multifarious physical properties. We called this mode of mental representation, *phenomenal perception*. In contrast, inquisitive mammals that actively explore the features of seen objects can learn about their multifarious properties. Sniffing, chewing, shoving, pouncing on, turning around and tearing apart the novel thing they encounter, mammals learn about its physical properties, such as its hardness, pliability, coarseness, slipperiness, durability, composition, and the like. We call this higher form of perception, the multimodal assessment of what things in the outside world are like, *substantive perception*.

The perception, or awareness, of what is seen as a concrete object with multifarious properties requires the ability to concurrently focus several senses on it and amalgamate that information centrally to form a comprehensive mental representation. Multisensory guidance of behavior is not absent in lower vertebrates. However, that does not necessarily mean perceptual integration. As Sjölander (1993) suggested, the hungry shark first chases a “visual fish,” which closer up becomes an “olfactory fish,” and then, as it is swallowed, turns into a “gustatory fish.” The sight of the prey, its image or portrait, is unlikely to have multimodal properties to the shark because that requires not only concurrent use of several senses—sniffing, palpating and manipulating the prey while visually examining it—but also multimodal central processing to integrate all that information and produce a single perceptual representation. We have argued earlier that the segregated sensory lobes of the piscine brain do not provide such a central mechanism (Section 3.14). The same may apply to the crocodile that sees an animal

on the shore or entering the water. Darting forward at high speed and quickly clamping down on the prey with its jaws, the crocodile finds out what it has captured after it has torn it apart and swallowed it. The hungry cat hunts differently. Following the olfactory trail of a mouse, it stalks its victim, faces the animal for a while as it rears to fight or freezes in panic and, then, through a perfect coordination of the visual, tactile and proprioceptive senses and its motor apparatus, the cat pounces on the mouse, grabs it, breaks its neck with a well-aimed strike of the paw, then retreats with it, tearing it apart, and consuming it. The cat can do all that because it has a multifaceted, substantive representation of the multifarious features and properties of its prey. Cross-modal integration adds a new dimension to the mental representation of what is perceived, as that becomes a complex amalgam of the object's visual, chemical and mechanical properties (Suddendorf, 1999).

Mammals differ greatly in their ability to form substantive representations of what they see. As we noted earlier, manual dexterity is better developed in omnivores, like shrews, rats, raccoons and bears, than it is in carnivores, such as cats and dogs, and it is virtually absent in hoofed herbivores. Manual dexterity is most highly developed in primates that rely on hand-eye coordination to gingerly pick fruits, shell them, groom one another, and, in some cases, manipulate simple tools, a stick or a stone, to achieve some end. There is, furthermore, evidence for an evolutionary trend from prosimians to apes in the ability to manipulate objects (to be described later) and in the cross-modal representation of perceived objects (Ettlinger and Wilson, 1990). Multimodal integration is, of course, a complex process, one aided by mnemonic and cognitive mechanisms.

From Slow Associative Learning to Fast Recollection-Based Cognitive Learning. Much of the habit formation displayed by mammals is the product of a slow, associative mechanism. It takes about 25-30 trials for dogs to learn to salivate in response to a conditioned stimulus (Fig. 5-6A), and for rats to master a T-maze (Fig. 5-6B) or a black-white discrimination (Fig. 5-6C). This type of slow learning is generally attributed to the gradual formation of new stimulus-response connections in the brain, a physiological process that may take place without mental mediation or awareness. This type of associative process may characterize much of the learning displayed by lower vertebrates. However, mammals can master problems much faster. In a pioneering study, Thorndike (1911) placed a hungry cat inside a cage with a door secured by a latch, and a fish outside to motivate the animal to learn how to open the latch and get the bait. Thorndike found that initially the cat engaged in aimless activities, biting and clawing, until by chance it pulled on the string that opened the latch. Eventually the cat learned to directly pull the string and open the door. Because of the gradual decrease in the time to get out of the cage, Thorndike argued that the animal solved the problem by a trial-and-error process rather than by insight. In fact, his own studies and those of others (Adams, 1929) indicated that the reduction in latency was initially slow, but then, after about half a dozen fumbling trials, there was a sudden change in the cat's behavior and henceforth the latch was opened rapidly, suggesting that the cat came to solve this procedural learning task by insight (Fig. 5-7).

FAST LEARNING MEDIATED BY IMAGERY-BASED RECOLLECTION: A HYPOTHESIS. We propose that when mammals display a sudden improvement in a learning task, they use mental imagery, i.e., recollect in quasi-perceptual form what previous act or event has led to a successful outcome.

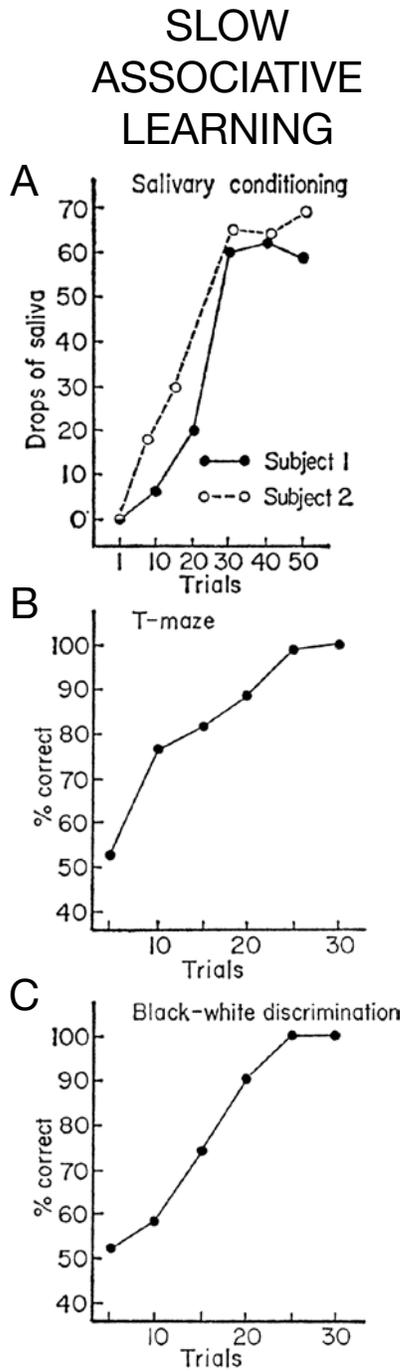


Fig. 5-6. Slow associative learning. **A.** Speed of acquiring an alimentary conditioned response in two dogs. **B.** Speed of spatial learning in a T-maze by rats. **C.** Speed of rats' learning a simple visual cue discrimination task. (A. After Anrep, 1920, from Macintosh, 1974. B and C, from Macintosh, 1974.)

INSTRUMENTAL LEARNING: FROM FUMBLING TO INSIGHT

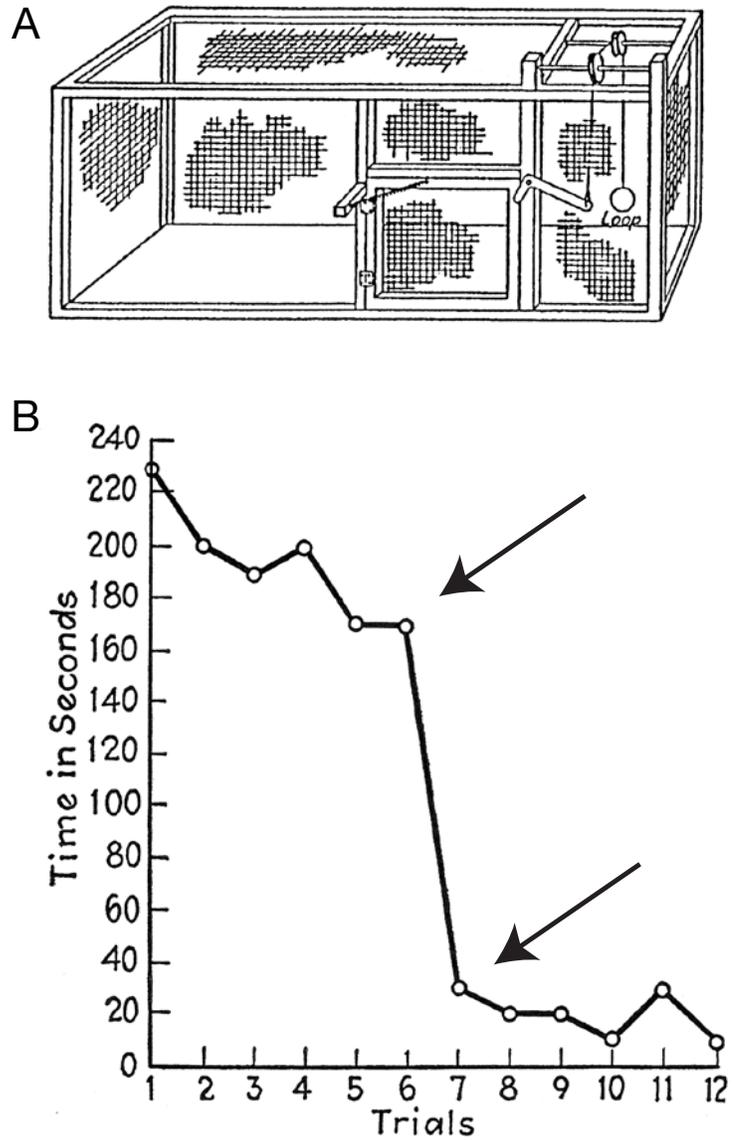


Fig. 5-7. **A.** The problem box used by Thorndike to train cats to open the door by pulling a string to gain access to food outside. **B.** After an initial period of fumbling, a cat suddenly learns how to pull on the latch and recollects that thereafter. (A, from Thorndike, 1911. B, after Maier and Schneirla, 1935.)

Consider the daily behavior of squirrels. Squirrels bury nuts in the ground during the fall to which they return in the winter when food becomes scarce. Do squirrels find the buried nuts by searching and sniffing for them or can they recall the exact site where they have buried them? Field observations have established that squirrels locate buried food items, without searching, with errorless precision (Devenport and Devenport, 1998). This ability must be based on a recollection image, rather than on some sensory process, because if the cache is displaced just a short distance by the experimenter, the squirrel keeps searching at the site it has buried the nuts and ignores the site where the food has been reburied. Moreover, when there are multiple caches in a particular area, squirrels do not revisit those that they have already emptied but systematically move to the sites that have not yet been visited. That memory for the precise burial sites of nuts endures for several months (Macdonald, 1997).

The ultimate test of mental recall is one-trial learning. Seward (1949) allowed rats to explore a T-maze with two distinctive goal boxes and later fed them in one of them. When the rats were returned to the starting area, the majority of them proceeded to the box in which they were previously fed. This illustrates one-trial *appetitive learning*. Tolman and Gleitman (1949) placed rats into a T-maze with two distinctive arms and shocked them upon entering one of the arms. When they were returned thereafter, the majority of them avoided entering the arm in which they were previously shocked, suggesting that they could recollect where they were punished. When a mouse is placed on a pedestal in a cage, it tends to step down and explore the cage. But once shocked upon touching the electrified floor, most of them refrain from stepping down on the next trial (Jarvik and Essman, 1960). These are examples of one-trial *passive avoidance learning*. *Active avoidance learning* requires more trials. In that test, the animal is typically given a warning signal of the imminence of a shock and can avoid punishment by performing some required action, such as move to another compartment. Rats master such an active avoidance task in less than five trials (Theios, 1963). That is faster than learning by conditioning. In another experiment, dogs had to jump over a hurdle to reach the safe compartment and thus avoid getting shocked (Solomon and Wynne, 1954). The record of a single dog indicates that it needed ten trials to learn that by performing that action it could avoid punishment (Fig. 5-8). However, it needed only a single successful avoidance experience to learn to calmly jump over the obstacle in response to the warning stimulus and it never got shocked again in that situation.

We postulate that slow learning is mediated by associative processes without insight; fast learning by awareness of what cue to heed and what to do in order to achieve a desired outcome. Lashley's (1929) investigations of pattern discrimination learning in rats clarified a facet of this process. Having initially used a T-maze, the rats had great difficulty in learning to make the simplest of pattern discriminations. Lashley then designed an apparatus in which, placed on a pedestal, the rats had to jump some distance to one of the two hinged doors marked by different visual patterns, where making the wrong choice made them fall into the net below. The rats learned to make pattern discriminations more readily and much faster (Fig. 5-9). Apparently, the experimental setup forced the animals to pay attention to what they were doing. There is also evidence for interplay in rats between slow trial-and-error learning, presumably without awareness, and a shift to fast learning once the animal becomes aware of the salient cue. An example is the design referred to as "latent learning." In this experimental design, rats

AVOIDANCE LEARNING: FROM AGITATION TO COPING

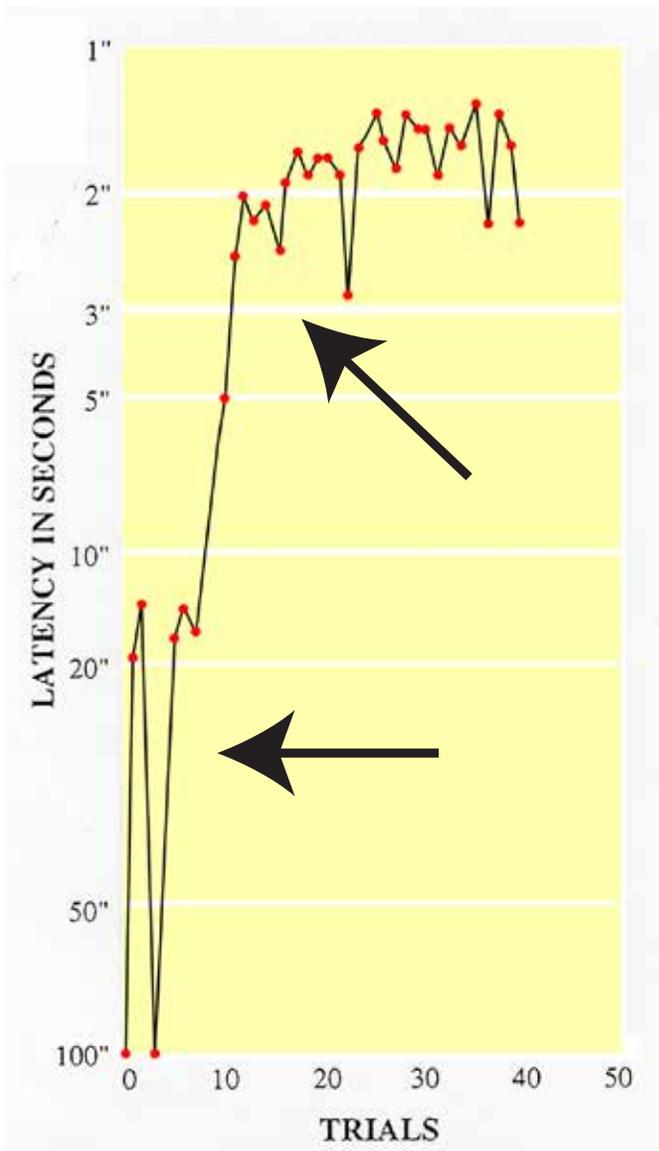


Fig. 5-8. In this experiment dogs could avoid an electric shock if they responded within 10 seconds to a warning cue. Here is the record of a single dog that learned after 10 trials (*lower arrow*) how to avoid getting shocked and recollected that permanently thereafter (*upper arrow*). (After Solomon and Wynne, 1954.)

FORCED PATTERN DISCRIMINATION TRAINING IN RATS

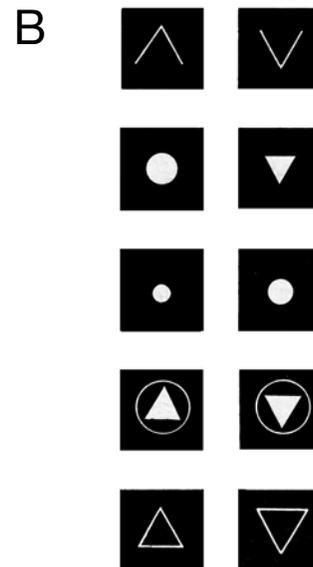
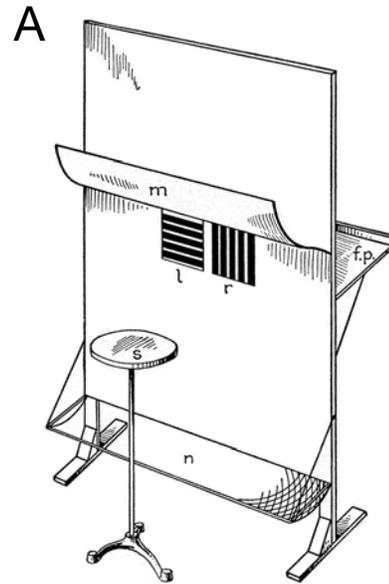


Fig. 5-9. A. Lashley's jumping apparatus for training rats to make visual discriminations. B. Pairs of patterns that the rats learn to discriminate. (From Lashley, 1930.)

are allowed to meander through a multiple-unit maze without receiving any reward. When thereafter the rats were rewarded with food in the goal box, they ran the maze after one or two trials as effectively as the rats that received lengthy training with a food reward (Blodgett, 1929; Tolman and Honzik, 1930). From a subjective perspective, mental imagery is an experience

in which something not perceptually available is replayed in the “mind’s eye” in a quasi-perceptual form. Recollection of a past experience produces “hindsight” and that, in turn, allows “foresight,” the anticipation of what will happen in the future.

The Role of Learning in the Behavioral Adaptability of Mammals. Learning studies indicate that the increased behavioral plasticity and versatility of mammals relative to lower vertebrates is due to their advanced mnemonic abilities. To be able to recognize the myriad of things, beings and situations that constitute an animal’s singular environment cannot possibly be preprogrammed by genetic mechanisms; they have to be learned through experience. And how much an animal can learn about its environment is a function of its mnemonic capacity. Consider two pets that a family adopts, say, a turtle and a dog. After some lapse of time, the family is pleased to see that the turtle has learned some of the routines of the household: it emerges regularly from its box at the time of feeding, proceeds to the kitchen to feed, and returns to its box thereafter. But contrast these few habits that the turtle acquires with what the dog might learn. In little time after its adoption, the dog becomes thoroughly familiar with the layout and contents of the house and the surrounding area: where its food and water dish is located, where there are comfortable chairs and couches to lie on, and where there are some quiet corners to withdraw for privacy. The dog comes to recognize all members of the family as distinct individuals, as well as some visiting neighbors and friends, whom it will regularly greet and follow, and distinguishes them from strangers that it will bark at or attack. It will learn not to urinate or defecate in the house and, lacking linguistic skills, it will learn to communicate its particular needs, whether to be fed, petted, or let out of the house to relieve itself. If so trained, the dog will learn to abstain from climbing on the table and grab food from there; it will learn what it can chew on or play with in the house, and what it must leave unharmed. Although without the ability to speak, many dogs learn to respond appropriately to a smaller or larger repertoire of verbal commands. With some effort, some breeds of dogs can be trained to guard and corral sheep, fetch rather than consume the killed bird in a hunt, or become the patient guide of a blind person. This ability to acquire habits and skills through experience, and follow customs and traditions learned early in life, is widespread among mammals. Domesticated species learn to perform tasks that they do not exhibit under natural conditions. Cows readily subject themselves to be milked and may voluntarily line up at a particular time at the barn for that purpose. Horses learn to tolerate and eventually enjoy to be ridden or to pull a cart or a wagon. Elephants learn to carry out such chores as carrying large logs and stack them as their master commands.

THE ROLE OF EARLY LEARNING. Lower vertebrates require little experience, rehearsal or practice to gratify their needs. Indeed, when reared in isolation without opportunity to learn from elders or peers, lower vertebrates behave much like their naturally developing peers do (Lorenz, 1950; Eibl-Eibesfeldt, 1970). This ability has its advantages. However, the inborn disposition to respond to select “sign stimuli” with a “fixed action pattern” has many drawbacks. Being a product of natural selection, it tends to benefit the species as a whole rather than the individual. An individual may be exposed to an infinite variety of conditions but genetic mechanisms prepare it only for a finite set of conditions or situations. It is for this reason that species survival among lower vertebrates is typically achieved through high fecundity rather than increased individual survival. Mammals also inherit many inborn behavioral dispositions

and abilities but their enhanced life expectancy is due to their ability to learn from individual experience and practice.

Mammals begin their life with a prolonged infantile period. This provides them with the opportunity to master skills tailor-made for the demands of their particular physical and social environment. In one experiment, juvenile female rats were raised on powdered food in empty cages devoid of solid objects they could manipulate (Eibl-Eibesfeldt, 1963). Then, at about 2-3 months of age, they were provided with nesting material. Within a few hours, most of them proceeded to build a nest. However, the nests built by them, unlike those built by normally raised rats, were assembled haphazardly. Apparently, rats have an innate disposition to gather material to build a nest but to do that properly requires prior experience with object manipulation. Another illustration of the importance of early experience is the way rats learn what food items are suitable for consumption. As omnivores, rats are opportunistic feeders, making best use of nutrients available to them in their particular habitat. However, omnivorous feeding is hazardous because some substances are not fit for consumption and others are poisonous. The selection of suitable nutrients is guided by a combination of social learning and neophobia. After rats are weaned, juveniles begin to consume solid foodstuff by nibbling on what their mother consumes and scatters about; they are reluctant to ingest anything else (Barnett, 1958). If deprived of food, rat pups may wait up to five days and starve before they venture to ingest some novel nutrients made available to them (Galef and Clark, 1971). This neophobia has survival value. It has been reported, for instance, that a poison used for pest control that decimated a rat population over several generations, eventually became ineffective (Steiniger, 1950). Observations indicated that the young raised by surviving mothers, those that learned not to ingest the bait, themselves learned not to ingest the bait. Perhaps their mothers displayed a negative emotional reaction (retching) when coming upon the bait and that induced the young to shun it. Once poisoned, the bait-shyness of rats endures for life (Garcia et al., 1966).

Another illustration of the importance of early learning is the report of how a group of wild rats learned to survive in a forest where only pine seeds were available as nutrients (Zohar and Terkel, 1991; Aisner and Terkel, 1992). To gain access to these nutritious seeds, the rats had to learn how to remove the tough scales of the pinecones. This is a difficult task because it requires, first, breaking the base of the pinecone, followed by successive removal of the spiral scales, starting at the base and proceeding to the apex. Experiments showed that food-deprived adult rats not reared in this unique environment failed to learn how to perform this task and thus supplement their insufficient diet with pine nuts. However, young laboratory rats reared by mothers that were competent in stripping pinecones, readily mastered the skill. Conversely, young rats born to mothers that were efficient in stripping pinecones but reared by inexperienced females, failed to acquire this skill. Further observations indicated that juveniles learn how to open pinecones by working on ones that have been partially opened by adults (or by the experimenter using a pair of pliers), suggesting that the juveniles' mastery of this complex skill is facilitated by the behavior of adults. However, there was no evidence that the young directly imitated the adults, or that the adults explicitly trained them. There is currently little evidence for imitation or deliberate instruction in lower mammals, like rats; however, felines may train their young in the art of hunting (Caro and Hauser, 1992; Galef, 1998).

