CHAPTER 7

THE EVOLUTION OF HIGHER LEVEL NEURAL AND MENTAL FUNCTIONS IN MONKEYS

Motivational, Affective, Mnemonic, and Cognitive Advances

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7.1 Simian Motivational and Affective Advances: Behavioral Manifestations and Neural Mechanisms

7.1.1. Motivational and Emotional Advances in Monkeys. We have attributed the superior perceptual and motor abilities of monkeys to certain unique somatic traits and their possession of a large brain, in particular a well-developed neocortex. We now turn to the more difficult issue of examining to what extent these advanced neurobehavioral processes depend upon mental support, in particular affect-based motivational forces, advanced mnemonic and cognitive faculties, and a greater awareness of what they are doing and what transpires in the world around them.

We begin by considering the superiority of monkeys relative to most other mammals in several motivational and affective domains. (*i*) The slowly maturing simian infants and juveniles tend to be more inquisitive and exploratory than most other mammals. This suggests great curiosity. That motivational force helps monkeys to become, over a long period of apprenticeship, well acquainted with the complex features of their physical and social environment. (*ii*) Young monkeys are also more playful and exuberant than most other mammals, and both their solitary play and play with peers tends to be more complex. That enables them to become, as they mature, more agile and dexterous, and socially more competent. (*iii*) The bonding between the simian young and its mother, sustained by intense affectional relationship between them, is more enduring than in most other mammals, and that provides the young with greater security. (*iv*) Monkeys are also more gregarious than most basal mammals, and that amicability helps them to cooperate with one another and form larger social groups. All these factors combined, empowers monkeys to roam about with some confidence over wide areas to feed themselves and their young, and procure the most desirable nutrients available.

The Affective Basis of Motivation. Although the behaviorists sought to describe animal motivation in physical terms, such as "drive" or "reinforcement," the motive forces they referred to are feelings and emotions. For instance, Thorndike's (1911) theory of learning postulated that a "satisfying" outcome (such as food reward) strengthens the formation of stimulus-response connections, and "annoying" outcomes (such as an electric shock) weakens them. Satisfaction and annoyance, as we know them from subjective experience, are emotional rather than physical forces. Experiences that were accompanied by rewarding outcomes in the past motivate our behavior positively because they produce anticipatory pleasure or hope; punishments motivate us negatively because they produce anticipatory displeasure or anxiety. This, of course, is not to deny that both anticipated pleasure and suffering have a host of endocrine, autonomic and other physiological corollaries but merely to stress the important motivational role played by the accompanying subjective feeling states. When monkeys move from one feeding site to another, they are prompted not only by hunger by the hedonic motive of finding other appetizing nutrients elsewhere.

Simian Affective Advances: A Preview. Basic emotions act as motivating forces that mobilize the individual to engage in behaviors that satisfy its metabolic needs and avoid injury, stress, and situations that threaten its welfare and survival. They typically form bivalent

(positive and negative) pairs by serving as "carrots" and "sticks," luring the individual as well as prodding it, to achieve certain ends (Table 7-1). We have identified earlier—relying on covert endocrine and autonomic manifestations and overt emotional expressions—the following affect categories in fish (Section 3.2). (*i*) The *ecological* affects: putative feelings of like and dislike, which instigates the sentient animal to seek and settle in favorable habitats and avoid or leave unfavorable ones. (*ii*) The *dietary* affects: sensations of hunger, appetite, and satiety, which drive the individual to procure nutrients and regulate what and how much it consumes. (*iii*) The *prophylactic* affects: sensations of pain and itch, and feelings of comfort or malaise, which aid the individual to avoid tissue damage or bodily injury, and keep it clean and healthy. (*iv*) The *agonistic* affects: fear, which instigates the individual to flee from dangerous situations, and rage, which induces it to engage in offensive and defensive behavior. (*v*) The *sexual* affects: amorousness and lust, which instigate the reproductively primed individual to engage in courtship behavior and mate. In the few piscine species that care for their young, there is suggestive evidence for (*vi*) *parental* affects; and in fish that form schools, there is indication for (*vii*) the *social* affects of gregariousness. We found covert and overt evidence for the preservation of these affects in amphibians (Section 4.1.3) and reptiles (Section 4.2.3). As we proceed from lower vertebrates to mammals, focusing here on primates, there is evidence for the elaboration of these ancient affects as well as the emergence of novel ones. In particular, there has been a great evolutionary elaboration of parental and social affects. Elaboration of the parental affects is indicated by the prolongation and intensification of maternal care, and of the social affects by increased amicability among group members. Particularly pronounced in higher primates are (viii) the *exploratory* affects and (ix) the *mastery* affects. The former is manifested positively as the affect of curiosity, being attracted by novelties in one's surroundings and examining them and, negatively, as tiring of the familiar and hackneyed. The latter as the affects of courage in undertaking challenging tasks, and pride in achievement, and negatively, as timidity and humility (Table 7-1). These new classes of affects, manifest in the play of the young, are motivating forces that greatly contribute to their cognitive development and acquisition of motor skills.