Short-Term and Long-Term Mental Imagery. The mental image may be the persistence of something experienced recently, short-term recall, or something stored in the brain and retrieved, long-term recollection. As described earlier, short-term memory (also called working memory) is indicated by the performance of rats in a radial arm maze, when they successively explore arms that they have not previously visited. Another test of short-term recall is the delayed reaction test (Fig. 5-10A). Hunter (1913) reported that rats could successfully solve that task if restrained for 5 seconds, whereas dogs could solve it with delays as long as 5 minutes. A more recent comparative study suggests (Fletcher, 1965) that the duration of working memory is shorter in the cat or raccoon than in primates (Fig. 5-10B). In a recent variation of this approach, dogs were given the task to search for a disappearing object (Fiset et al., 2003). The dogs' performance declined as a function of delay length but their searching behavior was still better than random after a delay of 240 seconds. In another experiment, cats were trained to locate a desirable food item hidden behind several boxes marked with visual cues (Fiset and Dore, 2006). As the delay was increased, the ability of the cats to locate the correct box declined but remained above chance level up to 60 seconds. We assume that the cats and dogs relied on a dissipating search image in their behavior.

DELAYED RESPONSE: WORKING MEMORY IN DIFFERENT MAMMALS

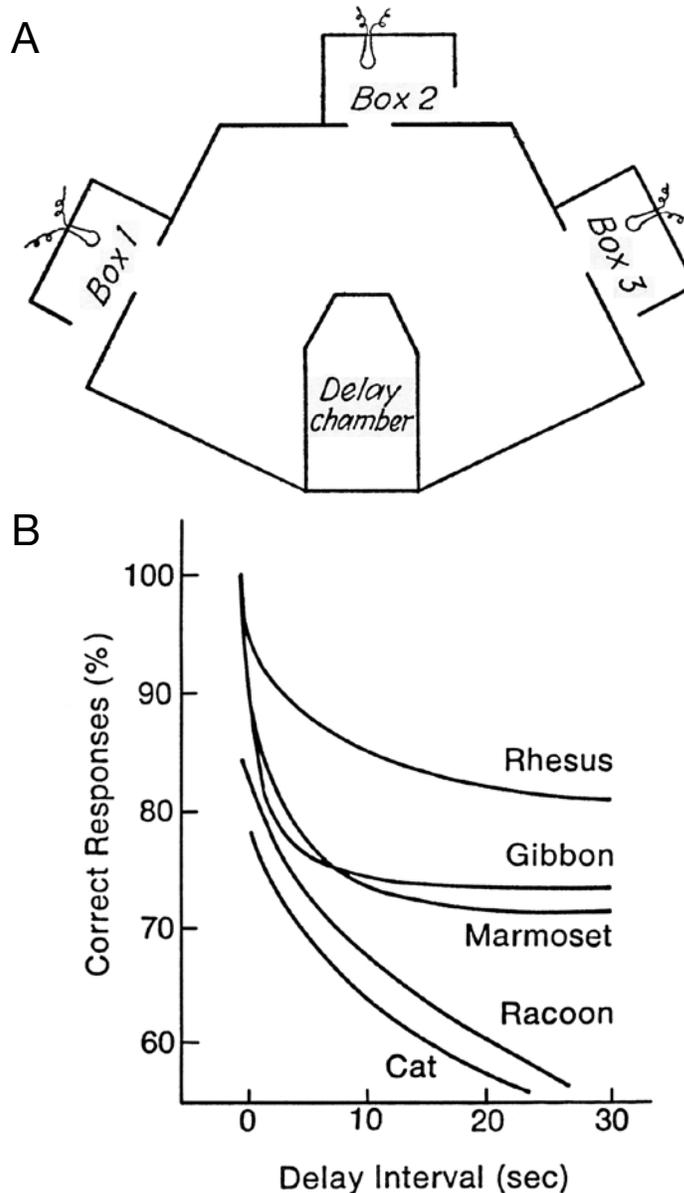


Fig. 5-10. A. Design of Hunter's delayed reaction apparatus. B. A comparative study of the performance of different mammals in a delayed response task, with the interval increased up to 30 seconds. (A, after Hunter, 1913. B, after Fletcher, 1965.)

Long-term recall of past experience has also been demonstrated in rats. Elliott (1928) reported that rats master a maze faster when rewarded with a preferred food (bran mash) than

a less favored one (sunflower seed). This could be explained in the behaviorist tradition as an association-mediated learning by postulating that the preferred reward produces stronger “reinforcement” or greater “habit strength” (Hull, 1943). However, Elliott also found that if the rats were trained to master the maze for the preferred bran mash but then the reward was surreptitiously changed to the less-favored sunflower seed, their performance suddenly deteriorated. Indeed, the performance of the “frustrated” animals fell below those that received the less preferred reward all along. Others obtained similar results, using different learning tests or rewards (Crespi, 1942; Zeeman, 1949; Flaherty et al., 1983). These findings are easily accounted for if we assume that a rat running a maze is guided by a specific search image and is frustrated if it does not receive what it anticipates (Amsel, 1958; 1992).

Imagery-Based Deliberation in the Rat. Does a primitive mammal, like the rat, fumble mindlessly as it acquires a new habit or does it deliberate (“think”) before opting for one course of action rather than another? In an early investigation, Lashley (1912) observed that rats trained to choose one of two visual patterns in a simple discrimination box, often turned their head back and forth before making a choice. This behavior was even more pronounced when the rat was tested in a jumping apparatus (Lashley, 1938; Dennis and Russell, 1939). The hesitating rat would typically crouch and turn its head in succession toward one door then the other door before jumping.

VTE AS A TEST OF DELIBERATION. Muenzinger (1938), who called this head movements in the jumping stand “vicarious trial and error” (VTE), undertook to quantify VTE frequency in relation to the rat’s progression in mastering the task. He found that VTE activity became particularly pronounced just before the rat began to make a series of correct responses. Tolman and Minium (1942) trained rats to make a white-black discrimination and found that VTE frequency was low as the animals initially adopted a position habit (jumping to the same door irrespective of the visual cue) but increased during the active learning period, and decreased substantially once the task has been mastered. When the discrimination task was made more difficult, VTE increased again, and then declined as the problem was solved. Similarly, VTE activity was pronounced during a maze-learning task, particularly when an alley directly pointed toward the goal box (Jackson, 1943).

IS IMAGERY-BASED DELIBERATION POSSIBLE? We generally hesitate when challenged with a difficult choice and that indicates that we engage in thinking before acting. VTE in the rat is rarely interpreted as a manifestation of thinking because of our reluctance to attribute such an advanced cognitive faculty to this “primitive” animal. Indeed, human thinking is largely a verbally mediated process, something that nonverbal rats cannot engage in. But is it possible that the VTE behavior of rats reflects a simpler imagery-based deliberation? Specifically, is VTE based on a combinatorial process of retrieving in the form of recollected imagery instances where jumping to one cue (say, square) led to falling, and jumping to the other cue (triangle) produced the desired reward? Can recollection imagery, without having verbally mediated concepts and ideas, aid an animal to decide what to do in a choice situation? The fact is that in some cases, for instance when we try to assemble a machine, we ourselves engage in such perceptually guided and imagery aided thinking, with little or no reliance on verbally mediated concepts and ideas. We use visual guidance to select from the shelf the correct

screwdriver to turn a screw, or the correct wrench to tighten a nut, rather than verbally based assessments of their respective sizes or features. And if we have to look around for other tools, we tend to keep in our short-term memory the image of a tool with desirable features to get the job done rather than its name. We propose that the phenomenon of VTE indicates that lower mammals are capable of imagery-based deliberation, a process that may constitute a primitive, incipient form of thinking.

THE CONSTRUCTION OF COGNITIVE SPATIAL MAPS. Other experimental approaches support this cognitive interpretation. An example is the way rats construct a topographically organized mental map of their environment (Tolman, 1948). Spatial learning is a prerequisite for getting to know the boundaries of a one's home range and the location of salient things within it. Spatial learning enables finding the shortest route to different foraging sites at different times or seasons and return home after a long expedition; it is vital to remember where one can find shelter when in need of rest and where to hide when threatened or pursued. The experimental approach to spatial learning in rats was introduced over a century ago by using mazes with choice points, blind alleys, and longer or shorter routes to a goal box baited with a reward (Small, 1901). Rats readily learn to navigate a maze with few errors, i.e., avoid blind alleys. The behaviorist explanation of the superior maze learning ability of rats is the acquisition of a series of egocentric stimulus-response habits in proper sequence rather than the acquisition of an allocentric mental representation, a picture or map, of the layout of the maze (Hull, 1943). In a pioneering study, Krechevsky (1932) used a simple maze in which rats could reach the baited target by relying either on a visual cue (e.g., consistently turn into the lit alley at the choice point) or a position cue (e.g., consistently turn to the left). He found that individual rats tended to use either the visual cue or the position cue at the outset and then, if not successful, switched to the alternate strategy. Krechevsky called these strategies "hypotheses." Tolman et al. (1946) designed a cross-shaped maze (Fig. 5-11) to test whether rats mindlessly acquire response habits when they master a maze or use a "cognitive map." Rats were trained to start at one arm of the maze, and were later tested by starting them at another (novel) arm. One group of rats was rewarded if they learned to consistently turn, say, to the right at the choice point; these were the "response learners." For the other group of rats, the location of the target remained the same irrespective of where they were started. That is, rats had to learn to turn either to the right or to the left, depending where they were started; these were the "place learners." Contrary to the "stimulus-response habit" theory of spatial learning, place learning proved to be an easy task for most rats, response learning very difficult. This indicated that rats tend to construct an allocentric mental representation of the layout of the environment.

MASTERING A RULE: REVERSAL LEARNING WITH THE SAME OR NEW SET OF CUES. It has been repeatedly demonstrated (Dufort et al., 1954; Pubols, 1957; Bitterman et al., 1958; Gonzalez and Shepp, 1961; Gonzalez et al., 1967a; Macintosh et al., 1968) that when rats are given a simple two-choice task, e.g., choose the alley cued by a black card to obtain a food reward and shun the alley cued by a white card, they reliably learn to select the correct cue after a few trials (Fig. 5-12A; 0=before reversal). If the cues that signals reward and nonreward are then reversed in the next session (A+B-, A-B+) the rats persevere with the old choice and may require close to 20 trials before selecting the correct cue (Fig. 5-12A, reversal 1). A within-session analysis indicates that while this pattern prevails in the first two reversal sessions (*dashed line*, Fig.

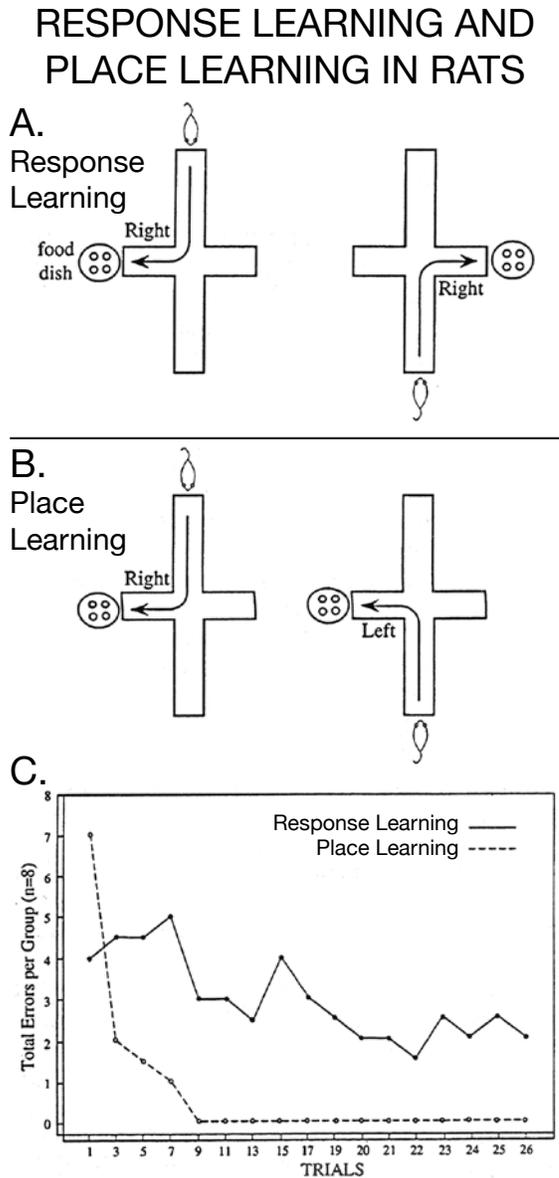


Fig. 5-11. **A.** One group of rats was trained in a cross maze to make the same turn (e.g., right) to obtain a reward, irrespective whether started from the north or the south; these were the response learners. **B.** Another group was trained to turn in the same direction (e.g., west); these were the place learners. **C.** Place leaning proved to very easy, response learning very difficult for the rats. (Modified, after Tolman et al., 1946.)

SIMPLE REVERSAL LEARNING IN RATS

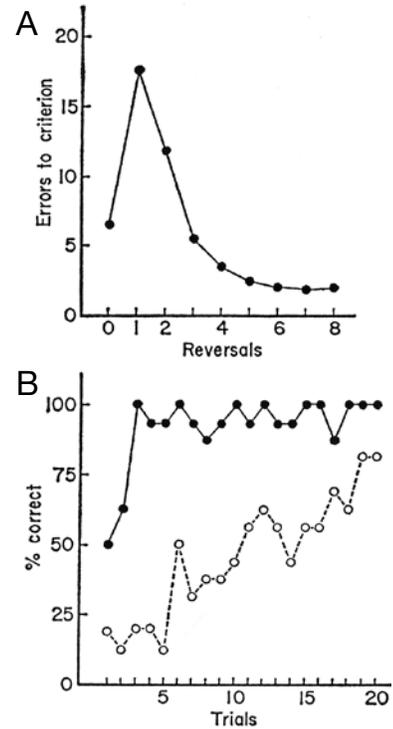


Fig. 5-12. **A.** Number of errors made by rats mastering a black-white discrimination task (zero=before reversal) and after a series of 8 reversals. **B.** Within-session (20 trials) performance during reversal tests 1 and 2 (O--O), and reversal tests 7 and 8 (●—●). (From Mackintosh, 1972.)

5-12B), after 7-8 reversal sessions, rats make the correct choice by the third trial (*solid line*, Fig. 5-12B). This suggests that rats gradually learn the rule to select the cue that is rewarded and refrain from selecting the cue that is not rewarded within any particular session. Fish, in contrast, require the same number of reversal learning trials as acquisition trials of the original discrimination (Gonzalez et al., 1967; Sutherland and Mackintosh, 1971).

A related but more complex form of rule learning is what Harlow called “learning set.” Instead of being tested with the same set of stimuli in a two-choice situation, the animal is given the task to select in successive sessions the correct cue with a new set of stimuli. After having learned to select, say, the black square instead of the white square, the animal has to learn in the next session to select the triangle instead of the circle, then the diamond instead of the cross, and so forth (A+B-, C+D-, E+F- ...). If the animal has been given enough problem sets and has reasoning power, it ought to select the correct cue after a single trial within a given session (one-trial learning) by applying the rule: “win, stay—lose, switch.” If the first random selection in any given session is rewarded, it has obviously stumbled upon the correct choice and, therefore, ought to stay with that throughout the session. If, on the other hand, the first random selection is not rewarded, it obviously made the incorrect choice and ought, therefore, switch to the alternate cue. Preschool children master this task after a few trials (Harlow, 1949; Shepard, 1957; Berman, 1973), with performance improving as a function of intelligence and age (Harter, 1965). Most rhesus monkeys solved this problem with a 90 percent probability after 200-400 problem sets, and some, apparently the brightest, succeeded in this task after exposure to a few problem sets (Warren, 1965, 1966). Cats, marmosets, and squirrel monkeys made about 70-80 percent correct choices (significantly above chance level) after the same number of problem sets. In contrast, rats tested on as many as 800 successive sets of two-choice discriminations still performed little above chance level on the second trial, indicating that they cannot ideationally solve this problem (Harlow (1949; Warren 1965). Interesting in this context is the finding that pigeons, notwithstanding their superiority in mastering visual discriminations, and a relatively large brain but one without a neocortex, show poor performance in learning set tasks (Macintosh, 1974), and passerine birds, like mynas and blue jays, attain no better than 70 percent correct responses on the second trial after 600 problem sets (Kamil and Hunter, 1970; Hunter and Kamil, 1971).

These findings suggested that performance on the learning-set test measures the cognitive power (intelligence) of the phylogenetic status of a species. However, in contrast to Harlow’s results with visual cues, subsequent investigations showed that rats readily solve learning-set problems when tested with olfactory or spatial cues. Slotnick and Katz (1974) reported that rats trained on 16 successive novel two-odor discriminations, showed reliable one-trial learning by the end of the problem series. This finding has been confirmed in other studies (Slotnick et al., 2000). Moreover, it has been reported that rats retained this ability to solve novel olfactory discriminations after a single trial when tested following a 6-week break in training (Bailey, 2006). Similarly, it has been reported that rats readily master spatial learning-set problems when successively tested in different rooms with different extra-maze cues, with some rats displaying one-trial learning by the third discrimination test (Fagan and Olton, 1987). Evidently, the failure of rats to display one-trial learning in visually-mediated, two-choice discrimination tasks is not due to cognitive disability but rather to the fact that, as nocturnal animals, they rely on other sense modalities. In summary, to the extent that the two-choice, learning-set task can be taken as a test of a simple cognitive ability—the realization of a rule that can be generalized across tests with different cues—that ability is displayed even by such “primitive” a mammal as the rat, one with a relatively small and unfolded (lissencephalic) neocortex. However, this need not mean that there are no phylogenetic differences in the cognitive abilities of mammals. To examine that issue, we now turn to an analysis of the

neural and mental abilities of select mammalian species, beginning with such basal mammals as insectivores and *tupaias*, and follow that with primates, beginning with prosimians.

5.2. Brain, Behavior and Mind in Basal Mammals: Insectivores and *Tupaias*

5.2.1. Generalists and Specialists in Mammalian Evolution. In turning to a discussion of the neural, behavioral and mental evolution of the mammalian line that led to the emergence of humans, it is useful to distinguish between two different mammalian trajectories, the specialists and the generalists. Specialists achieve reproductive fitness by evolving distinctive traits that make them better and better adapted to the distinctive niche they occupy. Generalists achieve fitness through opportunistic flexibility. This distinction between the two modes of adaptation is important from the perspective of human evolution because man's descent is traceable to a long line of generalists rather than specialists.

SPECIALIST MAMMALS. Specialists are more common among extant mammals than generalists. Broadly speaking, there are insectivores, herbivores, and carnivores among specialists. Specialized insectivores are the moles that occupy subterranean niches and forage underground. They favor earthworms, although they may also consume nuts. Less specialized insectivores are hedgehogs that scurry under bushes and are protected from predators by their spiny armor. Among highly specialized herbivores are grazers like the horse, browsers like cattle, and species with unique adaptations, such as the elephant, giraffe, hippopotamus, rhinoceros, and manatee. Among highly specialized carnivores are cheetahs, tigers and lions; and otters, sea lions and dolphins. All of them have distinctive traits that make them successful in exploiting the resources of their particular niche.

The specialization of extant mammals has been the product of a long evolutionary selection process. Best known is the evolutionary history of the modern horse (Simpson, 1951; MacFadden, 1992). The story begins with the small four-toed, browsing *Eohippus* that lived at the beginning of the Eocene, about 60 m.y.a., and ranged widely from Europe to North America. The somewhat larger four-toed *Orohippus* lived in the middle of the Eocene, about 45 m.y.a, replaced *eohippus* which, in turn, was replaced by the much larger three-toed *Mesohippus* and *Miohippus* during the Oligocene, about 30 m.y.a. All the early ancestral horses were browsers. Next in line was *Merychippus* of the Miocene, about 18 million years ago, a grazer that ran on a single large toe (its hoof) with the other toes becoming vestigial. This change, coupled with further increases in body size, continued as *Pliohippus* emerged during the Pliocene, about 5 m.y.a. and modern *Equus* during the Pleistocene, about 2 m.y.a. In the course of this evolutionary specialization, the extant horse—a large animal with powerful grinding teeth and long legs—became perfectly adapted to extract nutrients from low-calorie, hard and abrasive grasses, roam widely from one grazing ground to another, and defend itself by either kicking or fleeing from the large canines and felines. Their increased size conferred many advantages to horses. Greater bulk and strength reduced their vulnerability to small predators; reduced surface area relative to volume guaranteed less heat loss, hence enhanced ability to withstand cold; and the longer legs with single hooves improved their ability to outrun even the fastest predators. However, that specialization came with hazards. While specialization fosters

optimal adaptation to an existing habitat, it makes re-adaptation to a changing habitat more difficult if not impossible. The transformation of the horses teeth for grinding grass, their gastrointestinal system into a specialized mechanism for digesting the pulp, and their limbs into a single-purpose locomotor apparatus meant that horses could survive only in grasslands. Horses became extinct in North America as grasslands turned into forests or became glaciated, and human hunters appeared about 12 k.y.a.

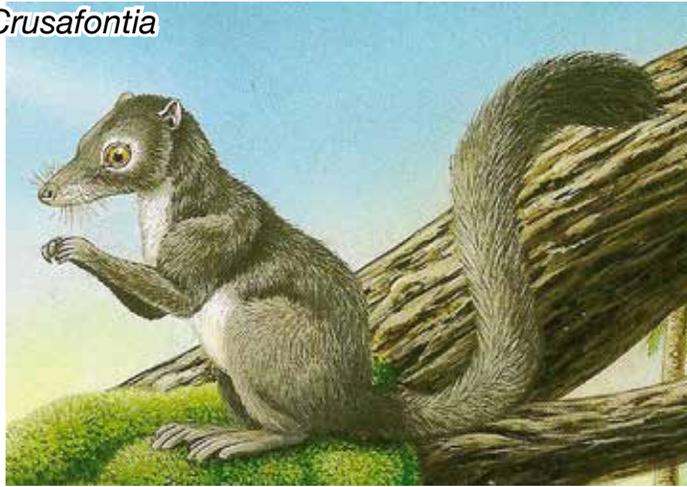
GENERALIST MAMMALS. Generalists followed a different evolutionary trajectory. To begin with, generalists tend to be omnivorous. An omnivorous diet allows animals to use a greater variety of nutrients, permitting them to shift from one food source to another, depending on what is available at different sites and during different seasons. Living on diverse nutrients, of course, requires greater behavioral flexibility than living on a calorie-poor but abundant resource, like grasses or leaves. Omnivorous foraging requires great sensory acuity for finding particular nutrients, variable and complex skills suitable for the acquisition of different resources and, above all, the ability to learn from experience what is palatable and not toxic, economically and hedonically more preferable. The rat, raccoon or bear will ingest anything that is digestible and has to learn how to choose among available foods. Nutrients are assessed in terms of their caloric content, their availability at different sites in different seasons, and the risk involved and the effort and skill needed to procure them. Bears have to learn to climb up a tree and extract honey from the beehive without being stung; how to position themselves on a rock to catch fish that swim upriver during their breeding season; or beg for food on a highway or open the garbage can in a backyard and go through its contents. It is not coincidental that generalists, like rats, raccoons and bears have several features in common. First, their body has retained several ancestral mammalian traits, like prehensile amphibian digits; second, they are unusually inquisitive and resourceful; third, by virtue of their behavioral flexibility and adaptability they are dispersed through virtually all climatic zones of this planet.