We describe below profound advances in the emotional life of monkeys in three domains: the important role played by curiosity, exuberance and playfulness in their behavioral and mental development; the intense and prolonged affectional relations between mother and her offspring; and the admixture of amicability and hostility in the development of the complex social relations of many monkey species.

7.1.2. Curiosity and Exuberance: The Affects of Exploration and Playfulness. Monkeys are inquisitive animals and spend a considerable amount of their waking hours exploring their physical environment (Jay, 1965; Symonds, 1965; Baldwin and Baldwin, 1977; Fragaszy and Mason, 1978). They are also very playful, particularly as juveniles (Symons, 1978; Fagen, 1981, 2002; Huffman and Quiatt, 1986; Nahallage and Huffman, 2007). While exploratory behavior and playfulness make great contributions to the cognitive growth and instrumental competence of monkeys, the motivational foundation of both of these higher-level functions are affective in nature. Exploratory behavior is driven, on the positive side, by the pleasure derived from having novel experiences and mastering new skills and, on the negative side, by the displeasure of being bored, confined and constrained.

TABLE 7-1
BIVALENT AFFECTS THAT MOTIVATE SIMIAN BEHAVIOR

CATEGORY	+/-	AFFECTS	BEHAVIOR	FUNCTIONS
1 ECOLOGICAL (Habitat selection)	+	Likes	Moves toward	Aggregates in favorable habitats
	-	Dislikes	Moves away	Avoids unfavorable habitats
2a DIETARY (Nutrient procurement)	+	Hunger, thirst	Seeks food and water	Gratifies nutritional, metabolic needs
	-	Satiety (fullness)	Rests, sleeps	Fosters metabolic processes
2b DIETARY (Nutrient consumption)	+	Relish	Ingestion	Consumes palatable and savory nutrients
	-	Distaste	Expulsion	Rejects unsavory, toxic, substances
3 PROPHYLACTIC (Tissue and organ protection)	+	Coziness	Relaxation	Rests in shelter and comfort
	-	Pain, suffering, malaise	Withdrawal	Avoids damage to tissues and organs
4 AGONISTIC (Self defense)	+	Anger, rage	Fights	Subdues predators and aggressors
	-	Fear, terror	Flees	Escapes from danger
5 SEXUAL (Courting, mating)	+	Lust (libido)	Mates	Courts, engages in sexual intercourse
	-	Abhorrance (revulsion)	Avoids courtship	Avoids sex
6 PARENTAL (Caretaking, dependence)	+	Affection, tenderness	Clings, caresses	Promotes bonding of mother and young
	-	Loss, anxiety	Pines, searches	Restores bond between mother and young
7 SOCIAL (Gregariousness, sociability)	+	Cordiality	Affiliation	Fosters friendship with others
	-	Animosity	Hostility	Quarrels with others
8 EXPLORATORY (Inquisitiveness)	+	Curiosity	Seeks novelty	Gets acquainted with new objects and places
	-	Boredom, ennui	Tired of the familiar	Loses interest in familiar places and objects
9 MASTERY (Exercising, seeking, achievement)	+	Manic exu-berance, pride	Competence, haughtiness	Social dominance
	-	Apathy, timidity, depression	Cowardice, meekness	Social subservience