Basal Generalists: Shrews, Tupaias, and Prosimians. Although with our modified hands and feet we are specialists, the fossil record suggests that we descend from a line of generalists among mammals, shrew-like insectivores, primate-like *tupaiids*, and primitive primates, the prosimians. We have referred earlier to *Eomaia*, a small placental mammal dated to about 125 m.y.a. Another shrew-like fossil, the Jurassic *Crusafontia*, which occupied the woodlands of Western Europe, has been dated to the early Cretaceous, about 110 m.y.a. It is assumed that between these periods and the extinction of the dominant dinosaurs 65 m.y.a., these small warm-blooded mammals led a nocturnal existence, hunting and foraging while the cold-blooded reptiles were lying dormant. Locating nutrients in the dark can be achieved either by reliance on olfaction or large eyes adapted to nocturnal vision. The two basal lines may have coexisted, and *Crusafontia* (Fig. 5-13A) with its large eyes may be illustrative of the latter. As we describe below, among extant basal mammals, shrews (Fig. 5-13B) that have large snouts are distinguished by a large and complex central olfactory system, and *tupaias* with large eyes (Fig. 5-13C) by a large and complex central visual system, closely resembling that of primitive primates, the prosimians.

The earliest prosimians with large medial eyes, and with nails rather than claws, appeared in the late Paleocene about 60 m.y.a., with features resembling lemurs (Benton, 1991).

EXTINCT AND EXTANT BASAL MAMMALS

A. *Crusafontia*



B. Elephant Shrew



C. *Tupaia*



Fig. 5-13. A. The Jurassic *Crusafontia*. B. An elephant shrew. C. A tree shrew. (A from mrugala.net, B from true-wildlife.blogspot.com, C from flickriver.com)

Lemurs evolved in the early Eocene, about 55 million years ago (Simons and Rasmussen, 1994; Seiffert, et al., 2003). However, since lemurs are specialists, they are not likely to be in the direct line of human evolution. Presumably, some generalist prosimian gave rise during the Miocene to simians—about 40-35 m.y.a.—the New World (platyrrhine) and the Old World (catarrhine) monkeys (Fleagle, 1988). An Old World generalist monkey, perhaps one resembling macaques, was the progenitor of apes. The earliest apes, such as *Aegyptopithecus*, evolved about 30 m.y.a., and species that more closely resembled extant apes, like Proconsul and Dryopithecines, emerged by the early Miocene about 22 m.y.a. (Walker, 1997; Potts, 2004; Singleton, 2004). Specialist apes, like gibbons, which have long brachiating arms and spend most of their time in the trees, are far removed from the ancestral line of hominoids and hominins. Generalists, like the knuckle-walking chimpanzees and bonobos, which readily alternate between foraging and moving about on the ground and trees, and readily consume fruits, insects as well as larger prey, are closer to our early ancestors.

We shall consider below what is currently known about the behavior, brain, and mental disposition and abilities of insectivores, *tupaids*, and some prosimians. We shall deal with monkeys and apes in greater detail in Chapters 6-8.

5.2.2. Somatic Traits, Behavior, and Brain Organization of Insectivores. Insectivores, such as shrews, moles, hedgehogs and tenrecs, are the most primitive extant placental mammals. They are typically nocturnal and secretive, living in such concealed habitats as dense vegetation or debris, the crevices of rocks or tree stumps, or in underground dens and tunnels (Burnie and Wilson, 2001). Most shrews are terrestrial, moles are burrowing, and tenrecs are semi-aquatic. All shrews are small (some only 2-3 inches long) and in order to maintain their body temperature, they all have a high basal metabolic rate. Although they have short legs, most of them can run fast on the ground, are skilled climbers, and are busy foragers. Notwithstanding their name, insectivores are omnivorous. They feed on whatever is locally available, such as worms, beetles, slugs, scorpions, bird's eggs, frogs or small fish, as well as berries and nuts. Because of their great speed and agility some small shrews can successfully prey on victims larger than themselves. Most insectivores have small eyes and ears but all of them have a prominent mobile snout. The snout serves both as an olfactory and tactile sense organ, and one specialist, the star-nosed mole, palpates and manipulates prey with the tentacles of its snout.

Most insectivores are solitary, but males and females interact with one another during their reproductive periods. Musk shrews scent their body during the mating season and this appears to facilitate their affiliation during the mating season. The female musk shrew is an induced ovulator, ovulating when raised in the vicinity of a male or on soiled bedding from a male (Rissman, 1987; Rissman et al., 1990). Females signal their sexual receptivity by tail wagging and there is evidence that that behavior is associated with elevated blood levels of cortisol (Schiml and Rissman, 1999). Likewise, the male's sexual maturation, as judged by testicular growth and testosterone levels, is enhanced when raised in the vicinity of a female, or with soiled bedding from a female. In the male, castration abolishes body scenting but the administration of testosterone restores that behavior (Tennant et al., 1987). The finding that removal of the olfactory bulb in musk shrews abolishes ovulation and copulation, establishes

the important role of olfaction in reproductive processes (Rissman and Lee, 2000). In the female, steroid implants in the medial preoptic area or hypothalamic ventromedial nucleus activate feminine sexual behavior (Veney and Rissman, 2000).

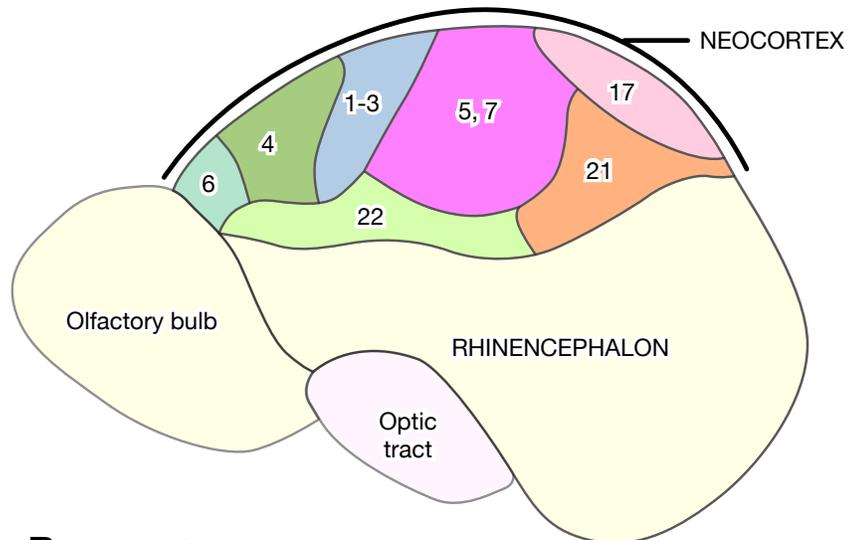
THE SENSE ORGANS AND PALEOCEPHALON OF INSECTIVORES. Most insectivores have small eyes and ears (Fig. 5-13B), although both senses appear to play some role in their behavior, with the exception of some moles that are virtually blind. The retina of insectivores contains a much higher proportion of rods than cones. Cones constitute only 2% of the photoreceptors in the nocturnal tenrec and 13% in the partially diurnal common shrew (Peichl et al., 2000). The type of cones identified in insectivores suggests dichromatic color vision. In the hedgehog and the musk shrew, retinal fibers have been traced bilaterally (with a contralateral preponderance) to the superior colliculus, the pretectal area, the dorsal and ventral nuclei of the lateral geniculate body, the accessory nuclei of the optic tract, and the suprachiasmatic nucleus (Dinopoulos et al., 1987; Tokunaga et al., 1992). In the tenrec, the superior colliculus also receives somatosensory projection from the dorsal column nuclei and the trigeminal complex (Künzle, 1993, 1996, 1998c). Efferent projections of the superior colliculus target the hypothalamus, the subthalamic region, the brainstem reticular formation, and the medullary inferior olive (Künzle, 1997a). In the mole, most of the auditory nuclei of the medulla and pons—including the dorsal and ventral cochlear nuclei, the superior olivary complex, and the nuclei of the lateral lemniscus—are well developed, and there is a large afferent projection to the inferior colliculus (Kudo et al., 1990). The inferior colliculus, the homologue of the torus semicircularis of lower vertebrates, also receives a somatosensory projection (Künzle, 1993).

THE OLFACTORY SYSTEM AND RHINENCEPHALON. The olfactory bulb, the first-order central target of olfactory sensory cells, is very large in macrosomatic insectivores when compared with such microsomatic mammals as primates, and has a complex laminar organization (Lopez-Mascaraque et al., 1986; Künzle and Radtke-Schuller, 2000; Radtke-Schuller and Künzle, 2000). Second- or higher-order olfactory fibers have been traced in the hedgehog to the large rhinencephalon (Fig. 5-14A), which includes structures such as the anterior olfactory nucleus, the nucleus of the lateral olfactory tract and the piriform cortex, and such basal telencephalic limbic structures as the septum, the diagonal band of Broca, and the amygdala (De Carlos et al., 1989). Most of these structures are more prominent in insectivores than in higher mammals (Baron et al., 1987). Among different insectivore species, those with exclusive nocturnal life styles, have larger olfactory brains than those with partial diurnal life styles or those occupying aquatic habitats (Barton et al., 1995).

THE NEENCEPHALON OF INSECTIVORES. While the rhinencephalon is a far more prominent component of the forebrain of extant insectivores (Figs. 5-14, 5-15A, 5-16A) than the neencephalon, they have a neocortex, a structure altogether absent in reptiles. However, the neencephalon is much smaller relative to the rest of the brain than it is even in such a primitive mammal as the mouse (Figs. 5-15B) or *Tupaia* (Fig. 5-16B, D). The density of synapses in the hedgehog neocortex is similar to that seen in primates (Schuz and Demianenko, 1995) but cortical lamination is not distinct (Ferrer, 1992, Frahm et al., 1982). The corpus callosum, the neocortical commissure, is small in insectivores (De Carlos et al., 1989). Cytoarchitectonic studies indicate (Fig 5-14A) that much of the hedgehog neocortex is composed of the projection

THE EARLY MAMMALIAN NEOCORTEX IN HEDGEHOG (*ERINACEUS*)

A CYTOARCHITECTONIC MAP



B PHYSIOLOGICAL MAP

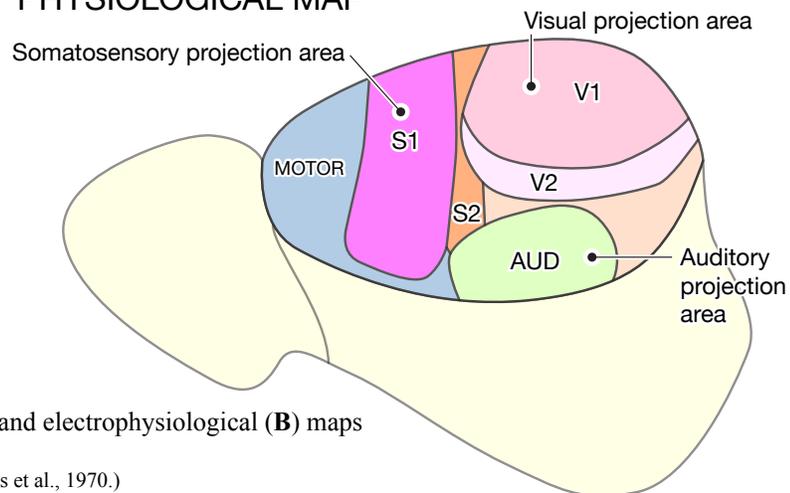


Fig. 5-14. Cytoarchitectonic (A) and electrophysiological (B) maps of the hedgehog forebrain.

(A, after Le Gros Clark, 1971; B, after Kaas et al., 1970.)

fields of the visual (Brodmann area 17, BA17), somesthetic (BA1-3), and auditory (BA22) systems, and a motor area (BA4) (Brodmann, 1909; Le Gros Clark, 1971). Physiological studies (Fig. 5-14B; Kaas 1980; Batzri-Israeli et al., 1990; Krubitzer et al., 1997; Catania et al., 1999, 2000) indicate the presence of two visual areas (V1, V2) and two somatosensory areas (S1, S2).

There is a distinct lateral geniculate nucleus in the tenrec with afferents from the retina, but its major input is from the superior colliculus (rather than the retina) and its projection to the visual cortex is small (Künzle, 1996; 1998b). The ventrolateral thalamic nuclei receive somatosensory afferents from the dorsal column nuclei and the trigeminal complex and there is a cerebellar input (Valverde et al., 1986; Künzle, 1994, 1998a, b). But in contrast to advanced

FOREBRAIN OF AN INSECTIVORE AND A RODENT

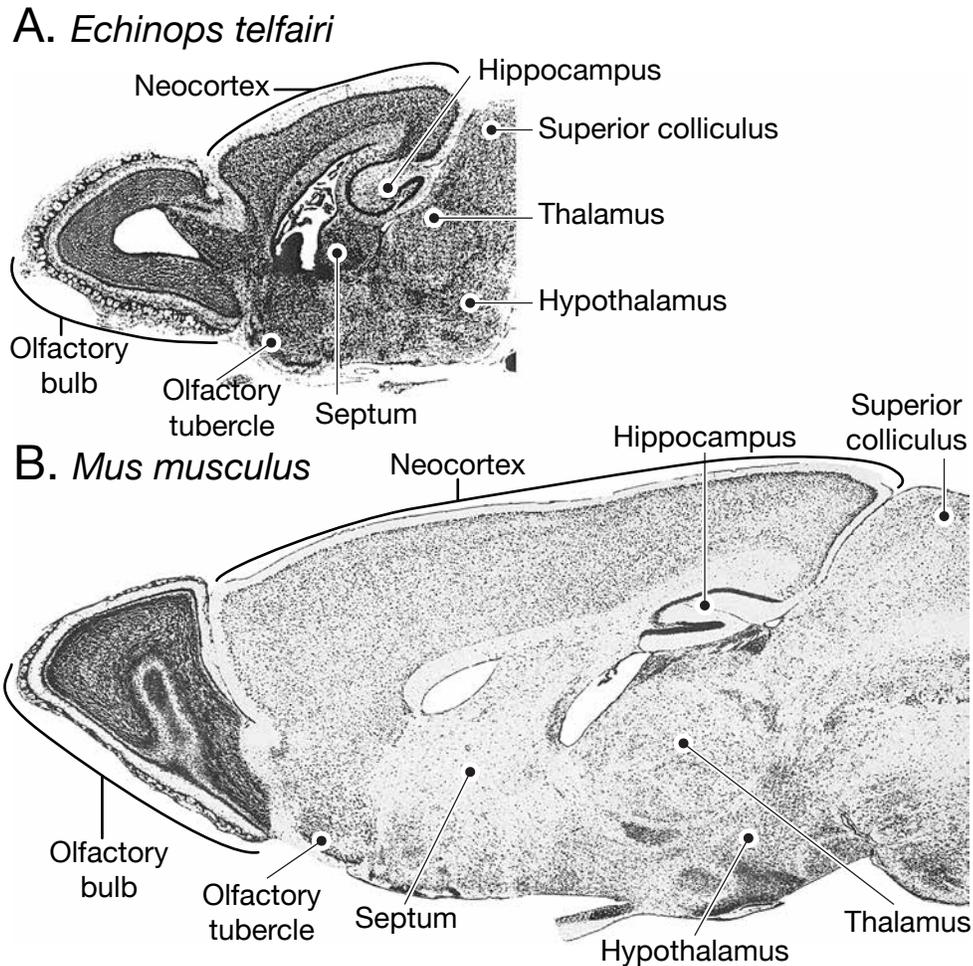


Fig. 5-15. The relatively small neocortex of an insectivore (A) compared with that of the mouse (B). Sagittal sections, with the olfactory bulb shown at approximately the same magnification. (A, after Rehkamper, 2001. B, after Sidman et al., 1971.)

mammals, in which the thalamocortical projection is strictly ipsilateral, the somatosensory projection to the hedgehog cortex is bilateral (Regidor and Divac, 1992; Dinopoulos, 1994). In the mole, the visual cortex is small and has a poorly developed internal granular layer, the target of visual radiation fibers (Ferrer, 1986). The medial geniculate body receives afferents from the inferior colliculus but the latter also projects to the lateral geniculate body and the suprachiasmatic nucleus (Kudo et al., 1997), perhaps a unique specialization of moles with poor eyes. A specialization in the star-nosed mole (which, as we noted, has tactile snout appendages) is a well-developed cortical region where each nasal ray is represented by a stripe of tissue in the somatosensory cortex (Catania and Kaas, 1997; Catania, 2000). This is reminiscent of the discrete representation of each vibrissa in “barrels” of the somatosensory cortex of the mouse (Woolsey and van der Loos, 1970).

With regard to the neocortical motor system of insectivores, there is a direct but small neocortical outflow to the spinal cord in the hedgehog (Michaloudi et al., 1988), the tenrec (Künzle and Rehkamper, 1992), and the mole (Catania and Kaas, 1997). The origin of this corticofugal projection, which does not descend beyond the upper cervical segments, are layer V cells in the small motor cortex and adjacent somatosensory areas. Most of these corticospinal fibers descend ipsilaterally (Künzle and Rehkamper, 1992; Palmieri et al., 1993), which is unlike the pattern found in more advanced mammals in which the majority of corticospinal fibers cross to the opposite side in the medullary pyramids. Moreover, the most prominent terminal target of these corticofugal fibers is not the spinal cord but the hypothalamus, the periaqueductal gray, the midbrain tegmentum, and several brain stem nuclei (Künzle and Lotter, 1996). Indeed, no motor deficits are observed following ablation of the motor cortex in the hedgehog (Palmieri et al., 1993). Resembling the pattern seen in reptiles, the diencephalic subthalamus and hypothalamus, and the mesencephalic tectum, tegmentum and reticular formation are the principal source of efferents to the spinal cord.

In summary, the neencephalon is present in insectivores, the most primitive of extant placental mammals, but it is poorly developed. In contrast to advanced mammals, the thalamic projection to the neocortex is bilateral rather than unilateral. Moreover, the principal target of descending cortical projections in insectivores is the diencephalon and mesencephalon, and the few fibers that descend to the spinal cord do not decussate and terminate only at upper cervical levels. Extant insectivores, as we noted, are basal mammals that are closely related to the earliest placental mammals of the Jurassic and Cretaceous periods. However, they are typically nocturnal animals with a prominent rhinencephalon, distant relations of primates. Closer to the ancestral line of primates are the *tupaias* (tree shrews), marked by a well-developed visual system and diurnal adaptations.

5.2.3. Somatic Traits, Behavior, and Brain Organization of Tupaias. *Tupaias* are small, squirrel-like animals. They are of great interest from the perspective of human evolution because they show close affinities with both insectivores and prosimians (Van Valen, 1965; Campbell, 1966; Le Gros Clark, 1971; Emmons, 2000). Indeed, it has been argued that *tupaias* are primitive primates (Carlsson, 1922; Le Gros Clark, 1925). However, they are now considered to belong to a separate order, the *Scandentia* (Luckett, 1980).

LIFE STYLE AND FEEDING. Unlike most insectivores, *tupaias* are diurnal animals. In their natural habitat, they tend to leave their nest at dawn, forage for food all day long, and return to their nest at dusk (Emmons, 2000). They are active omnivorous feeders with a voracious appetite, searching in the clutter of the forest floor for caterpillars, ants, crickets, cockroaches, beetles, and the like, and, climbing up trees with great agility, consuming berries, fruits and bird's eggs. Hence, *tupaias* are neither arboreal nor terrestrial specialists but rather scansorial (climbing) generalists (Jenkins, 1974). The main survival strategy of tree shrews is their great alertness, cryptic coloration, and quiet way of moving about in the dense vegetation of the forest. Observations in the wild indicate that while *tupaias* tend to use their mouth to capture insects, they use their paws to reach for fruit and hold it while consuming it.

Similar observations have been made in a large colony of *tupaia*s in captivity (Hasler and Sorenson, 1974). They are strictly diurnal and omnivorous. They consume insects and mice, seeds and nuts, but prefer juicy fruits. When offered live grasshoppers, they usually track them with their eyes and catch them with their mouths; peanuts and sunflower seeds are shelled before eating. In the typical feeding posture, they sit on their haunches, hold the food item with their forepaws, and use their incisors as scoops when consuming soft fruits and their molars to grind hard nutrients. Both adult males and females are cannibalistic and consume newborns and adults that die.

SOCIAL BEHAVIOR. In the wild, many species of tree shrews live as loosely bonded monogamous pairs; in other species the family unit is polygynous, with one male living with two or three females. The family shares a territory, which they patrol by frequent scent markings with skin-gland secretions and urine, and is defended by the male against intruding conspecifics (Kawamichi and Kawamichi, 1982; Holst and Eichmann, 1998). Scent marking is affected by testosterone levels and by the presence of conspecifics of the same or opposite sex (Eichmann and Holst, 1999). However, the bonded male and female rarely occupy the same nest; they forage separately and meet periodically to reinforce their social bond. During the reproductive season, which occurs when food is abundant, the parents build a separate breeding nest in a tree cavity above the ground. After a gestation period of 46 to 60 days, the female delivers 2-4 young with closed eyes and little fur. However, the mother does not stay with the young or take care of them, as most mammals do; rather, she visits the nest once every other day for no longer than 5 minutes for the sole task of nursing the young (Martin, 1966, 1968; D'Souza and Martin, 1974). Within this short period, the young consume as much as one-third of their body weight of milk. It has been suggested that since adults have a strong odor that can easily be tracked, this "absenteeism" is a way of protecting the young from predators (Emmons, 2000). The young leave the nest at about 30 days of age but now the parents stay with them for a short period every day, licking them and guiding them to feeding sites. When the young are about 60 days old, parenting ends. Indeed, the father may display hostility towards its sons and treats its daughters as potential mates. The young reach adult size at about 3-4 months of age and shortly thereafter become ready to breed themselves.

In captivity, the social behavior of male and female *tupaia*s differ considerably (Hasler and Sorenson, 1974). From the outset of being housed together, the confined males are extremely hostile toward one another, displaying threat postures, chasing, lunging and biting each other, until one of them emerges as the tyrant. The males rarely bite the females. The emerging tyrant marks its acquired domain with glandular secretions and urine, keeps harassing the vanquished males. Henceforth the tyrant male has exclusive access to the receptive females and most of the other males in the group die within a 2-month period. The females initially chase each other, without biting, and in time establish a linear social hierarchy by periodically displaying threat postures towards subordinates. However, the females often rest together and sleep on top of one another. While both males and females frequently groom themselves, combing their fur with their teeth and licking themselves with their tongue, allogrooming and reciprocal grooming was infrequent. Males were not observed grooming others; the females occasionally groomed each other or the tyrant male.

The Olfactory System of Tupaia. Although diurnal tupaia rely much more on vision in their daily life than do insectivores, olfaction still plays an important role in their behavior, and the rhinencephalon takes up a large part of their telencephalon. (Compare the relative sizes of the rhinencephalon between the hedgehog and *Tupaia* in Fig. 5-16). *Tupaia* have a wet nose pad that they frequently moisten with their tongue and they use their sense of smell in foraging as well as in social relations by creating scent-marked odor trails (Martin, 1968; Emmons, 2000). Corresponding with this role of olfaction, the rhinencephalon is more prominent in *tupaia* than it is in primates (Baron et al., 1983, 1987). Afferent projections from the *tupaia* main olfactory bulb has been traced to several brain regions: the anterior olfactory nucleus, the olfactory tubercle, the entorhinal cortex, and parts of the cortical amygdaloid area (Ferrer, 1969; Skeen and Hall, 1977). The accessory olfactory bulb, which is related to the vomeronasal organ, projects to the bed nucleus of stria terminalis and the medial amygdaloid area. The olfactory fibers terminate in layer I of the allocortical rhinencephalon, which is unlike the termination pattern of visual, tactile and auditory fibers in layer IV of the neocortex.

The Visual System of Tupaia. Most *tupaia* have large eyes but in contrast to prosimians and monkeys, their eyes are positioned laterally rather than medially, much like in insectivores (Fig 5-13B, C). The photoreceptor layer of the *tupaia* retina is composed mostly of cones, with some rods (Polyak, 1957; Samorajski et al., 1966; Kuhne, 1983; Foelix et al., 1987; Muller and Peichl, 1991). Their color vision is dichromatic, with two peaks at 440 and 550 nanometer (Jacobs and Neitz, 1986). The *tupaia* retina contains several classes of physiologically characterized ganglion cells. (i) Fast-conducting Y-cells that have a large visual receptive field and respond with a transient discharge to optic stimulation. These are well suited for rapid scanning of the visual world. (ii) Slow-conducting X-cells that have a smaller receptive field, and respond with a sustained discharge to contrasting stationary stimuli. These are well suited for pattern discrimination and object recognition. (iii) W-cells that are sensitive to the orientation of the stimulus and their direction of movement (van Dongen et al., 1976; Wong-Riley and Norton, 1988) may play a role in tracking objects. Some ganglion cells are characterized as “on-center” neurons. These are maximally activated by bright light against a dark surround, i.e., are enhanced bright spot detectors. Others, the “off-center” neurons, respond maximally to a dark spot against a bright surround; these are enhanced dark spot detectors. The optic tract fibers project to the superior colliculus and the pretectum in the midbrain, the suprachiasmatic nucleus of the hypothalamus, as well as the lateral geniculate body and pulvinar of the thalamus.

THE SUPERIOR COLLICULUS. The superior colliculus of *tupaia* (Fig. 5-16C), the homologue of the optic lobe of lower vertebrates, is large and is composed of several layers. The superficial layers have been implicated in sensory processing, the deep layers in motor control (Hall and Lee, 1993). The superficial layers receive a large input from the optic tract (Graham and Casagrande, 1980). The optic tract projection to the superior colliculus is predominantly contralateral, with some patchy ipsilateral projection (Conley et al., 1985). A high proportion of collicular neurons have small visual receptive fields that provide high visual resolution (Hilbig et al., 2000). There is an outflow from the superficial layers of the superior colliculus to the lateral geniculate body and the pulvinar, and these two may originate in different layers (Albano et al., 1979). The deep layers of the superior colliculus receive an input from

THE NEOCORTEX IN TWO BASAL MAMMALS

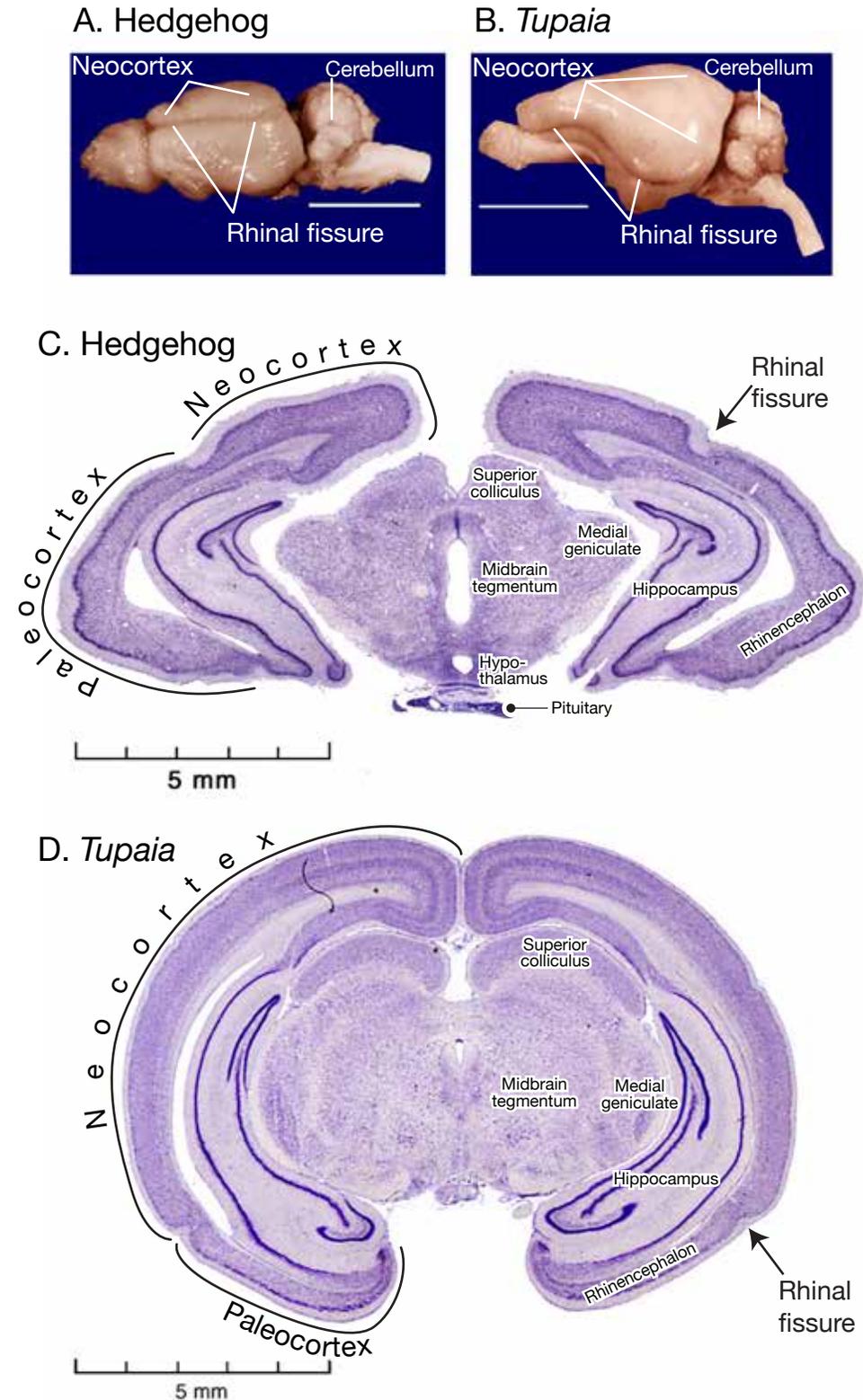


Fig. 5-16. Lateral view of the brain of a hedgehog (A) and *tupaia* (B), with cell-stained, coronal sections of the hedgehog (C) and *tupaia* (D) brain. (After W. Welker, www.brainmuseum.org.)

the neocortex (Casseday et al., 1979) and project to several tegmental nuclei, the reticular formation, and the inferior olive (Harting et al., 1973b). Collicular lesions produce severe pattern discrimination deficits in *tupaia*s. The organization of the descending brain stem (paleocephalic) motor system has not been systematically investigated. Perhaps an important component of that system, in addition to the reticulospinal tract, is the rubrospinal tract, which unlike the neencephalic corticospinal tract, reaches the lumbosacral cord in *tupaia*s (Murray et al., 1976).

THE LATERAL GENICULATE NUCLEUS. The thalamus of *tupaia*s, with its large neothalamic components, resembles that of primates (Fig. 5-17). The dorsal nucleus of the lateral geniculate body (dLGN) has an advanced six-layered organization (Diamond, 1970; Schroeder and Jane, 1971; Simmons, 1979-1981) where contralateral and ipsilateral optic nerve fibers are segregated (Glickstein, 1967) and are monocularly activated (Sherman et al., 1975). The ipsilateral fibers terminate in lamina 1 and 5, the contralateral fibers in lamina 2 and 4. The different layers contain different classes of neurons in different proportions: (i) on-center (bright-spot detector) cells predominate in lamina 1 and 2; (ii) off-center (dark-spot detector) cells in lamina 4 and 5; and (iii) W-cells (movement detector) cells are located mostly in lamina 3 and 6 (Holdefer et al., 1988; Wong-Riley and Norton, 1988). Input to the latter comes from the superior colliculus (Diamond et al., 1991). There are dLGN neurons of different sizes and dendritic configurations. Some of them provide interconnection between the different layers while others are relay neurons that project to the visual cortex (Hajdu et al., 1982a; Saini et al., 1987). This arrangement presumably facilitates the use of binocular cues for depth perception. However, notwithstanding its laminar complexity, the dLGN of *tupaia*s is the target of only 20 per cent of optic nerve fibers (Hajdu et al., 1982b). This is a far smaller proportion than that found in primates. While the majority of optic nerve fibers target the paleocephalic superior colliculus, some terminate in the pulvinar (Ohno et al., 1975; Somogyi et al., 1981) and the suprachiasmatic nucleus (Murakami and Fuller, 1990; Reuss and Fuchs, 2000). *Tupaia*s also have a ventral LGN with several components (Agarwala et al., 1992; Conley and Friederich-Ecsy, 1993a). The vLGN receives input from the retina, the superficial layers of the superior colliculus, the pretectum, and the striate cortex; and its principal output is to the deep layers of the superior colliculus, the hypothalamus, midbrain tegmentum, and the vestibular nuclei (Conley and Friederich-Ecsy, 1993a, b). These connections suggest that the ventral nucleus is not part of the neothalamic-neocortical visual relay system.

THE PULVINAR. In addition to the direct visual pathway from the dLGN to V1, there is in *tupaia*s also an indirect pathway from the superior colliculus (optic lobe) to the large pulvinar nucleus of the thalamus (Lyon et al., 2003; Luppino et al., 1988; Chomsung et al., 2008). The pulvinar (Figs. 5-17, 5-18B), which may not exist or is poorly developed in insectivores, in turn, projects to V1 (Lyon et al., 2003), the visual association areas of the posterior cortex (Chomsung et al., 2010), and to the striatum and the amygdala (Chomsung et al., 2008). This relay from the dorsal pulvinar of *tupaia*s to the striatum is topographically organized, whereas that from the central pulvinar is diffuse (Luppino et al., 1988; Day-Brown et al., 2010). The latter authors speculated that the topographic pathway to the striatum is involved in the visual guidance of precise motor activities, whereas the diffuse pathway to the amygdala functions as an alerting mechanism to dangerous visual stimuli.

THE THALAMUS OF *Tupaia*

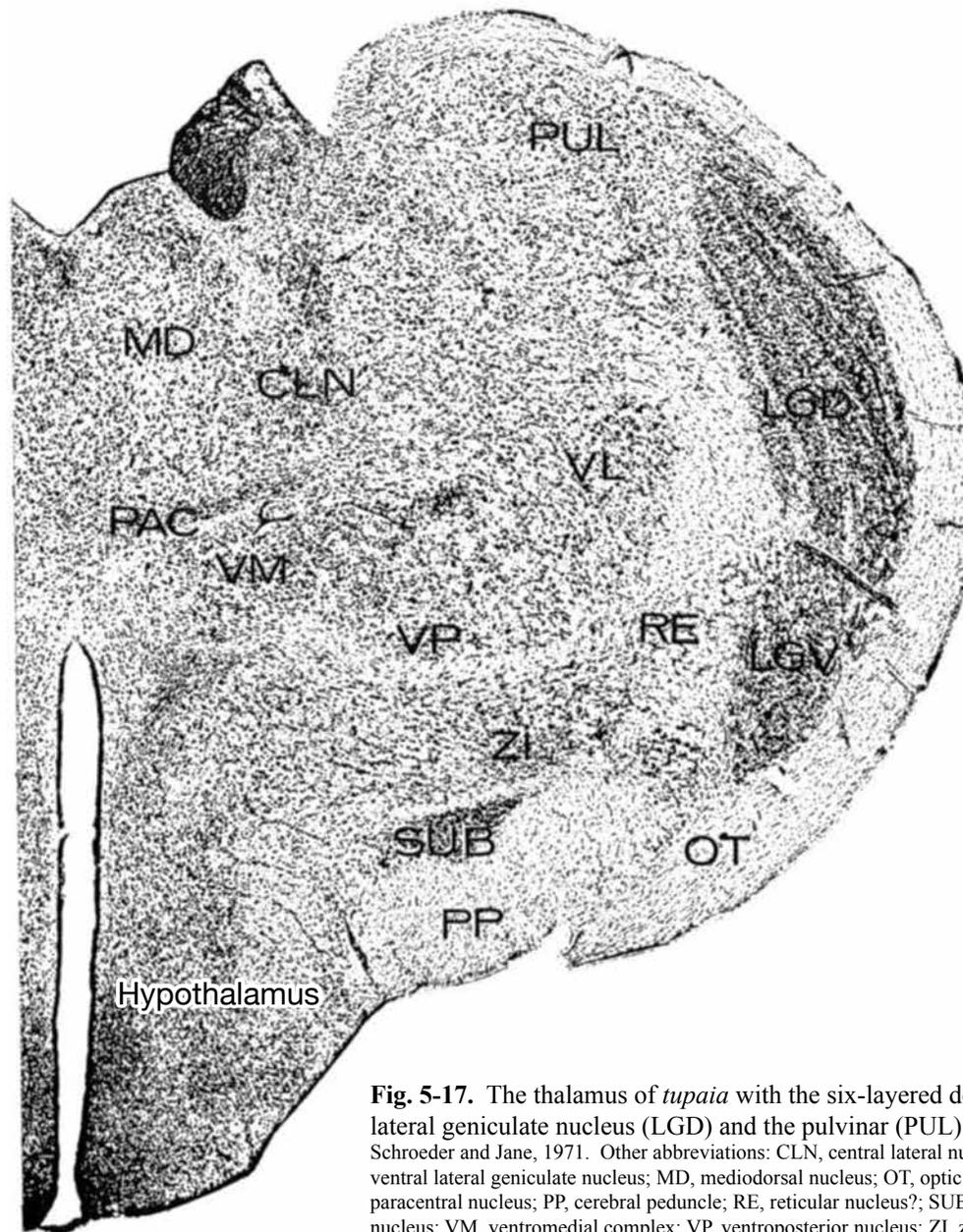


Fig. 5-17. The thalamus of *tupaia* with the six-layered dorsal lateral geniculate nucleus (LGD) and the pulvinar (PUL). (After Schroeder and Jane, 1971. Other abbreviations: CLN, central lateral nucleus; LGV, ventral lateral geniculate nucleus; MD, mediodorsal nucleus; OT, optic tract; PAC, paracentral nucleus; PP, cerebral peduncle; RE, reticular nucleus?; SUB, subthalamic nucleus; VM, ventromedial complex; VP, ventroposterior nucleus; ZI, zona incerta)

The Neocortex of Tupaia. The neocortex is larger and more differentiated in *tupaia*s than in insectivores (Fig. 5-16A-B), and it resembles more closely the neocortex of primates than that of shrews or rodents, like the rat (Diamond, 1970; Cusick et al., 1985; Remple et al, 2006, 2007; Wong and Kaas, 2009). It is composed of large projection areas of the visual, somatosensory, and auditory systems that are targets of thalamic relay nuclei (Fig. 5-18A) as well as occipital, parietal, and temporal association areas that are interconnected with each other and with the pulvinar nucleus (Fig. 5-18B).

ORGANIZATION OF *Tupaia* NEOCORTEX

Fig. 5-18.

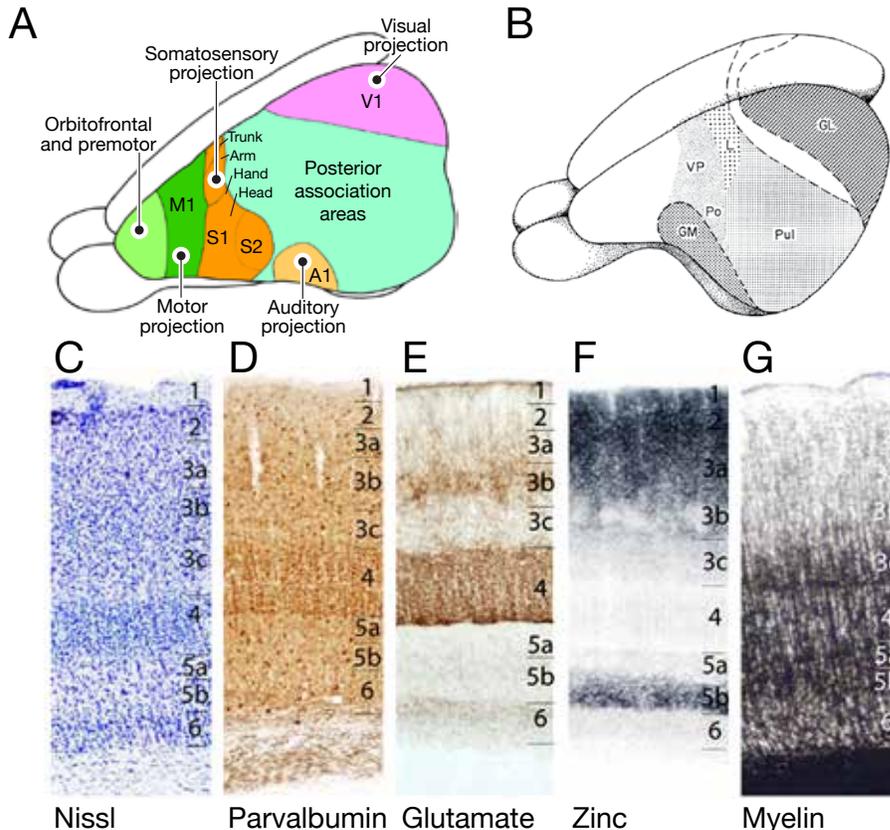
A. Projection areas and association areas of the tupaia neocortex.

B. Corresponding terminal fields of the different thalamic relay nuclei and of the pulvinar.

(Abbreviations: GL, lateral geniculate; GM, medial geniculate; L, lateral nucleus; Po, posterior nucleus; Pul, pulvinar; VP, ventral posterior.)

C-G. The organization of the tupaia striate cortex, revealed by different staining procedures.

(A. After Kusick et al., 1985; Remple et al., 2006, 2007. B. After Diamond et al., 1970. C-G. After Wong and Kaas, 2009.)



THE VISUAL CORTEX. Correlated with their primate-like dLGN, *tupaias* have a distinctly laminated visual cortex (striate cortex or V1) with a prominent layer 4 (Figs. 5-16D, 5-18C). Staining of V1 with different reagents (Wong and Kaas, 2009) has revealed some differences in the organization, and possible functions, of these layers. Parvalbumin staining shows the partitioning of layer 4 into two cellular bands (Fig. 5-18D). Glutamate staining, a marker for thalamocortical fibers, indicates that these terminate principally in granular layer 4, with a smaller terminal band in supragranular layer 3 (Fig. 5-18E). Zinc staining may reflect the rich network of locally arborizing neuron processes in supragranular layers 3 and 2 (Fig. 5-18F). Myelin staining shows the concentration of cortical afferents and efferents in the lower portion of the gray matter (Fig. 5-18G).

Neurons in different lamina of the dLGN send axons in a precise retinotopic order to subdivisions of the granular layer of V1: lamina 1 and 2 project to cortical layer IVa; lamina 4 and 5 to layer IVb (the granular layers); and lamina 3 and 6, chiefly to layer III (Diamond et al., 1970, 1985; Harting et al., 1973a; Conley et al., 1984). We may recall that laminae 1 and 2 of the dLGN contain bright-spot detecting neurons, laminae 4 and 5 dark-spot detecting neurons, and laminae 3 and 6 motion-detector neurons. That is, the functionally distinct visual channels remain separate in layer IV of the striate cortex (Norton et al., 1985; Kretz et al., 1986). This is the starting point of the complex cortical process that allows pictorial representation of external objects, images with sharp contours against their background. The first step in that process

is the amalgamation of bright and dark *spots* into bright lines or dark *lines* of a particular orientation, the elements that form the outline of objects. Hubel and Wiesel (1959, 1968) demonstrated in cats and monkeys that different cortical neurons respond preferentially to bright or dark bars or edges of a particular orientation in the visual field, ranging from vertical to horizontal. They called these orientation-specific, line-detector neurons “simple cells.” These line-detectors neurons form radial cell columns (minicolumns) throughout the striate cortex. Hubel and Wiesel also described “complex cells” in the cat and monkey visual cortex that respond to lines with a specific orientation that move in a particular direction irrespective where they are located in the visual field. Studies in *tupaia*s have shown that, as in cats and monkeys, a high proportion of V1 neurons preferentially respond to either dark or white lines of a particular orientation (Skeen et al, 1978; Kaufmann and Somjen, 1979; Humphrey and Norton, 1980). These orientation-specific line detectors form patches (hypercolumns) across V1 (Fig. 5-19A-C). Complex neurons are also present in the V1 of *tupaia*s (Kaufmann and Somjen, 1979). And some evidence has been presented that neurons with horizontally extended axons in layers 2-3 (the supragranular layers) interconnect these patches with one another (Rockland et al., 1982; Bosking et al., 1997) (Fig. 5-19D). (Kaschube et al., 2010, discuss the evolutionary origins and significance of this organization.) Neurons in the supragranular layers are also the source of commissural fibers that cross in the corpus callosum and interconnect the visual areas in the two hemispheres

ORIENTATION AND SELECTIVITY OF COLUMNS AND PATCHES IN *Tupaia* VISUAL CORTEX

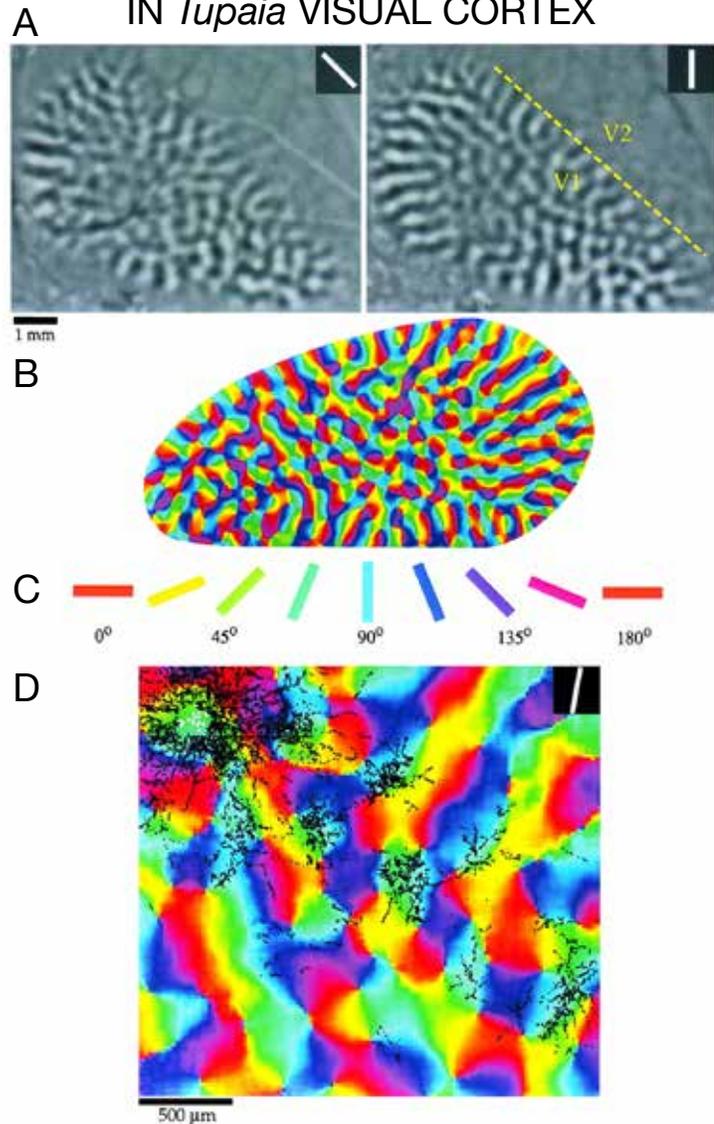


Fig. 5-19. A. Patchy distribution of neurons in V1 of a *tupaia* preferentially responding to lines in the visual field with two different orientations (upper right corners). B-C. Color-coded reconstruction of patches in which neurons preferentially respond to lines with different orientations. D. Synaptic terminals of horizontal axons (boutons in black) that interconnect neurons with a particular line orientation (upper right corner). (Modified, from Bosking et al., 1997.)