Curiosity: The Affective Basis of Inquisitiveness. In human experience, curiosity is the positive affect that draws our attention to whatever is unfamiliar and novel, one that becomes manifest as the emotional expression of surprise when we witness something unexpected or spectacular. In the absence of stimulation by new things or events, we become bored and that negative affect motivates us to move around and explore our surroundings. Many mammals display elements of curiosity by overcoming their fear of the unknown (neophobia) to venture forth to explore unfamiliar places and examine the properties of novel things they encounter. Most mammals display some degree of curiosity (Fig. 5-5). A rat placed at the entrance of an unfamiliar T-maze will explore first one arm of the maze than the other (Dember, 1956). When placed into an enclosure containing familiar and unfamiliar objects, a rat will sniff and inspect new objects more frequently than familiar objects (Berlyne, 1950). Exploring one's home range and examining the features and properties of the multifarious things it contains is a facet of novelty, or sensation-seeking (Zuckerman, 1984). Monkeys are particularly curious animals and use close vision to examine the properties of every new object they encounter (Fig. 7-1).

The curiosity of monkeys induces them to engage sometimes in novel activities of a complex kind. For instance, a macaque will solve a mechanical puzzle by unlocking several latches in a serial order for the sole reward of opening a door (Harlow et al., 1950; Fig. 7-2). Likewise, they may learn to operate a mechanical device that briefly opens a window in order to obtain a short glimpse of what goes on in the adjacent cage (Butler, 1954). Novelty seeking may be a species-specific affective trait, as it is more pronounced, for instance, in spider monkeys

SIMIAN CURIOSITY

Fig. 7-1. A capuchin monkey closely inspecting an object, while another monkey looks on. (From Wikipedia, Cebus capucinus.png.)

SIMIAN EXPLORATORY BEHAVIOR

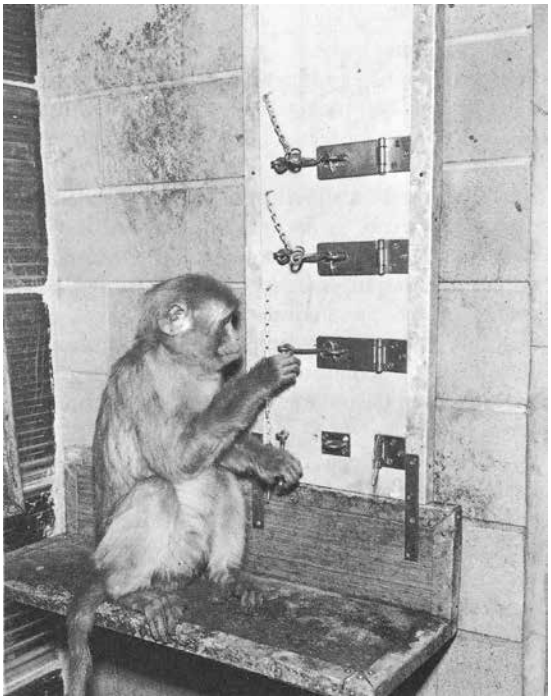


Fig. 7-2. A rhesus monkey disengaging hooks in a serial order for the sole reward of mastering skill of opening a door. (After H. F. Harlow.)

than in stump-tailed macaques (Santillán-Doherty et al., 2010). This interest in exploring the environment and manipulating objects emerges in macaques as early as 20 days of age and becomes more prevalent as they become older (Mason et al., 1959). The great long-term utility of curiosity is that it aids the maturing animal to learn more and more about the features of its habitat.