(Kretz and Rager, 1990). Neurons of the infragranular layers (V and VI) are the source of long distance axons that target subcortical structures.

The dLGN projection to V1 is not the only visual channel to the neocortex in *tupaia*s (Lyon et al., 1998). V2 receives a large input from the pulvinar (Diamond et al., 1970; Harting et al., 1973a), a thalamic structure that appears to be absent in some lower mammals. V1 also has reciprocal connections with V2, traditionally known as association area 18 (Sesma et al., 1984). V2 neurons have larger receptive fields than neurons in the striate cortex (Kaas et al., 1972). In addition to V1 and V2, visual association areas have also been identified in the temporal cortex of *tupaia*s and these have been hypothesized to play a role in the added processing of optic information (Killackey et al., 1971; Lyon et al., 1998; Wong and Kaas, 2009).

THE SOMATOSENSORY CORTEX. The dorsal column nuclei and the trigeminal sensory nuclei of *tupaia*s convey somatosensory information from the body and the head to the ventral complex (VL, VP) of the thalamus (Fig. 5-17). The latter relays topographically organized input to the somatosensory areas of the neocortex, S1 and S2 (Schroeder and Jane, 1971; Weller et al., 1987; Sur et al., 1980a; Remple et al., 2006, 2007). In S1, the topographic organization of the contralateral body surface is mapped “upside-down,” in S2 the somatosensory map is “right-side up” (Sur et al., 1981). S1 and S2 are interconnected ipsilaterally, and also across the two hemispheres by fibers of the corpus callosum (Cusick et al., 1985). Significantly, the snout and the mouth are enlarged in these cortical representations but the hands and digits are much less so when compared with prosimians (see Fig. 5-29C below). The relatively poor cortical representation of the hands and digits parallels their limited use for object manipulation. Unlike primates, *tupaia*s have claws rather than nails on their digits and the tactile pads—epidermal friction ridges that aid primates in palpating and grasping objects—are distributed patchily over the palms of their hands. The clawed digits of *tupaia*s are better suited for grasping tree branches, although occasionally they use their hands to pick small objects, such as fruits or berries. However, they are not adept in using their digits for precision gripping (Napier, 1961; Sargis, 2001).

THE AUDITORY CORTEX. *Tupaia*s are very sensitive to noise and their hearing has a broad frequency range from 300 Hz to 40 kHz (Peterson, 1968). If alarmed, they chatter, whine or whistle (Emmons, 2000), and much of their vocalization is in the frequency range of human hearing (Gould, 1978). The central auditory system of tree shrews is similar to that of most mammals. Medullary components of that system are the ventral and dorsal cochlear nuclei, the superior olivary complex, and the trapezoid body (Covey et al., 1984). Fibers of the ascending tract, the lateral lemniscus, have been traced to the mesencephalic inferior colliculus, and hence to the thalamic medial geniculate body, and from there, to the auditory cortex (Casseday et al., 1976). The medial geniculate body has several subdivisions that appear to project to different components of the auditory cortex (Oliver and Hall, 1978). In a functional mapping study, glucose utilization was found elevated in the auditory cortex of *tupaia*s exposed to conspecific vocalization (Binz et al., 1990).

THE MOTOR CORTEX. In addition to the differentiated thalamocortical sensory channels, tree shrews also have a well-developed corticofugal motor system. This output channel—comparable to the human pyramidal tract implicated in voluntary movements—originates in the somatosensory and motor areas, crosses to the opposite side in the medullary pyramids, and descends to thoracic levels of the spinal cord (Jane et al., 1965, 1969). Shriver and Noback (1967) distinguished three components in this system in *tupaia*s. (i) The ipsilateral corticopontine projection that terminates in the deep pontine gray. This tract is presumably part of the cerebellar feedback loop to the cerebellum by way of pontocerebellar fibers (middle cerebellar peduncle). (ii) The bilateral corticoreticular projection that penetrates the bulbar nuclei of the reticular formation in the vicinity of the sensory nuclei of the cranial nerves. (iii) The crossed corticospinal tract that descends in the ventral portion of the dorsal funiculus and terminates dorsally in the spinal cord. The descent of this system in the dorsal funiculus and its termination in the dorsal spinal cord is different from what is seen in higher primates, in which the corticospinal fibers descend in the lateral funiculus and terminate in the vicinity of the ventral horn. This suggests that the principal function of the *tupaia*d corticospinal tract is not direct motor neuron control, as in higher primates, but rather the control of lower-level pattern generators.

5.2.4. Affect and Cognition in *Tupaia*s. The affective disposition of *tupaia*s and their cognitive abilities have features that may be conceived of as intermediary between that of insectivores and primitive primates, the prosimians.

AFFECTIVE MANIFESTATIONS IN *TUPAIAS*. We supported our claim that feelings and emotions play a role in the behavior of fishes, amphibians and reptiles by the following arguments. First, these lower vertebrates show many of the same physiological reactions when stressed, injured, threatened, food deprived, and sexually aroused as do mammals, man included. These reactions include activation of the autonomic nervous system, secretion of pituitary hormones that regulate metabolic processes, and release of various neurotrophic factors and neurotransmitters by brain structures implicated in emotional arousal and motivation. These physiological reactions mobilize the animal's energy resources to flee when frightened, fight when angered, search for food when hungry, and pursue a mate when sexually aroused. Second, in association with these physiological reactions, lower vertebrates display emotional expressions that communicate to conspecifics their feelings and mood. Among these emotional expressions are skin color changes, vocalizations, postural displays, and body movements that convey the individual's affective disposition, and conspecifics respond to these expressions by fleeing, fighting or becoming sexually receptive. Third, the brains of lower vertebrates contain many of the structures that play a role in mammals and man in the physiological and behavioral regulation of emotions. These include the brainstem reticular formation, the periaqueductal gray, the hypothalamus, the preoptic area, the septum, the nucleus accumbens, and the amygdala.

*Tupaia*s share with both lower and higher vertebrates (including humans) many of the physiological manifestations of emotional arousal. Confining two tree shrews in a small cage prompts territorial fighting and the submissive male shows a series of changes that include the following: increase in blood pressure (Fuchs et al., 1993), changes in peripheral adrenergic

reactions and central serotonergic reactions (Flügge, 1995; Flügge et al., 1997); increases in the adrenal secretion of corticosterone and cortisol (Collins et al., 1984; Magariños et al., 1996; Kozicz et al., 2008); gonadal tissue regression (Fischer et al., 1985); loss of body weight (Magariños et al., 1996), and reduction in locomotion and scent marking (Flügge et al., 2001). These reactions are not seen in the dominant male. Psychosocial stress, or the administration of ACTH, are also accompanied by an increase in adrenergic binding sites in components of the affective brain circuit—the anterior hypothalamus, the medial nucleus of the amygdala, and the cingulate cortex (Flügge et al., 1988, 2001). Other biochemically or morphologically affected brain regions in vanquished *tupaia*s are the hippocampus (Fuchs and Flügge, 1995; Magariños et al., 1996; Fuchs et al., 2001), amygdala (Kozicz et al., 2008) and the prefrontal cortex (Flügge et al., 1997).

There are both similarities and differences in the emotional expressions of mammals when compared with lower vertebrates, and some of these new expressions are evident in *tupaia*s. For instance, instead of skin color changes as a medium of emotional communication, *tupaia*s convey their agitation to conspecifics by bristling the hair of their large tail (Fig. 5-20). This is a mammalian trait, as furry mammals raise their body hair, called piloerection, when excited. (An atavistic manifestation of this response is our “goose pimples” when frightened). Frequency and duration of hair bristling increases greatly in social conflict, such as territorial fights between two males (Holst, 1969; Ewert, 1980), but the fights usually result in few wounds (Blanchard et al., 2001).

HOSTILITY AND GREGARIOUSNESS. As noted, male tree shrews are extremely hostile toward one another but that disposition is manifested differently in the wild and in captivity. In the wild, each male inhabits a territory in the company of one or several females and defends that “property” against all intruding males, including closest kin. Since *tupaia*s live on scarcely distributed particulate nutrients, this egosocial behavior is highly adaptive as it assures sufficient resources for a small reproductive unit. This aggressive disposition leads to a pathological behavior in captivity, where males are constrained to live together in an enclosed space. Facing one another, the males engage in constant fighting, with the result that the strongest and most pugnacious of them eventually emerges as the colony’s tyrant and the stressed and injured

EMOTIONAL DISPLAY IN *Tupaia*

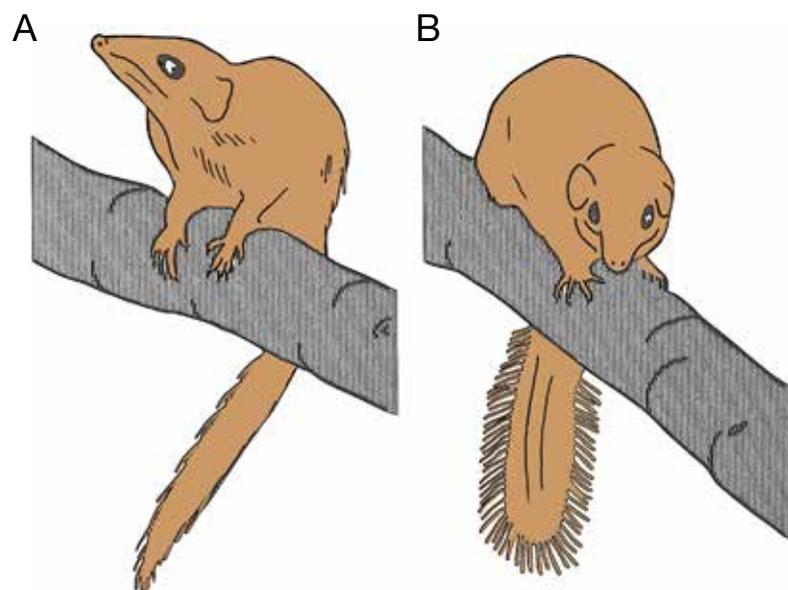


Fig. 5-20. The flat tail hair in the relaxed *tupaia* (A) is “bristled” when agitated (B). (After Holst, 1969.)

weaker males eventually die (Emmons, 2000; Blanchard et al., 2001). This contrasts sharply with the behavior of the females that display allosocial behavior even in captivity. Although they, too, are competitive, which leads to the establishment of a social hierarchy, they do not fight with one other but occasionally engage in mutual grooming and they huddle together when resting and sleeping.

With regard to the formation of affectional relations, it is interesting that the bonding of male and female *tupaia*s is supported by an unusual behavior, i.e., their smearing one another with glandular secretions and urine, as if making the other smell like oneself inhibits their basic aggressive disposition. Another phenomenon, the “absenteeism” of *tupaia* mothers from the nest where the young are “parked,” as described earlier, may also indicate limited parental affection. However, it has been noted that the parents guide the young to feeding sites after they are weaned, and they periodically engage in mutual licking (Emmons, 2000). As Emmons argued, absenteeism may have survival value in that the musky parents do not impart their pungent odor to the hidden young.

CURIOSITY AND EXUBERANCE. We noted earlier the apparent absence of curiosity and playfulness in lower vertebrates. Reptiles explore their environment when they are hungry in search of food but there is little evidence that, when sated, they move about to find out what goes on in their environment or examine the features of new objects for the sake of becoming more knowledgeable (Fig. 5-5). Although initially fearful in the laboratory setting, *tupaia*s become inquisitive once they become habituated and restlessly move about much of their waking hours exploring every nook and cranny of their surrounding (Polyak, 1957). Curiosity, so typical of primates, may be an emerging affective trait of *tupaia*s.

LEARNING AND COGNITION. *Tupaia*s readily learn simple color and pattern discrimination tasks for a food reward, and they learn to switch from one cue to the other in as few as 10 sessions in serial reversal tasks (Killackey et al., 1972; Casagrande and Diamond, 1974). They can even learn such complex tasks as shifting in successive experimental sessions from responding to differences in stripe width to differences in color, and vice versa. However, while they can learn to consistently discriminate stripe orientation in about 10-20 sessions, they may require as many as 30-50 sessions to discriminate between an upright and an inverted triangle (Casagrande and Diamond, 1974). With regard to using working memory, there is some evidence that tree shrews are superior to insectivores but inferior to prosimians in delayed alternation tasks. In the simple alternation test in a two-choice discrimination apparatus, such as a T-maze, an animal is required to successively alternate responses into obtain a reward. In the delayed alternation test this task is made more difficult because the animal has to wait for some time before it is allowed to make its successive choices. In a comparison of insectivores, *tupaia*s and prosimians, Masterton and Skeen (1972) found that hedgehogs could solve this problem with a maximum delay of 32 seconds, *tupaia*s with a delay of up to 128 seconds, and bushbabies with a delay of up to 256 seconds. The ability of *tupaia*s to master such a task with a delay of over two minutes suggests a short term working memory of significant duration. Ohl et al. (1998) developed an apparatus with a large number of holes, each covered by a lid, and placed food in a few holes and marked those with a visual cue. Tree shrews needed only five trials on the first day to find the marked holes, and from the second day onward solved

this problem with very few errors. It was noted that in searching for hidden food in the hole-board, tree shrews collect rewards according to a minimum distance principle, much like capuchin monkeys do, but unlike mice (Bartolomucci et al., 2001).

BRAIN STRUCTURES MEDIATING COGNITIVE FUNCTIONS. Both the superior colliculus and the visual cortex have been implicated in visual discrimination learning in *tupaia*s. Casagrande and Diamond (1974) found that the ability of tree shrews to relearn a simple visual discrimination task (horizontal versus vertical stripes) was little affected by superior collicular lesions, but lesioned subjects displayed severe deficits in mastering more difficult discriminations, such as circles differing in size, or an upright versus an inverted triangle (Fig. 5-21). The authors suggested that the deficit was due to visual neglect; i.e., the animals were able to see but failed to pay attention to the details of the cues to make the discriminations. The same deficit was obtained when the efferents of the superior colliculus were severed (Raczkowski et al., 1976). Small lesions in the striate cortex produced little deficit in visual pattern discriminations but large lesions with retrograde degeneration in both the dLGN and pulvinar resulted in severe deficits (Snyder and Diamond, 1968; Ward and Masterton, 1970; Ware et al., 1974). *Tupaia*s trained on a simple reversal task, showed amnesia after removal of the visual cortex, but they could relearn the task in about the same number of trials as normal animals did (Killackey et al., 1971). However, they failed when challenged with a complex reversal-learning task involving multiple cues. *Tupaia*s also showed severe reversal learning deficits after ablation of the temporal region that receives afferents from the pulvinar (Snyder and Diamond, 1968; Killackey et al., 1972).

We have described earlier Butler's (1995) theory, according to which the mammalian thalamic relay system has two components: the collothalamus that receives sensory input indirectly by way of the midbrain colliculi, and the lemnothalamus that receives direct

VISUAL DISCRIMINATION LEARNING IN *Tupaia* FOLLOWING SUPERIOR COLLICULUS LESIONS

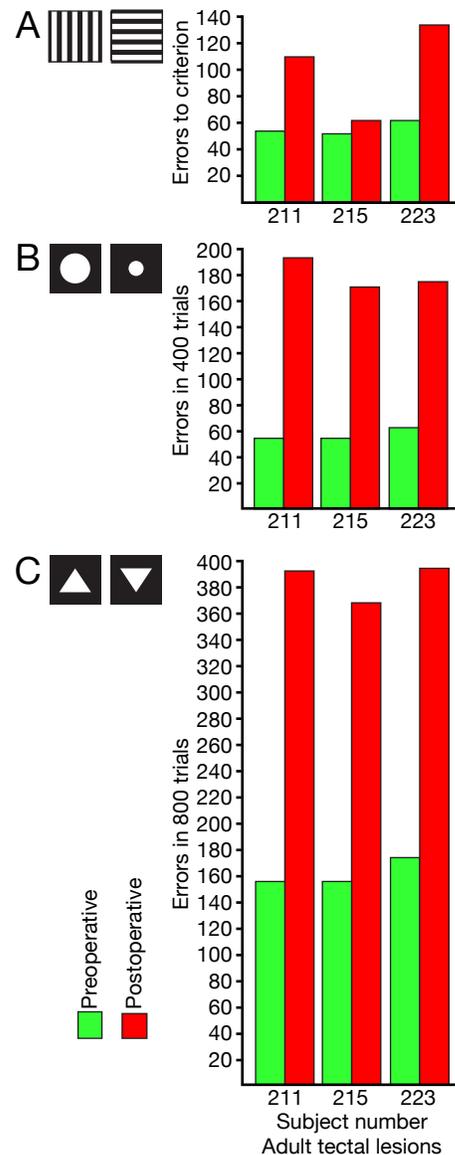


Fig. 5-21. Deficits in relearning visual discrimination tasks of increasing difficulty following ablation of the superior colliculus in *tupaia*s. (After Casagrande and Diamond, 1974.)

input from the visual, somesthetic and auditory systems (Section 4.2.2). We have suggested that the two constitute, respectively, the ancient vertebrate indirect pathways and the more recent mammalian direct pathways to the diencephalon and telencephalon. The findings just described—first, that *tupaia*s have a large pulvinar that relays collicular input to different components of the telencephalon as well as a highly differentiated dLGN and, second, that both systems play an important role in visual learning—suggest that *tupaia*s are a transitional species when compared with higher mammals, particularly primates, in which the role of the indirect collothalamic system diminishes relative to the direct lemnothalamic system.

In summary, the little evidence that is currently available about the emotional disposition and cognitive capacities of *tupaia*s, combined with what we know about their brain organization, suggests an admixture of basal mammalian traits with some advanced features that evolved in primates. Much like shrews, *tupaia*s are furtive animals that forage by themselves and are intolerant of conspecifics. The limited mutualism displayed by bonded *tupaia*s is regulated by hormonally triggered reciprocal scent marking, rather than by complex affectional bonds, as in primates, and the emotional bond between parents and young is an ephemeral one. With regard to their perceptual and cognitive abilities, *tupaia*s possess a complex and advanced visual system when compared with insectivores, and can master difficult visual discrimination tasks. However, because of their limited manipulatory skills—their clawed fingers are suited for grabbing but not for the dexterous manipulation of objects—their exuberance and cognitive faculties serve mainly their existential needs and wants, in particular their voracious appetite.

5.3. Brain, Behavior and Mind in Basal Primates: The Prosimians

5.3.1 The Origin and Arboreal Adaptations of Primates. The emergence of primates has been traced to the Paleocene, about 65 m.y.a. (Martin, 1990; Purvis, 1995). Early primate-like basal mammals (euprimates) may have emerged even earlier in the late-Cretaceous period, about 85 m.y.a., as flowering and fruit-bearing plants (angiosperms) became widespread (Sussman, 1991; Ravosa and Dagosto, 2007; Williams et al., 2010). With long fingers to grasp tree branches, euprimates could add flowers and fruits on the terminal branches of angiosperms to their omnivorous diet. By the Eocene, about 55 m.y.a., fossils resembling extant prosimians (*strepsirrhini*) appear in the paleontological record; with traits suggesting advanced arboreal adaptations (Simons and Rasmussen, 1994; Seiffert et al., 2003). Primate origins can be best understood as a mammalian adaptation to the exploitation of the bounties of the vast forests of the tropical and subtropical zones—leaves, berries, fruits and insects—and as a strategy to avoid powerful predators that roam on the ground (Campbell, 1974).

EVOLUTIONARY IMPLICATIONS OF THE TWO TYPES OF EXTANT PROSIMIANS. Prosimians have survived in the continents of Africa and Asia, and on the island of Madagascar. It is important to note that the two lines differ substantially in somatic, neural and behavioral traits. To begin with, all the continental prosimians are small-bodied animals; most of the Malagasy prosimians are considerably larger. According to data summarized by Burnie and Wilson (2001), the weight range of the South African lesser galago (bush baby) is 150-250 g, and of the greater galago, 1-2 kg; of the West African potto 0.85-1.5 kg; and the Indian slender loris of 85-350 g, and the slow loris, 225-650 g. Among the prosimians of Madagascar there are a few that are

also small, such as 175 g dwarf lemur, but most of them are above 2 kg. The aye-aye is in the range of 2.5-3 kg; the ring-tailed lemur, 2.5-3.5 kg; the brown lemur, 2-4 kg; the sifaka, 3-5 kg; and the indri, 6-7 kg. This difference in body weight is correlated, first, with the continental prosimians tending to live in small family units whereas many of the heavier lemurs form larger social groups. Second, as we shall see, the neocortex of continental prosimians is less differentiated than that of the larger Malagasy lemurs. Noteworthy in this context is the different trajectory of primate evolution at these sites. According to current paleontological evidence, the continental prosimians gave rise to small-bodied primitive monkeys, the eosimiids, which were subsequently replaced by the larger and more advanced extant monkeys (Beard and Wang, 2004; Egi et al., 2004; Williams et al., 2010). The prosimians of Madagascar, the island that became separated from Africa about 85 m.y.a., did not give rise to anthropoid monkeys. We speculate that the niches that were occupied by the larger monkeys of Africa and Asia were occupied in Madagascar by the larger and more advanced lemurs. Hence, from the perspective of human ancestry, the traits of continental prosimians are of greater interest than the Malagasy prosimians.

5.3.2. Advanced Somatic, Reproductive, and Developmental Traits of Prosimians.

Prosimians have a prominent rhinarium (snout), reflecting their persisting reliance on olfaction. In contrast to the dry-nosed monkeys (haplorhini), the prosimians are moist-nosed (strepsirhini) primates (Fig. 5-22A). But while the olfactory system of prosimians remains well developed, their eyes are big and medially situated (Fig. 5-22B). That contrasts with the laterally situated small eyes of most insectivores. Prosimians habitually use their eyes to scan the environment and, having evolved flat nails and sensitive terminal pads with friction ridges on their hands, they can grasp small objects, inspect it, and bring it to their mouths (Fig. 5-22C). Most prosimians are agile arboreal animals, although some lemurs spend time on the ground. They run swiftly up and down tree trunks and along branches in quadruped style. Some of them routinely jump from one tree to the next with great accuracy by relying on their excellent vision to judge distance. They use their sensitive fingers to grab a branch and grip it fast when landing (Petter, 1965). The diet of prosimians varies. Some are frugivores, consuming mostly fruits and flowers; others are opportunistic omnivores, digging tree barks for sap or grubs; still others are carnivores, preying on small animals, like insects, lizards and mice.

Advances in Reproductive Processes, Development, and Longevity. Prosimians tend to have much longer gestation and lactation periods than comparably sized mammals of other taxa. They typically bear only a few or a single offspring rather than a large litter, the weaned young develop relatively slowly, and it takes them longer to reach sexual maturity. For instance, the gestation period of the lesser galago is 132 days, the mother typically delivers only a single young, and females do not become pregnant until about 18 months of age (Hendrickx and Newman, 1978). In comparison, the gestation period of rats is only 21 days, litter size may be as high as 8-12, the young are weaned at 3 weeks of age, and females become sexually mature by 3 months. The gestation period of the slender loris is 166 days, she delivers a single young, which may weigh as much as 33 percent of the adult weight at birth, and the young is suckled for about 6 months after birth (Gursky, 2000). Maternal care is intensive in most prosimians, the mother transporting, grooming and protecting her young as she moves about, although some hide (“park”) their young in a tree hollow when leaving the nest to forage. Finally,

PROSIMIAN BUSH BABIES

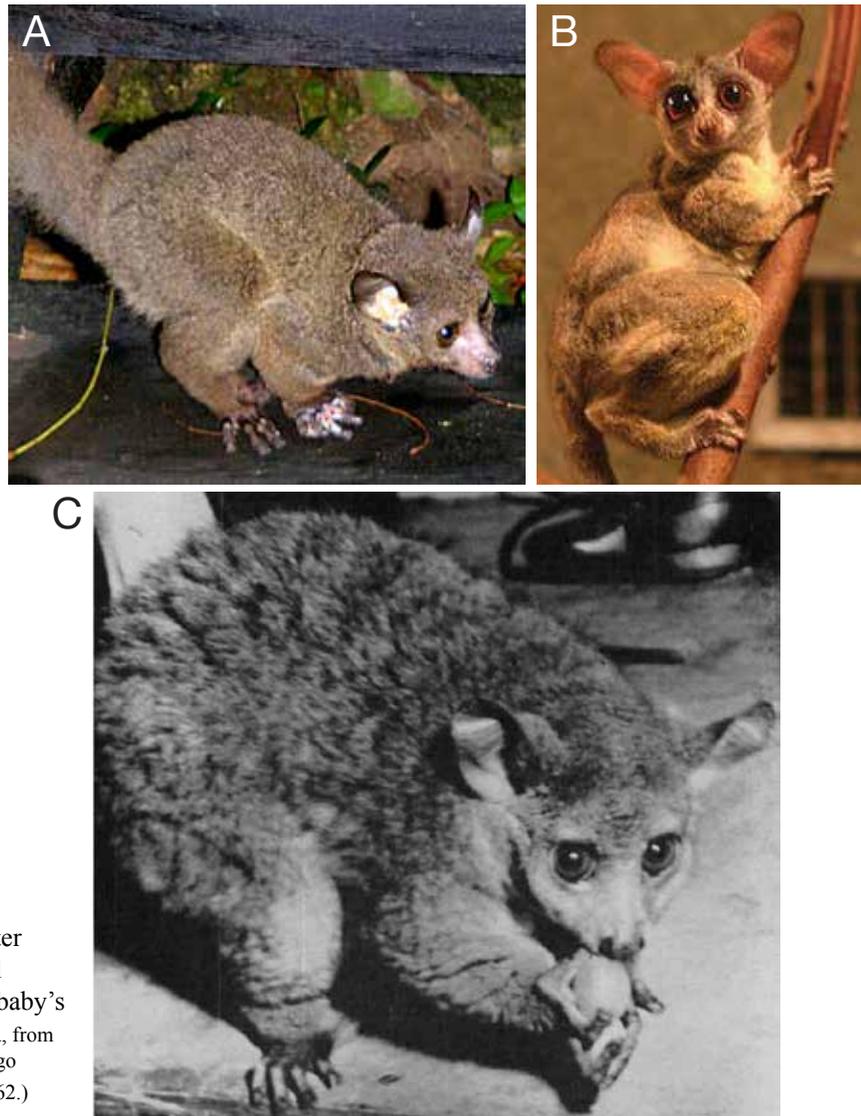


Fig. 5-22. The prosimian greater bush baby (A) and the Senegal galago (B). C. A greater bush baby's hand grip of a small object. (A, from Greater bush baby.jpg. B, from Galago senegalensis.jpg. C, from Bishop, 1962.)

prosimians tend to be long-lived. Whereas a rat lives about 2 years, the life span of the mouse lemur is 12-14 years (Aujard and Perret, 1998), the ring-tailed lemur 20 years (Gould et al., 2003), the potto over 25 years (Burnie and Wilson, 2001), and female sifakas may live as long as 32 years (Wright et al., 2008).

5.3.3. Behavioral and Neural Advances in Prosimians. Prosimians occupy an intermediate position between basal mammals like *tupaia*s and monkeys. They are active animals but their exploratory behavior is mainly limited to finding food to satisfy their enormous appetite. They have prehensile hands with fingers but, under natural conditions, display little inclination to use their hands for object manipulation. And they are either solitary or their social relations is limited to interaction with family members. Only prosimians that evolved in Madagascar, such as the ring-tailed lemur, form troops consisting of up to dozens of individuals.

Visual Guidance of Behavior. All prosimians have large frontal eyes, a fovea with great resolving power, and color vision (Polyak, 1957). And unlike the dichromatic *tupaia* retina, the retina of diurnal prosimians is trichromatic with three types of pigmented cones (Blakeslee and Jacobs, 1985; Jacobs, 1993, 1996; Tan and Li, 1999). Trichromatic color vision aids arboreal prosimians to detect ripe fruits in the densely foliated trees and discern immobile and well-camouflaged insects against their background. With their elongated arms and mobile digits, prosimians can reach for and grasp objects effectively under visual guidance. And even though most prosimians have retained the original quadruped body stance of mammals—the trunk being aligned parallel to the substratum during locomotion—many of them often assume a sitting or upright posture (Fig. 5-23). The sitting posture frees their hands to pick fruits, and the vertical stance, sustained with tail support, helps them to visually scan their surrounding. However, reliance on vision in the guidance of behavior has only been partially accomplished by prosimians. Olfaction persists in playing a paramount role in many aspects of their behavior. Bush babies use scent marking to demarcate the boundaries of their territory (Charles-Dominique, 1977). Aye-ayes recognize the odor of conspecifics and are attracted to the odor of females with offspring (Price and Feistner, 1994). The forearms, armpits, and the chins of lemurs are studded with secretory glands, which they rub against tree trunks to mark their territory (Petter, 1965; Mertl-Millhollen, 1988). They also rub their urogenital region against one another and moisten their paws with urine and with glandular secretions, and spread these over themselves, their partners, and various objects in their surroundings. In mouse lemurs, the urine of the dominant male contains a chemical that inhibits the sexual activity of subordinate males within the group (Perret, 1992).

PROSIMIANS IN A SITTING OR STANDING POSTURE

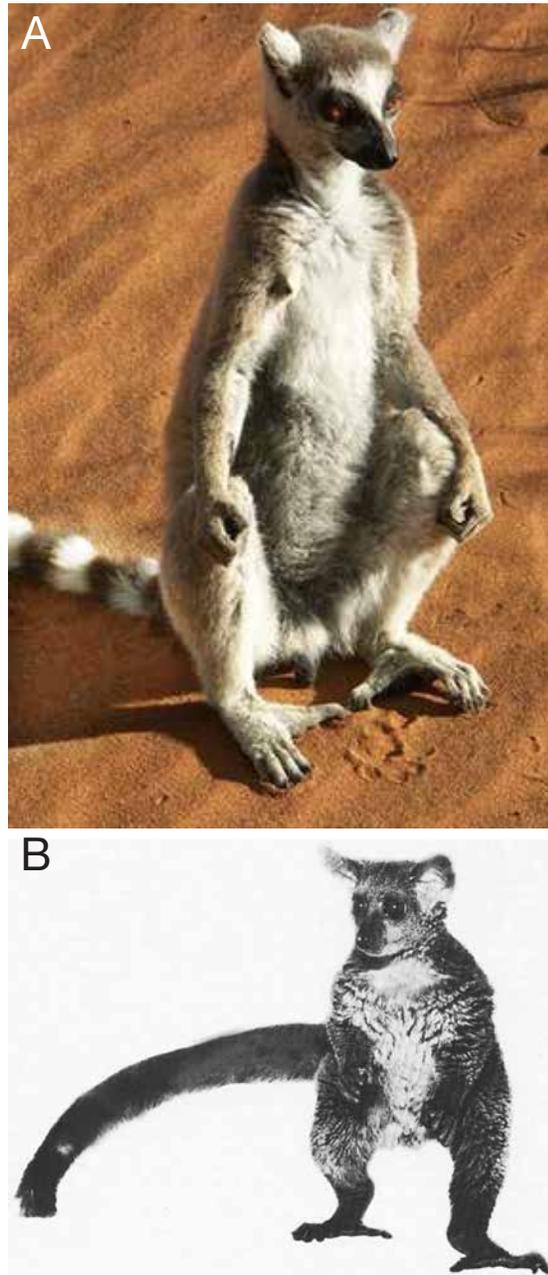


Fig. 5-23. **A.** Ring-tail lemur in a sitting posture with liberated hands. **B.** Greater galago assuming an upright posture. (A, after Madagascar.org. B, after Carlson and Welt, 1980.)

Manual Dexterity and Object Manipulation. Manual dexterity varies in different species of prosimians. In many, the fingers have broad terminal pads that are better suited for power grip, such as to latch on to a tree branch, than for the nimble object manipulation. Other prosimians, including galagos (Fig. 5-22C) display considerable dexterity when holding objects with their fingers. In the laboratory, galagos (Cantalupo et al., 2002b) and lemurs (Forsythe et al., 1988) consistently use their hand to reach for and grasp food. Galagos display hand lateralization, with a preference for using either the right or left hand when reaching for food (Milliken et al., 1991). These activities imply that prosimians are able to use their hands and fingers for effective object manipulation under visual control.

According to one study, the ability of galagos to discriminate size differences by touch alone is comparable to that of monkeys although they are inferior to monkeys in texture discrimination (Carlson and Nystrom, 1994). However, object manipulation is not as diverse in prosimians, in terms of the complexity of actions involved, as it is in most Old World monkeys (Torigoe, 1985). Lemurs may be more dexterous than galagos and engage in extractive food consumption. When eating fruit, the aye-aye consumes not only the flesh but also opens the protein-rich hard shelled kernel (Petter, 1965). When feeding on coconuts, the aye-aye first removes the fibers on one side of the nut, creates a small hole in the shell with its incisors, drinks the liquid through the hole and, finally, uses its third finger to scrape away the inside flesh (Feistner et al., 1994). Aye-ayes also use their third finger to tap the bark of trees to find hidden larvae or insects (percussive foraging), and the combination of the third and fourth fingers to carry the prey to the mouth. Finally, aye-ayes may also use vines as tools to extract food from hidden sources (Sterling and Povinelli, 1999).

Playfulness, Curiosity, and Exuberance. Young prosimians engage both in solitary play, like leaping, running about and hanging upside down from branches, and social play, such as chasing, tail pulling, play-biting, and wrestling with one another (Ehrlich, 1977; Doyle, 1979; Nash, 2002). Sex differences have been noted in prosimian play behavior: males tend to play vigorously with other males; females play more gently with siblings or their mothers. A behavior that suggests curiosity in prosimians is the head cocking of galagos, the rotation of the head in one direction or alternately from side to side (Rogers et al., 1993; Cantalupo et al., 2002a). Head cocking is more frequent in young galagos than in old ones, is most readily elicited by novel visual stimuli but may also occur in response to auditory stimulation. Head cocking is elicited not only by solid objects but also by pictures.

The Development of Sociality. A notable behavioral advance in most prosimians is the change from the solitary existence and furtive life style, characteristic of insectivores, towards a more family- or group-oriented life style. This may be due, at least partially, to reliance on the more abundant nutrient supply of fruiting trees than scattered prey. There is great variability in different prosimian species in group size, group composition, dominance hierarchy, and other facets of social relations (Petter, 1965; Charles-Dominique, 1977; Bearder, 1987; Muller and Thalmann, 2000; Gron, 2008). *Nuclear family* units are common in galagos (Ehrlich, 1977; Doyle, 1979), slender lorises (Nekaris, 2003), and red-fronted lemurs (Pereira and McGlynn, 1997). The social bond of these units, typically consisting of an adult female, her young, and 1-2 males, is reinforced by mutual licking and grooming, and by marking themselves and

one another with urine and glandular secretions. The bond between mother and daughter is typically more enduring in these nuclear units than between mother and son. A tendency toward affiliation with conspecifics has been observed in “solitary” nocturnal galagos (Clark, 1985) and among dwarf lemurs. Although solitary foragers with individual home ranges, female dwarf lemurs tend to form *huddling* companionships by resting and sleeping together (Radespiel, 2000; Kapeller et al., 2002). Huddling has also been reported in redfronted lemurs (Ostner, 2002).

Gentle lemurs form larger, *extended family* units. They live in groups of up to 8-9 individuals, consisting of two breeding females and one adult male, and several offspring, including subadult males (Nievergelt et al., 1998, 2002). Group living, of course, has many advantages by fostering cooperation among females in feeding and raising the young and, in general, promoting the security of group members. As a sign of social cooperation, gentle lemurs and brown lemurs provide aid to their partners (third-party intervention) in conflict with outsiders (Pereira and McGlynn, 1997; Roeder et al., 2002). Finally, ring-tailed lemurs live in *small troops* consisting of up to 30 members, with equal numbers of males and females in the troop (Petter, 1965; Mertl-Millhollen, 1988; Gould et al., 2003). Members of the troop feed together and huddle together when resting. Both sexes have separate dominance hierarchies, with the females forming a matriline core. In this species, females dominate males irrespective of body size and hormonal status (Engelhardt et al., 2000). This matriarchal pattern is widespread among prosimians; for instance, female mouse lemurs are dominant over males in captivity (Radespiel and Zimmermann, 2001). The social organization of larger lemurs suggests the evolution of amicable cooperative relationships between mating partners and their progeny, a pattern quite common among many higher primates.

Neural Advances in Prosimians. The behavioral advances of prosimians are correlated with the growth and elaboration of the neencephalon. In Fig. 5-24 we illustrate two advances by comparing the brain of a *tupaia* with the brains of two small African prosimians, the lesser and greater galago, and two larger Malagasy prosimians, the mongoose and ring-tailed lemur. The manifest advances are, first, an increase in the size the cerebral hemispheres and, second, a trend toward increased fissurization of the neocortex (Fig. 5-24). The cerebrum of the lesser galago (bush baby) has only a single fissure, the ubiquitous prosimian lateral sulcus (Fig. 5-24B). This fissure separates the frontal lobe from the temporal lobe. There are also shallow fissures within the frontal, temporal and parietal lobes in the greater galago (Fig. 5-24C) and these fissures are more pronounced and deeper in the ring-tailed lemur (Fig. 5-24D) and the mongoose lemur (Fig. 5-24E).

Two other facets of cortical expansion and elaboration are illustrated in coronal sections of the brains of *tupaia*, potto, and mongoose lemur at frontal-cortical (Fig. 5-25), mid-cortical (Fig. 5-26), and posterior-cortical (Fig. 5-27) levels. These are the expansion of the white matter in correlation with the foliation of the neocortex, and an increase in the size of the neocortex relative to the paleocortex in the rhinencephalon. The great increase in the white matter includes an expansion of the following structures: (i) the medullary layer of the neocortex composed of cortical afferents and efferents; (ii) the corpus callosum composed of cortical commissural fibers; (iii) the internal capsule composed of descending corticofugal fibers; and

Tupaia AND PROSIMIAN BRAINS

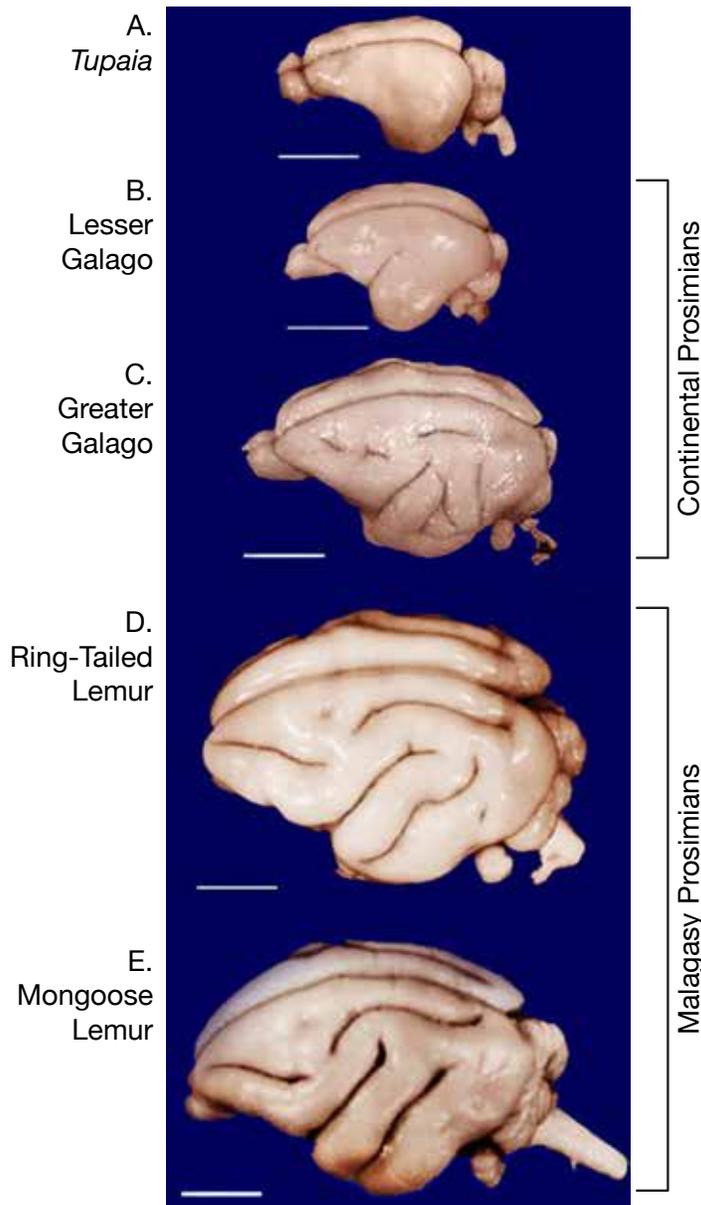


Fig. 5-24. Photographs of dissected brains of *tupaia* (A), two African prosimians (B, C) and two prosimians of Madagascar (D, E). (Modified, from University of Wisconsin-Madison Brain Collection.)

(iv) the ascending thalamocortical afferents of the thalamic radiation. The great increase in the descending corticopontine and corticospinal fibers (pyramidal tract) is illustrated in Fig. 5-27.

Advances in the Organization of the Prosimian Neocortex. The foliation of the cortical gray matter reflects an increase in the number of cortical neurons, and the expansion of the white matter an increase in the nerve fibers that link the cortex with subcortical structures. Experimental studies have revealed that this volumetric growth is partly attributable to the expansion of the cortical association areas of the frontal and parietal lobes in galagos relative to *tupaias* (Fig. 5-28).

FRONTAL CORTEX IN *Tupaia* AND PROSIMIANS

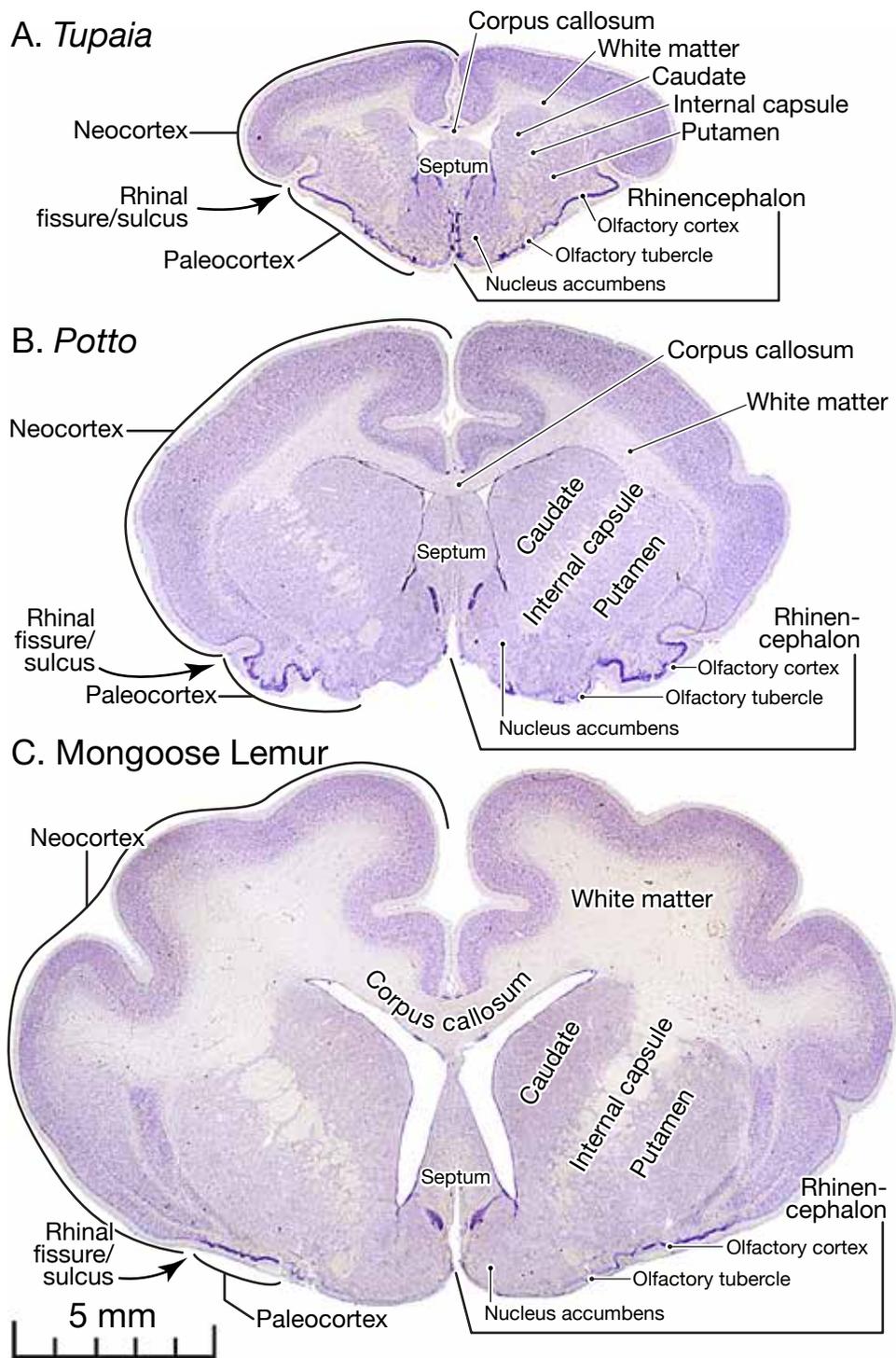


Fig. 5-25. Stained coronal sections of the brains of a *tupaia* (A), *potto* (B), and mongoose lemur (C) at the level of the frontal cortex. (Modified, from University of Wisconsin-Madison Brain Collection.)