Exuberance: The Affective Basis of Playfulness and Achievement Drive. As soon as an infant monkey is able to walk and run, it will start climbing up and down trees, and swing and jump from one branch to another, for no other obvious reason but the joy and thrill of the exercise (Symons, 1978; Fagen, 1981, 2002). The play of monkeys is more complex and varied than that of most other mammals, irrespective whether they play by themselves or with their peers. Simian solitary play includes handling, chewing on and carrying objects around; running, hopping, and somersaulting; hanging from a vine and swinging and leaping from branch to branch; looking at the world upside-down or between their legs. An unusual behavior that has been recorded is young Japanese macaques carrying a snowball (Fig. 7-3). A common form of social play is chasing and wrestling with peers with an open mouth "play face," without any expression of fear and anger (grimacing and screaming) or by jointly handling various objects. Social play style changes in the course of development (Simonds, 1965). One-month old bonnet macaques hop together for several minutes. By the second month, they start chasing one another, and that becomes more vigorous as their locomotor coordination improves with age. By 6 month of age, they start to wrestle, and henceforth wrestling becomes one of their favorite pastimes. The play of male infants is generally more exuberant than that of females, and males spend more time in play fighting than females (Symons, 1978; Hayaki, 1983). The offspring of higher-ranking females, perhaps due to their greater confidence, play more than the offspring of lower-ranking females (French, 1981). Play diminishes in adult monkeys but does not altogether disappear. Free-ranging Japanese macaques play with stones—collecting, transporting, rolling and hitting them together (Huffman, 1984; Huffman and Quiatt, 1986; Shimada, 2006; Nahallage and Huffman, 2007). Captive baboons will play with whatever is available, such as containers, drinking utensils and other artifacts (Westergaard, 1989).

SIMIAN PLAYFULNESS

Fig. 7-3. A Japanese macaque carrying a snowball around. (After Mitsuaki Iwago.)

Play has the short-term benefit of contributing to the strengthening of muscles and improving postural and limb coordination. Among its the long-term benefits are the following. First, as a form of practice, solitary playful activities contribute to the mastering of motor skills that may become part of the animal's behavioral repertoire as it matures. Second, play teaches the young how to transact with peers socially and acquaints it with the scope and limits of its abilities (Dolhinow and Bishop, 1970). When raised in isolation from peers, the social development of a monkey is greatly retarded (Harlow and Harlow, 1969). Third, play

fighting contributes to the establishment of a dominance hierarchy, a prominent feature of the organization of simian societies. Play can be a strenuous activity, costly in energy expenditure, and it is hazardous. Infants fall and injure themselves, and while playing away from adults, they often become the target of predation. Therefore, it is not unreasonable to assume that the juvenile period is also a phase in life during which the lesser fit young become either socially marginalized or fail to survive. But as a proximate factor, it is the positive affective force of enthusiasm and the negative affective force of boredom that motivate the exuberance of juvenile monkeys.

7.1.3. Maternal-Filial Affection and Dependence. We have described earlier the evolution of maternal-filial emotional bonding in mammals, such as rats, cats and dogs (Section 5.1.4). Although intense for a relatively short period, once the rapidly maturing infant becomes self-sufficient (typically several weeks to a few months) it tends to leave its mother and the affectionate relationship between them is severed. In monkeys, the mother's solicitous caregiving and the young's attachment are typically much longer—enduring several years, and in many cases for a lifetime—and far more elaborate than in many other mammals.

SIMIAN MATERNAL/ FILIAL ATTACHMENT

Fig. 7-4. Affectional relationship between a rhesus macaque mother and her infant. (From pbs.org/nature episodes.)

MATERNAL LOVE AND INFANT ATTACHMENT. Following delivery, the lactating mother does most of the parenting in most monkey species. (In a few species of monogamous monkeys, the male also plays a role in parenting. For instance, in the South American titi monkeys it is the father's task to carry the young around [Dunbar and Barrett, 2000]). For several days after birth, the doting mother does not let the infant get separated from her. She grooms and cleans the infant, supports it when suckling (Fig. 7-4), may hold it when moving about, and resists the attempt of other troop members (who are also attracted to the young) to touch and play with the infant. It is hazardous to attribute subtle affects to animals but observing the relationship between a monkey mother and her infant warrants the use of the term *love*, as she is apparently no less motivated to care for her young than human mothers are. After a few days, the mother lets the infant move about, and allows siblings and other kin to hold, caress and play with the infant. But as soon as the agitated infant starts to whimper and cry, signaling its emotional distress, the mother retrieves it. As the mother approaches, the infant coos, and it becomes quiet and relaxed when physical contact is re-established (Kalin et al., 1992). When the mother moves about, the infant initially clings to the mother's fur with all its strength; later, as the young gets stronger and more agile, it may ride on the back of the mother.

DEPRESSED MONKEY INFANT

Fig. 7-5. Isolated monkey infant showing the expression of grief. (After I. C. Kaufman.)