CENTRAL CORTEX IN *Tupaia* AND PROSIMIANS

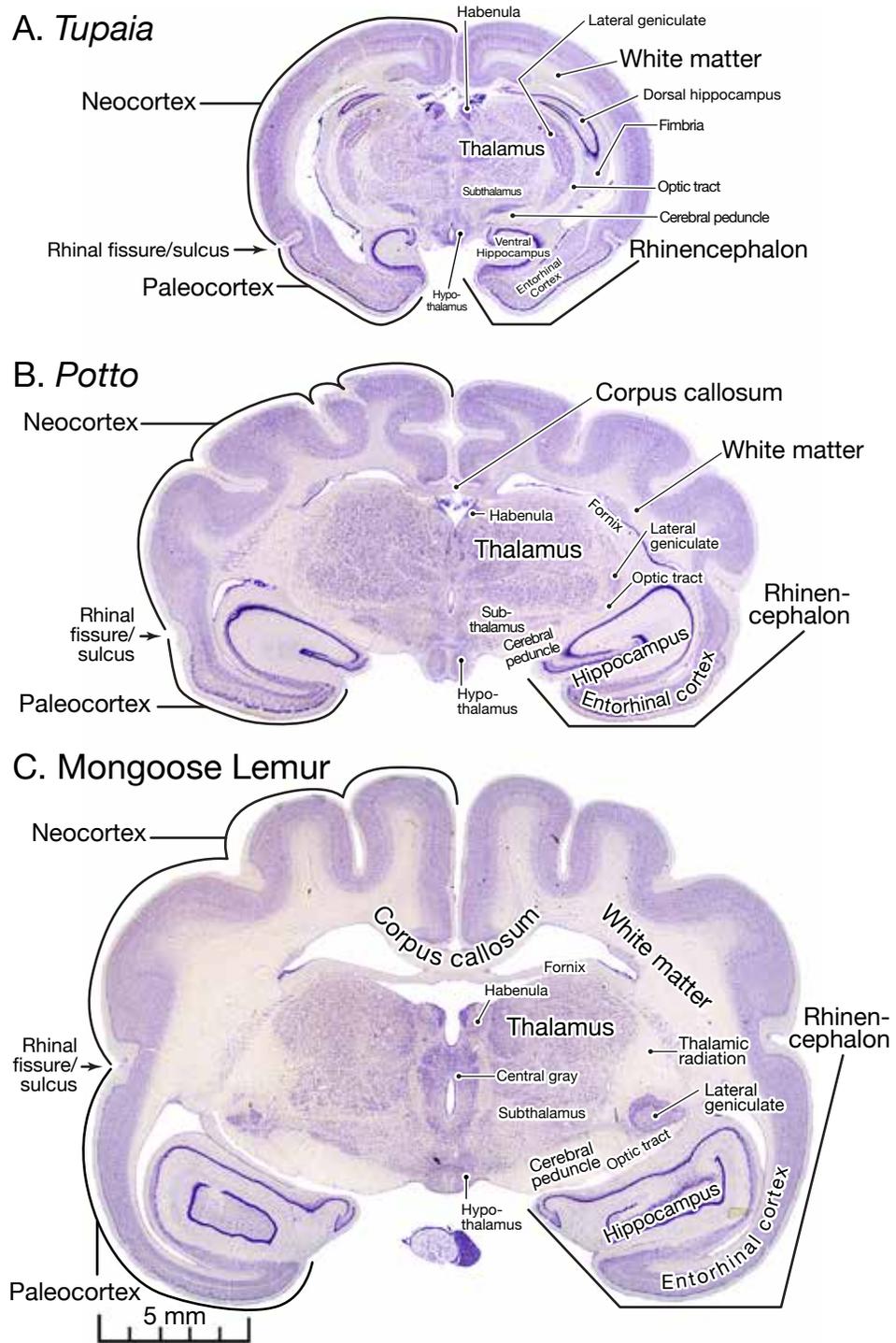


Fig. 5-26. Stained coronal sections of the brains of a *tupaia* (A), potto (B), and mongoose lemur (C) at mid-cortical level. (Modified, from University of Wisconsin-Madison Brain Collection.)

POSTERIOR CORTEX IN *Tupaia* AND PROSIMIANS

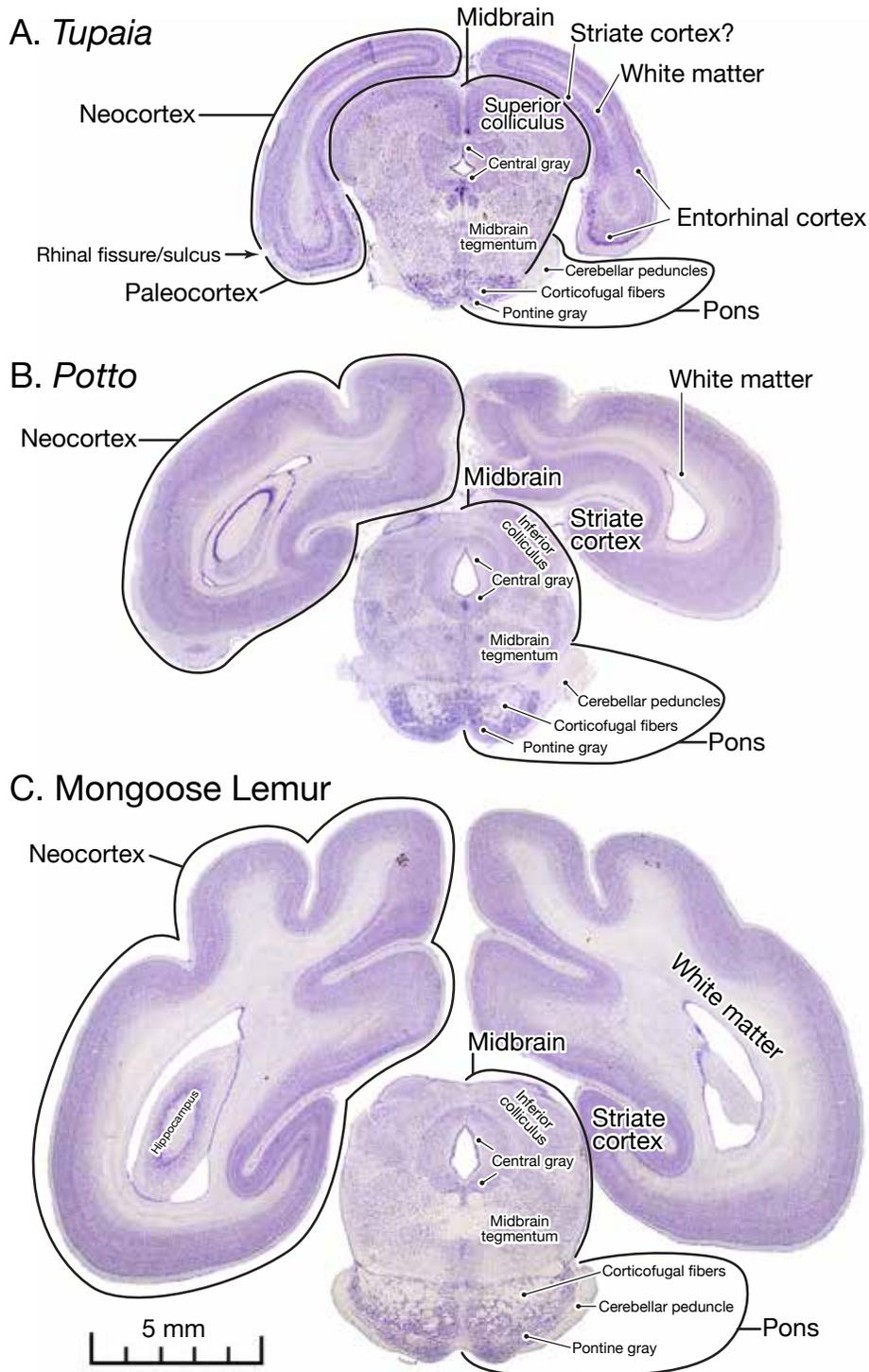


Fig. 5-27. Stained coronal sections of the brains of a *tupaia* (A), *potto* (B), and mongoose lemur (C) at the level of the midbrain. (Modified, from University of Wisconsin-Madison Brain Collection.)

“ASSOCIATION” AREAS IN THE NEOCORTEX OF *Tupaia* AND *Galago*

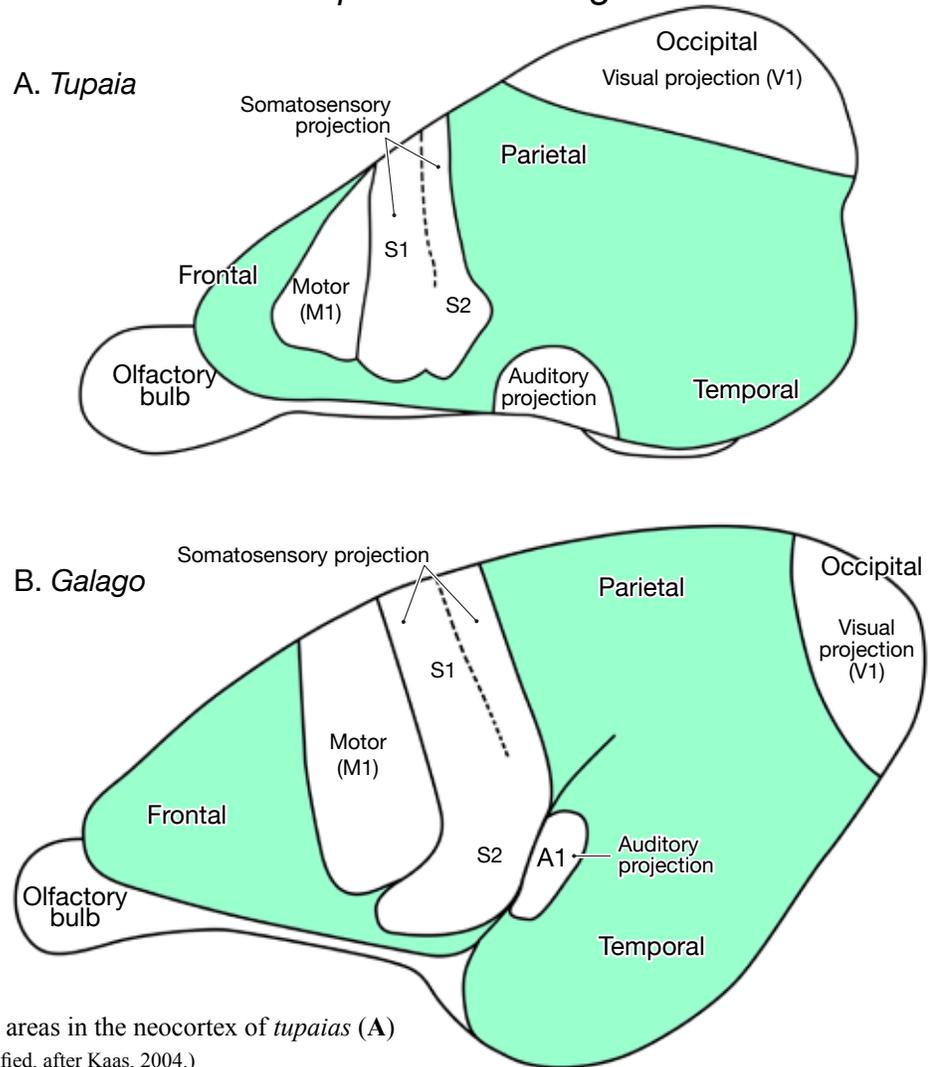


Fig. 5-28. Association areas in the neocortex of *tupaia*s (A) and *galagos* (B). (Modified, after Kaas, 2004.)

THE PROSIMIAN VISUAL PROJECTION AND ASSOCIATION AREAS. Cortical gray matter expansion in prosimians is paralleled by the growth and differentiation of the thalamic relay nuclei, such as the dorsal lateral geniculate nuclei (Fitzpatrick and Diamond, 1979; Diamond et al., 1985). Neurons in different layers of the galago dLGN provide parallel channels for the transmission of information of different perceptual features of the visual world to the striate cortex, or V1 (Norton and Casagrande, 1982; Norton et al., 1988; DeBruyn et al., 1993). V1 contains “simple” cells that selectively respond to stationary, oriented lines as well as “complex” cells that respond to other visual features. Flanking V1 in the occipital lobe are the visual association areas V2 and V3 (Rosa et al., 1997; Collins et al., 2001) and there are several multimodal association areas more anteriorly in the parietal and temporal lobes (Allman and Kaas, 1971; Allman et al., 1973; Tigges et al., 1973; Kaas, 2004). These areas may be involved in the enrichment of the visual input with information derived from the other senses.

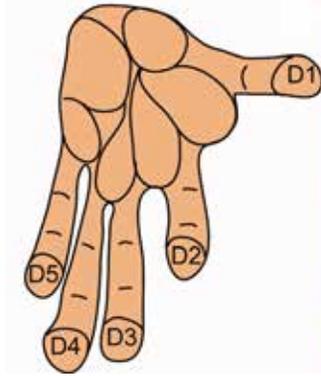
THE PROSIMIAN SOMESTHETIC PROJECTION AND ASSOCIATION AREAS. Paralleling the change in prosimians from the clawed digits of insectivores and *tupaia*s to digits with nails for improved object palpation and manipulation, the ventroposterior thalamic nucleus of galago has been shown to have distinct compartments for each digit of the hand (Qi et al., 2011; Figs. 5-29A, B). And, correspondingly, the primary somesthetic area (S1) of the galago neocortex has an enlarged somatosensory representation of the limbs and digits, relative to the representation of the muzzle (glabrous nose) in *tupaia*s (Kaas et al., 1981; Fig. 5-29C, D), with added representations of the body surface in S2 (Sur et al., 1980a, 1980b, Burton and Carlson, 1986). Moreover, there are several multimodal somatosensory areas in the parietal and temporal lobes of galagos that have extensive connections with the motor, premotor, cingulate and other regions of the neocortex (Wu et al., 2000; Wu and Kaas, 2003). These various somesthetic areas, we assume, make possible the complex task of hand-eye coordination displayed by prosimians as they reach for, grasp and manipulate objects.

THE PROSIMIAN MOTOR PROJECTION AND ASSOCIATION AREAS. In addition to the expanded primary motor area (M1), several premotor areas have been identified in the frontal cortex of galagos, including the frontal eye field (FEF), the supplementary motor area (SMA), the dorsal premotor field (PMD), the ventral premotor area (PMV), and the cingulate motor area in the medial cortex (Wu et al., 2000; Fang et al., 2005). Many of these regions project to the spinal cord and evoke movements when stimulated. The premotor areas, together with the somatosensory projection areas, and the parietal and occipital association areas that provide direct or indirect input to the motor cortex, presumably participate in patterning, monitoring, and correcting the skilled voluntary activities controlled by the motor cortex. While it is not yet possible to assign exact functions to these higher-order premotor and association areas, we assume that they represent the beginning of a trend seen in higher primates of increasing the number of parallel and serial processing stations that coordinate their skilled activities (Lewis and Van Essen, 2000).

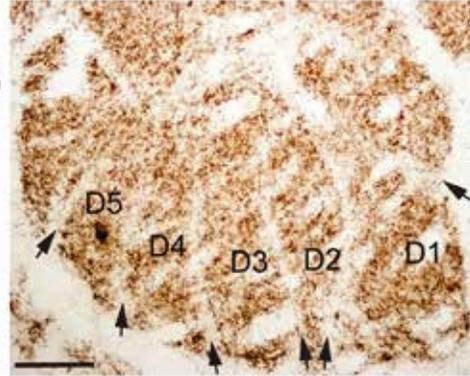
FUNCTIONAL SIGNIFICANCE OF NEENCEPHALIC EXPANSION. Cortical fissurization in prosimians, as illustrated in a few selected examples in Fig. 5-24, is correlated with increase in body size, brain volume, and behavioral complexity. The lesser galago with its minimally foliated neocortex, is a small nocturnal animal, with an average body weight of about 200 g, and a relatively simple social life. According to available descriptions, the males live separately in individual territories; the females form small matriline groups with their immature offspring. Greater galagos, which are also nocturnal, weigh about 1.5 kg. They aggregate in small groups while resting and sleeping but split up when foraging. Mongoose lemurs are larger, up to about 2.5 kg. Typically, a male and a female form a monogamous bond and rear their young jointly. They groom themselves and each other, using their specialized comb teeth. The behavior of mongoose lemurs is more versatile than that of galagos. During the hot season they forage at night, but when the weather gets cooler they forage during the day. When members of different families meet, they become agitated and vocalize aggressively and scent mark their disputed territories. Ring-tailed lemurs are still larger, about 3.0 kg. They live in troops of two-dozen or more individuals, consisting of several males and several females with their offspring. They move jointly when foraging and huddle together when it gets cold.

MAP OF DIGITS IN THE THALAMUS AND CORTEX OF *Tupaia* AND *Galago*

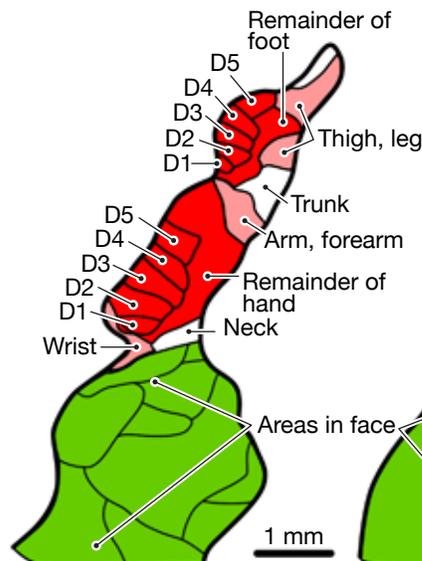
A. *Galago* hand



B. *Galago* digit representation in thalamus



C. *Tupaia* cortical representation



D. *Galago* cortical representation

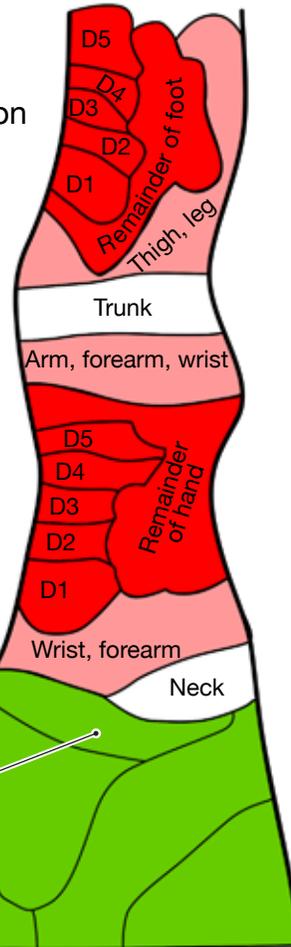


Fig. 5-29. The digits of galagos (A), and their representation in separate compartments of the ventroposterior nucleus of the thalamus (B). Somatosensory body maps of the head, trunk, and extremities in the neocortex of *tupaia*s (C) and galagos (D); anterior is left, posterior is right, medial is up, lateral is down. (A and B, from Qi et al., 2011. C and D, modified from Kaas et al., 1981.)

Contrasting with these generalizations, a recent study examined the relationship between brain size and several behavioral traits in 19 lemur species (MacLean et al., 2009). The study employed the allometric procedure of plotting brain/body weight ratios on a log scale. The results indicated that fruit-eating (frugivorous) lemurs had larger relative brains than leaf-eating (folivorous) lemurs, and that more active species had larger brains than less active species. However, the relationship reported in monkeys between brain size and social complexity (Sawaguchi and Kudo, 1990) or group size (Dunbar and Shultz, 2007) was not confirmed. Does this mean that there is no correlation between brain size and behavioral and mental complexity in prosimians? Before accepting that proposition, we should consider the pitfalls inherent in the allometric method. To appreciate that, let us first consider the relationship between brain weight and body weight in two great apes, the chimpanzee and the gorilla. The difference in their body weight is considerable; a gorilla silverback may weigh 2-3 times as much as a male chimpanzee. The large body of gorillas is related to their dietary adaptation. Since leaves and pith is their staple, they have to consume large quantities of these calorie-poor and hard-to-digest nutrients, and they have a hypertrophied hindgut (cecum and colon), where bacteria are harbored that ferment the fibrous carbohydrates. That dietary adaptation contrasts with the omnivorous chimpanzees that live on calorie-rich nutrients: fruits, nuts, insects and small mammals. In spite of the substantial difference in brain weight, there is relatively little difference in brain volume between gorillas and chimpanzees (Sherwood et al., 2004). Indeed, due to this drastic difference in their body weight, the encephalization index (the number of times the neocortex is larger than that of a basal insectivore of equal body weight) of the gorilla has been calculated to be about 30 (lemurs are about 20) and that of chimpanzees about 60 (Stephan and Andy, 1969; see Fig. 5-4). The brains of chimpanzees and gorillas are part of their shared heritage and so is their comparable cognitive abilities. Or consider the relationship between the brain/body ratio of a lean person in his youth and the same person in middle age: his body weight may have increased twofold but his brain weight has changed little. Another problem with the allometric method is that it is a statistical procedure and to obtain significant correlations requires large samples. Regrettably, many of the available allometric studies have used brains from different sources, disregarding whether the brains are from young or old animals, from males or females, from wild or captive provenance, from dry or wet specimens, or from estimates of cranial size. The exact relationship between neocortical size and behavioral and mental complexity—more broadly conceived than just social complexity—requires further investigation.

5.3.4. *Affective Advances in Prosimians.* As in the case of lower vertebrates, we infer the affective life of prosimians from their endocrine and physiological reactions, and their emotional expressions and overt behavior. The little information currently available along these lines indicates, first, a conservation of the ancient vertebrate mechanisms that regulate the imperatives of individual and kin survival, and second, a few advances in the domain of parental affection toward offspring, and amicable relations between close kin and, in some prosimians, among troop members.

Egocentric Hostility, Competition, and Aggression. Most prosimians are highly territorial. Whether they live in a small nuclear family unit, like galagos, or a troop, like ring-tail lemurs, outsiders are repelled or fought whenever they approach or enter their territory or home range.

Hostility towards outsiders concerns primarily the defense of habitats. There is also competition between males within the group during the breeding season. The testes of male mouse lemurs become enlarged as the days lengthen in the spring (or when exposed to a long artificial light cycle) and that is coupled with a substantial rise in blood testosterone levels (Perret and Schilling, 1993; Aujard and Perret, 1998; Schwab, 2000). Likewise, there is an increase in the size of the testes of galagos during the breeding season, particularly in the dominant male (Charles-Dominique, 1978). The testosterone-primed males engage in fierce competition for access to females, and the dominant male may prevent all the other males from gaining access to the females (Foerg, 1982; Morland, 1993; Ostner and Kapeller, 1999; Cavigelli and Pereira, 2000). The males begin to court the females as soon as the latter begin to develop their vaginal swellings but before they become sexually receptive (Lipschitz et al., 2001). Ovariectomized galago females retain their attractiveness to males but are sexually unreceptive and the males cannot copulate with them (Dixson, 1978). Ovariectomized females treated with estradiol become receptive but treatment with progesterone abolishes the facilitating effect of estrogen (Lipschitz, 1997). In many species, the dominant male is more vocal and has a stronger sexual odor than the subordinate males. When fighting on the ground, the ruffed lemur assumes a bipedal posture and swings one arm at the opponent or engages in cuffing (Pereira et al., 1988). The end result of the emotional displays and fights is that the larger and more aggressive males end up copulating most of the time with the receptive females (Pullen et al., 2000). In addition to its endocrine status and fighting ability, a male's social position also plays a role. Although aging mouse lemur males have reduced testosterone levels and sexual potency, they have greater reproductive success than the younger males (Aujard and Perret, 1998). These observations suggest that, as far as sexual relations are concerned, there is little or no affectional bond between mating partners among prosimians. The success of the larger, dominant males in copulating with females is dependent on their egocentric hostility toward competitors.

Allocentric Maternal Affection. The investment in offspring by the mammalian female differs from that of fishes and reptiles. That difference may be characterized as a shift from quantitative to qualitative investment, from producing numerous progeny but caring little for their survival to producing a few progeny and caring for them intensively. The care that mammals expend on their offspring is motivated by an altruistic emotion, maternal affection. All prosimians are solicitous of their infants—licking, grooming, carrying, and protecting them (Petter, 1965)—a behavior that heralds what we call in higher mammals and humans “mother love.” As we noted earlier, the care given to the young by the insectivore or *tupaia* mother is largely limited to “parking” them in a safe nest and periodically returning to feed them. Once the young become self-sufficient to feed themselves, they are abandoned. Most prosimian mothers display great affection toward their young while nursing them, and the maternal affection is reciprocated by the helpless young who clings to its mother. Thus a bond is formed between the two. Among social prosimians, like the ring-tailed lemur, even adult males seek the proximity of both the nursing mother and her infant, and lick and groom them (Gould, 1997).

There is variability in the endurance of the maternal-filial bond in different prosimian species. The mouse lemur infant is weaned at about 1 month of age, when it begins to leave its mother to play with peers; however, it returns to its mother when frightened and she displays

her affection by licking and grooming it and making it relax (Petter, 1965; Wright, 1999). The infant aye-aye, which develops more slowly than most other prosimians, begins to leave the nest at about 2 months, starts to consume solid food at 3 months, but does not feed itself regularly until 4-5 months, and may still try to suckle at 1 year of age (Feistner and Ashbourne, 1994). In most prosimians, sons that become sexually mature tend to leave their mother to find females, and father and son become hostile toward one another during the mating season. As mother and daughter start to compete for resources, their affectional bond is severed and the dispersing daughters may seek to establish their own home range (Foerg, 1982). In other prosimian species, the bond between mother and daughter is more enduring, and that results in the formation of matrilineal groups in which females of two or more generations cooperate and jointly raise their young. This sociability often results in females becoming dominant over males among prosimians, such as ruffed lemurs (Raps and White, 1995).

Prosocial Amicability and Trust. The maintenance of group cohesion presupposes the development of prosocial feelings, or amicability, between members of the group, whether they are close kin or not. One expression of this friendliness is grooming behavior, which is seen occasionally in prosimians with specialized teeth that serve as “combs” and “toilet claws” (Petter, 1965; Wright, 1999; Nakamichi and Koyama, 2000; Gould et al., 2003; Lewis, 2010). However, grooming with fingers, as monkeys and apes do, is rarely seen in prosimians. Amicable relations are better developed between females that jointly raise their young than between males that compete with one another for access to females during the mating period. However, in some prosimian species adult males often form resting and sleeping companionship, which indicates the replacement of fear or mistrust of the “other” (so prominent in insectivores) by a fraternal feeling of trust. Interestingly, prosimian companions engage in a seemingly bizarre behavior, washing themselves and each other with urine and pungent secretions. Perhaps, by making the “other” smell like oneself creates a sense of oneness in these animals that are also fearful of each other. Indeed, a new affect begins to emerge in social prosimians, a feeling of self-assurance or confidence. When ring-tailed lemurs awake in the cool morning, they “sunbathe” in the open with little display of fear or anxiety, and when the troop marches along well-trodden paths some members may engage in playful behavior (Palagi, 2009). This contrasts with the furtive behavior of insectivores and *tupaia*s.

5.3.5. Cognitive Advances in Prosimians. As we noted earlier, insectivores rely on olfaction as their principal source of information about the features and properties of their environment. The forward-projecting rhinarium (muzzle) of wet-nosed prosimians indicates a preservation of that primitive trait when compared with the receding face of monkeys. When they encounter things as they move about, prosimians tend to sniff them rather than handle them (Jolly, 1964; Torigoe, 1985). As we have noted before, olfaction is the primary source of sensory information about the properties of the organic world. The principal source of volatile chemicals are the odors that living and dead bodies emit or generate. It is by their odor that food is detected and offspring and kin, predator and prey are recognized; and it is by glandular secretions and pheromones that potential sexual partners signal their readiness to mate. These vital chemical stimuli typically evoke intense feelings and emotions—appetite, disgust, affection, fear, sexual craving—and through their motivating force instigate and control adaptive actions and reactions. However, olfactory qualia do not provide information

about the features and properties of the mainly odorless inanimate world and, the information they do provide has the character of subjective “secondary qualities” rather than objective “primary qualities” (Section 3.3.2). The partial shift in prosimians from sniffing to the visual scanning of the environment and the palpation of the objects it contains heralds the beginning of gathering realistic information about the physical world, perceiving things as they actually are independent of their promotion or retardation of life processes.

The Learning and Cognitive Abilities of Prosimians. The prolonged infancy of prosimians provides them with a period of apprenticeship when, being protected by their parents, they can learn about the spatial layout of their habitat, where to find nutrients, how to interact with peers, and many other skills needed to become adapted and successful individuals (Charles-Dominique, 1978; Bearder, 1987; Nash 2002). While there is no evidence that parents intentionally train their young, the young have the opportunity to learn what is edible or inedible, useful or harmful, dangerous or safe by following their parents. An example of learning by social facilitation is the report about a group of galagos learning to fish by adopting the behavior of a single animal that developed that habit (Welker, 1976).

Experimental studies carried out in the 1970s and 1980s indicated that galagos readily learn visual pattern discrimination tasks such as distinguishing stripes of different orientations or geometric shapes (Attencio et al., 1975; Wilson et al., 1979; Marcotte and Ward, 1980; Keys, 1981; Caldwell and Ward, 1982), and they can also master more complex spatial reversal and delayed alternation tasks (Skeen and Masterton, 1976). These abilities have also been demonstrated in slow lorises (Ohta, 1983) and more recently in mouse lemurs (Picq, 1995). It has also been found that removal of V1 in galagos interferes with their ability to judge distance and depth, and reach accurately for small objects (Marcotte and Ward, 1980). There are reports that the ability of prosimians to master complex pattern discriminations tasks is interfered with or abolished following ablation of V1 (Attencio et al., 1975; Wilson et al., 1979; Keys, 1981). That contrasts with *tupaia*s, in which removal of V1 produces little deficit in pattern discrimination learning. In addition, it has been found that lesions of the visual associations areas, and/or the temporal visual area (MT) produce deficits in complex visual learning tasks (Wilson et al., 1979), and that frontal lobe lesions interfere with learning delayed alternation and spatial reversal tasks (Skeen and Masterton, 1976).

ADVANCES IN HAND-EYE COORDINATION AND IN TOOL USE. A distinctive property of higher primates, such as apes, is the ability to concurrently use the scrutinizing eyes to guide the hands, and the palpating fingers to help the eyes, to manipulate objects. It is this ability that has further evolved in humans and has turned us into beings that can make and use tools and construct artifacts. Although there are no reports of prosimians spontaneously using tools in the wild or captivity, there is some evidence that they have made some inroads toward that ability. We have described earlier the disposition of prosimians to reach for objects with their hands and hold them with their fingers, and their aptitude to skin fruits or perforate nuts to get at their nutritious contents. Are these skills mastered by trial and error or is insight involved in comprehending means-to-end relations? One test relevant to this issue is observational learning, the ability of a naive animal to carry out a novel act by observing a skilled animal; that learning presumes the ability to translate what is seen into a visually guided motor action.

Stoinski et al. (2001) trained one ruffed lemur to use a sliding door to get a container filled with snacks, and another lemur to use a hinged door. Thereafter one group of lemurs was allowed to observe the first procedure, and another group, the second. On their first trial, the peers tested imitated the method used by the demonstrators. Evidently, some lemurs are capable of observational learning.

While prosimians have not been observed to use tools in their natural habitat or in captivity (Jolly, 1964; Torigoe, 1985), they can be trained to use tools and display some insight into the mechanics of how tools work. In an experiment by Santos et al. (2005), ring-tailed lemurs and brown lemurs were trained to select among two identical canes the one with its hook so positioned that it could be used to retrieve a reward (Fig. 5-30A). The animals were allowed to select only one tool in any given trial. After the animals learned to select the correct tool to achieve the desired outcome, they were tested whether they could transfer what they have learned to novel configurations of the canes and the reward (Fig. 5-30B). The animals performed better than chance on the transfer tests (Fig. 5-30C). In subsequent experiments, the animals were tested with novel canes with different features, and demonstrated some ability to ignore such irrelevant features as the color of the cane but select thicker canes that were easier to grasp or manipulate. These findings indicate that even though lemurs do not spontaneously use tools in the wild or in captivity, once they are trained to do so they have the reasoning power to use a tool appropriately to achieve a desired end, that is, they could appreciate the means-ends relationship involved. Importantly, this study also highlights the pronounced individual differences among the lemurs tested in gaining insight into the proper use of tool. Some understanding of the how tools aid the achievement of an end state is also suggested by the observation that lemurs adopt an unnatural grasping configuration with their hand when that facilitates success in a food extraction task (Chapman et al., 2010).

COGNITIVE RULE LEARNING. With reference to the cognitive powers of prosimians, a recent study examined the ability of ring-tailed lemurs to learn a rule based on numerical magnitude estimation (Merritt et al., 2011). The animals were trained to touch the display on a computer screen that contained smallest number of figures, which ranged from 1 to 4, to obtain a food reward (Fig. 5-30). The experimental procedure ruled out the use of non-numerical cues, such as the size or shape of the items. After the lemurs learned to choose the display with the smallest number of figures, at a probability level exceeding chance, they were given transfer tests with novel displays containing 5 to 9 items. The results indicated that the subjects learned the rule of selecting the display with the numerically smallest number of items. However, the performance of these prosimians appeared to be inferior to monkeys as found by other researchers.

The Dawn of Substantive Perception. We have described earlier two stages in the evolution of awareness in animals, the qualeous sentience of jellyfish and the phenomenal awareness of fishes, amphibians and reptiles. We have attributed *qualeous sentience* (sensation) to multicellular animals that have specialized sensory transducers and neural processing mechanisms to enable them to discriminate external things on the basis of their odor, taste, brightness, color or other subjective qualities. For instance, having eyes distributed over their bodies (Fig. 2-14), box jellyfish detect opaque obstacles along their path and avoid bumping

TOOL USE IN LEMURS

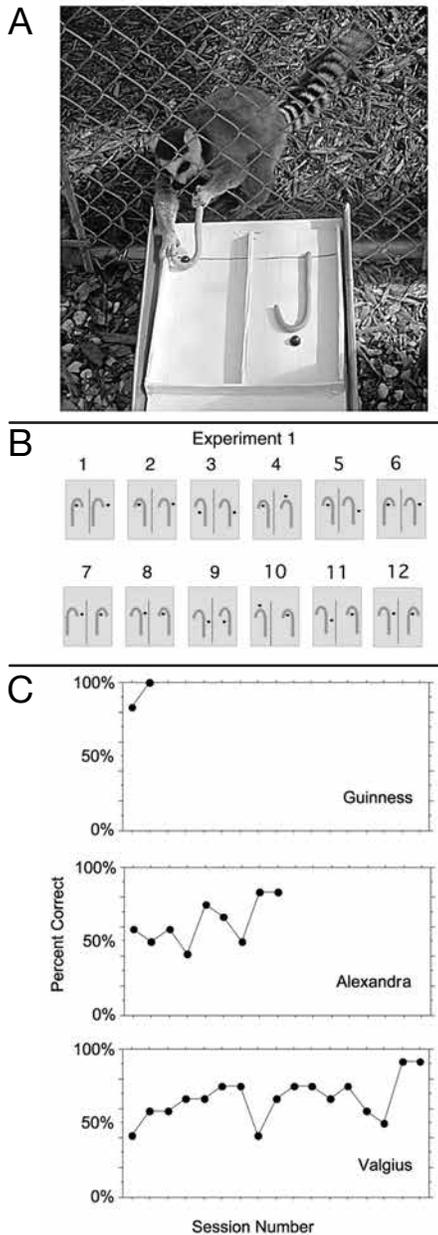


Fig. 5-30. A. Training of ring-tailed lemurs to select the appropriately placed cane to retrieve a food reward. B. Their testing with different arrangements of the cane's hook in relation to the reward. C. The performance of three different animals in the transfer tasks. (After Santos et al., 2003.)

into them (Fig. 2-17). However, because the eyes of jellyfish do not have enough retinal elements ("pixels") to form a pictorial representation of the objects they encounter, their visual system cannot form images, portraits of what different external objects look like in terms of their shape, texture, movement, and other phenomenal features. In contrast, fishes with well-developed ocular mechanisms, a large retinal surface, and large optic lobes, can see what different things look like, such as the bodily markings of conspecifics (Fig. 3-17). They can also learn to discriminate different geometric patterns in an experimental setting (Fig. 3-22). This image-producing ability has been preserved in amphibians and reptiles. Frogs use different methods to capture small and large prey, and snap at higher frequency at visual stimuli that mimic wriggling worms than those that do not (p. 189). However, we have also argued that animals devoid of extremities with dexterous fingers to palpate and manipulate objects lack the ability to centrally integrate visual and haptic information to engage in hand-eye coordination and are thereby capable of only *phenomenal perception*, not *substantive perception*. They may be aware of what objects look like from the outside but not how they are constituted in terms of their component parts and the distinctive properties of those parts. The behavior of submammalian vertebrates supports this idea. The large fish opens its mouth and swallows the small fish as a whole, scales, skeleton, and all. The frog does not remove the carapace of the insect it captures with its tongue, and the alligator does not get rid of the shell of the turtle or the feathery skin of the bird before swallowing them. Without manipulating and dissecting things, there is no way that these animals could learn about the substantive properties of the objects they encounter. That has changed to some extent in basal mammals because they are inquisitive creatures and often use their teeth and paws to tear apart objects under visual guidance. It is that ability that has led to extractive foraging in some lines of mammals, such as removal of the tough

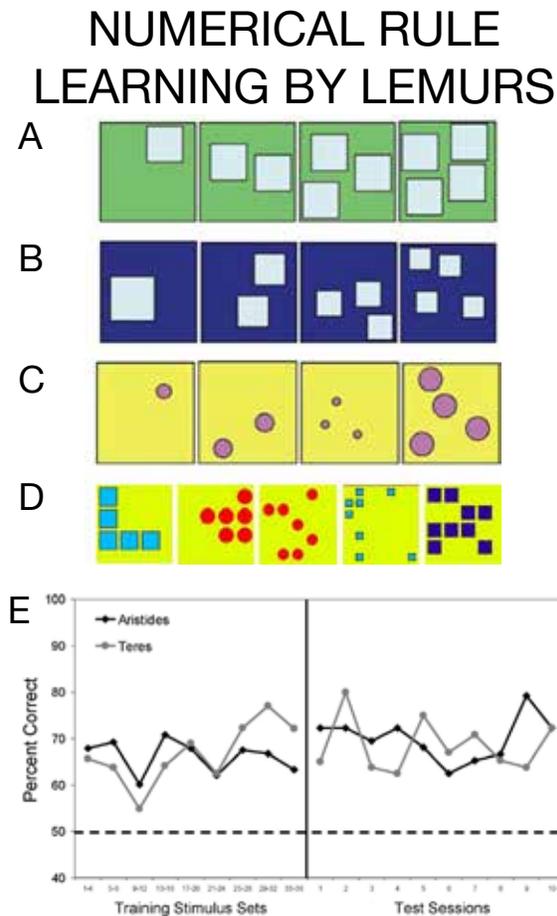


Fig. 5-31. A, B, C. Monitor displays used to test a lemur's ability to select the box that contained the smallest number of elements, from 1 to 4, irrespective of their location, color, size or shape. D. Transfer test of comprehending that rule with displays containing 5 to 9 elements. E. Performance of two different animals during the training and test sessions. (After Meritt et al., 2011.)

skin of fruits to get at their more tasty and juicy flesh, breaking open nuts to get at their nutritious kernels, and tearing open a prey and get to its better tasting and more easily digestible internal parts. We have described earlier how rats can master the skill of removing the tough scales of pine seeds, and we are all familiar with how squirrels hold acorns in their paws and open it with their sharp teeth. Notably, however, in most of these cases, the fingers work in unison as a vice, as when an animal holds a nut in power grip and cracks it with its teeth. Prosimians, as we noted, often reach for edible things with their hand, grasp it with all fingers, and bring it to the mouth (Fig. 5-22C). But can they use their fingers individually and palpate and manipulate objects in order to learn about their structural properties? One prosimian having this ability is the aye-aye (Lhota et al., 2008). Aye-ayes are specialized foragers that feed mostly on embedded food resources, such as wood boring insects, the nectars of flowers, and the flesh of nuts, and they have long, specialized fingers for this task. For instance, they use their thin third finger to tap the surface of trees to locate insects and then extract them, and the more robust fourth finger to scoop the flesh of broken coconuts. However, this ability to use individual fingers for palpation and manipulation is a highly specialized function, and the question remains how widespread this ability is among prosimians. As we shall see in the next chapter, this

ability, which is the foundation of substantive perception, is widespread in the simian world.

5.3.6 Our Basal Mammalian and Prosimian Legacies. Important visceral, somatic, neural, behavioral and mental advances evolved in basal mammals relative to reptiles, and the prosimians have acquired additional traits that herald anthropoid dispositions and abilities.

Basal Mammalian Legacies. Among the important visceral advances that evolved in insectivores relative to reptiles were the following: the ability to maintain optimal body temperature while the ambient temperature changes through its daily and seasonal cycles; carrying offspring inside the uterus of the gravid female during embryonic and fetal

development; and milk production by the mammary glands. Internal temperature regulation allows mammals to be behaviorally active in the heat of the day and the cool of the night, and to survive in cold climatic zones throughout the year. Live bearing ensures the nourishment and protection of offspring during a period when they are most vulnerable, and the same holds for nursing and caring for them from the time they are delivered until they are ready to be weaned. Important somatic advances include: versatile dentition for improved preparation of nutrients for digestion; transformation of the long tubular trunk into one shorter and barrel-shaped, allowing the assumption of a seated posture; elongation of the fingers with nails for object manipulation; and elongation and modification of the extremities for improved locomotor abilities. Most important among the neural advances was the evolution of the neencephalon. Whereas in lower vertebrates each sensory modality has its own segregated, paleocephalic processing station (such as the olfactory, optic, facial, lateral line and vagal lobes of fish), all mammals have a unified, superordinate thalamocortical processing mechanism. They all possess a neothalamus that consists of a set of dedicated relay stations where afferents from the visual, somesthetic, kinesthetic and auditory sensory systems terminate, and a neocortex where the afferents originating in these thalamic nuclei terminate in projection areas with a basically similar cellular organization. We speculate that the heterogeneous signals (trains and bursts of action potentials) conveyed by the differently organized sensory systems are “collated” and “recoded” in these neothalamic nuclei which then, by way of a new set of afferents that they give rise to, “route” the information obtained to dedicated neocortical stations for perceptual processing.

Basal mammals are also distinguished by novel mental dispositions and abilities. Paramount in the realm of affects is the evolution of maternal love. Unlike lower vertebrates, mammals suckle, cuddle, groom and protect their offspring until they are ready to fend for themselves. This provides the young with the opportunity to learn from experience how to survive and prosper in their particular habitat. That learning is aided by two novel affects, curiosity and exuberance, as manifested by their playfulness and exploratory behavior. Moreover, there is some evidence that primitive mammals can learn not only by the slow process of trial-and-error but the much faster, imagery-mediated recollection. With regard to advances in their perceptual abilities, basal mammals may learn something about the substantive properties of the objects they encounter by mouthing and manipulating them under visual guidance. We have paid particular attention to the tree shrews. Although not in our direct evolutionary line, we did that because *tupaia*s share several traits with primitive primates, the prosimians. Unlike insectivores, they depend considerably on vision in their daily behavior in addition to olfaction; they use their fingers for object manipulation; and their thalamocortical system closely resembles that of primates.

Prosimian Legacies. We have distinguished two lines of prosimians, the smaller species that survive in Africa and Asia alongside the typically larger monkeys, and those of Madagascar, where in the absence of monkeys, there are larger prosimian species that occupy simian niches. Prosimians resemble basal mammals in having a muzzle (rhinarium) rather than a reduced face but possess many advanced traits that herald anthropoid characteristics. Unlike insectivores, most prosimians are arboreal and rely greatly on chromatic vision to locate nutrients. Their well-developed eyes have shifted from a lateral to a frontal position and are embedded in a bony

orbit for protection. Frontal eyes provide improved stereoscopic vision, which aids prosimians to grasp branches when leaping from one tree to the next and reach for objects. They pick berries and fruits, and may even shell them, with their elongated fingers that are furnished with sensitive tactile pads and in which nails have replaced the claws of most vertebrates. Prosimians regularly assume a sitting posture when resting or socializing, and may briefly stand upright to scan their environment. While insectivores are mostly solitary and furtive, prosimians form family units, with the parents jointly caring for their young. Some species form larger troops, consisting of several males, females and their offspring, and they move about in their habitat with greater assurance. Litter size is typically small, gestation and lactation more prolonged, and maternal care more intense than in insectivores. Regarding neural advances, the forebrain of prosimians has a much larger neocortex relative to the rhinencephalon than do insectivores, and in many species the cerebral hemispheres are foliated and contain multimodal association areas. Their perceptual, mnemonic and cognitive abilities are also more advanced. Experimental studies indicate that some prosimians readily master complex discrimination tasks, display a limited ability to learn by observation, can appreciate simple rules, and may even master the use of a tool with some insight into its means-end relationship. As we describe in the next chapter, these mental abilities are far better developed in monkeys.