AFFECTIVE REACTIONS TO SEPARATION: PINING, DEJECTION, GRIEF, AND DEPRESSION. If separated for a longer period, both mother and young become agitated, justifying the idea that they are pining for each other. If the separation is prolonged, the infant becomes dejected and depressed, and withdraws from all other members of the group (Rosenblum and Kaufman, 1968; Kaufman and Rosenblum, 1969; Fig. 7-5), much as the separated human infant does (Bowlby, 1969; Ainsworth et al., 1978). When an infant dies, the grieving monkey mother may carry the dead body around until it disintegrates (see Fig. 6-4). Depression is a powerful negative feeling state that is overtly expressed in both monkeys and humans as a loss of appetite and avoidance of social contact with others. The biological utility of depression is not obvious. Indeed, it is one of the few emotions that, rather than spurring the individual to action, produces inactivity. Its function may be to assure the fidelity of the bonded pair by not getting distracted or consoled and thus abandon their desire to become reunited. This, of course, becomes impossible when either the mother or the young dies. Alternatively, the period of bereavement may provide the opportunity for the gradual dissipation of the strong affectional bond that existed between mother and young, allowing the surviving member to establish a new dyadic relationship.

THE BEHAVIORAL SIGNIFICANCE OF THE AFFECTIONAL NEXUS BETWEEN MOTHER AND YOUNG. In a seminal series of studies, infant monkeys were separated from their mothers and raised with artificial "surrogate mothers" (Harlow and Harlow, 1969). These were dummies, furnished with either a wire mesh body frame or one padded with foam rubber and covered with terrycloth (Fig. 7-6). When agitated, the infants invariably ran for protection to the softer cloth surrogate rather than the harder wire surrogate. In the absence of a soft surrogate, the separated infant would clutch a piece of cloth or, in its absence, hold on to its own body and rock itself. In one experiment, the feeding bottle was attached to the wire mesh surrogate. The infant developed the strategy of clinging to the cloth surrogate and reaching over to the wire surrogate to suckle. When frightened, this infant ran to the cloth surrogate rather than the wire surrogate, suggesting that its attachment was not based on nutritional conditioning but by the soft touch of the cloth that better simulated a mother's fur. Young raised without maternal affection may develop a compensatory, self-comforting behavior, such as thumb or toe sucking and self-clasping, and such aberrant behaviors as self-biting, swaying, and rocking.

The strong affectional bond established between mother and young has enduring consequences. Surrogate-reared monkeys, or monkeys reared in isolation, cannot interact socially and sexually with peers, and if they become pregnant, they reject, abuse and may even kill their infant (Harlow, 1962; Harlow and Mears, 1979; Caine and Reite, 1983; Lutz et al., 2007). Moreover, many of the young raised by abusive mothers become abusive mothers themselves, suggesting a trans-generational emotional disturbance (Maestripieri, 2005). Even

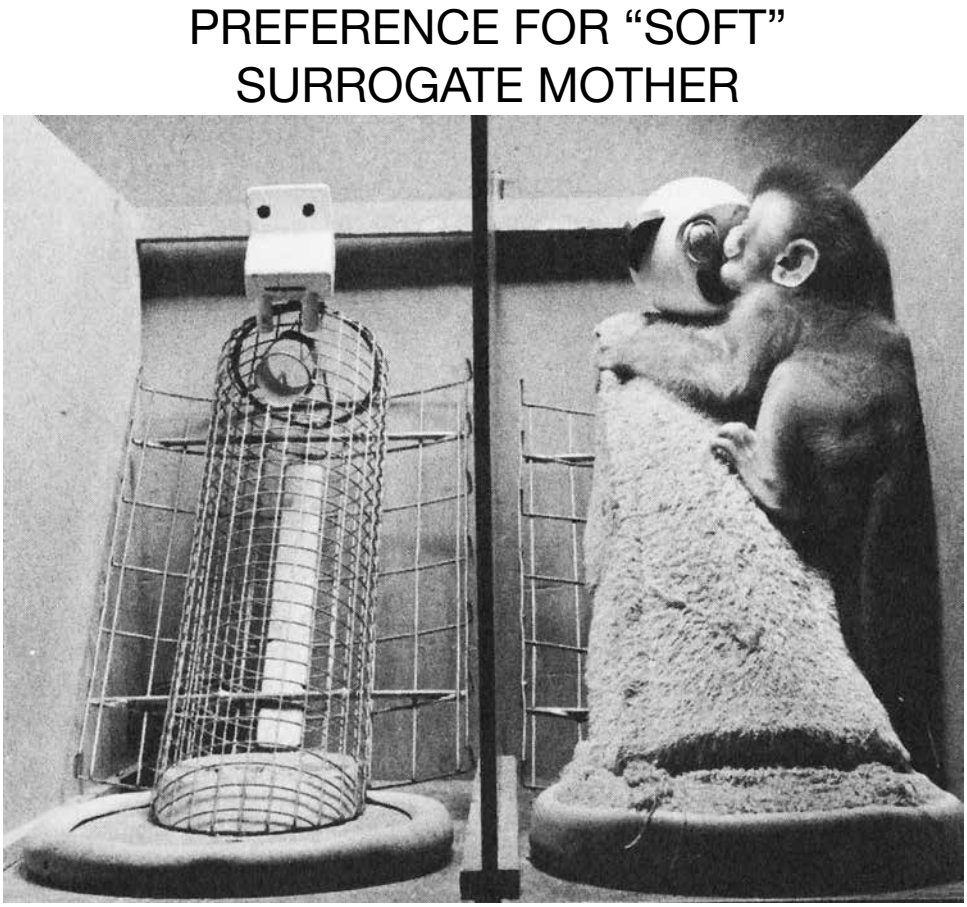


Fig. 7-6. The preference of an infant monkey reared with a wire and a cloth surrogate mother. (After H. F. Harlow.)

the quality of maternal affection has consequences. Monkeys that have experienced a secure attachment relationship with their mothers during infancy interact in a relaxed manner with their peers, whereas those with an insecure maternal attachment history develop an agitated style (Weaver and de Waal, 2003). Evidently, the affection and intimacy that develops between parent and young has enduring consequences.

7.1.4 Amicability and Hostility: Ambivalent Social Relations. Monkeys typically live with others of their kind but group size, group composition, and complexity of social relations vary considerable in different species (Kummer, 1971; Dunbar and Barrett, 2000; Burnie and Wilson, 2001). Colobus, patas and proboscis monkeys form small groups, consisting of a family with a single adult male, several adult females and their offspring. Hanuman langurs and several species of macaques and mandrills form larger groups, consisting of several adult males and females, and their young. Hamadryas baboon troops may consist up to hundreds of individuals that rest and sleep in close proximity on cliffs. Because baboons forage on the ground—where they are preyed upon by lions, leopards, and jackals—they tend to aggregate on cliffs when resting or sleeping, with some males serving as sentinels (Hall, 1960; Altmann and Altmann, 1970). As they awake in the morning, the baboon troop splits into smaller groups that take different routes to feeding sites. Upon getting there, the hungry group breaks up into still smaller units, typically consisting of families with one male, several females and their offspring, and proceed to forage separately. They stop feeding in the afternoon, gather

at a water hole to drink, and then return to their communal sleeping ground for the night. This changing "fusion-fission" relationship is highly adaptive in that it allows the exploitation of scarce and dispersed food resources (roots in the ground, leaves, berries and fruits on scattered trees) by smaller units as well as a collective defensive strategy when exposed at a water hole or a cliff.

The Ambivalent Affective Dynamics of Simian Social Relations. As we noted earlier (Section 5.2.3), tupaids and most small prosimians tend to forage separately in home ranges that each individual claims for itself and defends against others of their kind. Socialization is limited to intermittent meetings during the day and, in some species, same-sex or different-sex companions may huddle together at night to keep warm. This mostly solitary life style has been attributed to the dependence of these small-bodied species on scattered and scarce prey—like insects, frogs and lizards—that often have to be ambushed or approached stealthily. Monkeys typically exploit a more bountiful food supply, consuming fruits, nuts, leaves and barks that are often available in abundance in the forests they occupy. Exploiting these abundant resources in larger groups is safer than by oneself, hence most monkeys tend to live in larger groups. However group living often engenders conflicts. In times of scarcity, individual members of the group compete with one another for preferred nutrients and life in large groups creates conflicts among the males that compete with one another for access to receptive females.

AMICABLE RELATIONS FOSTERED BY MUTUAL GROOMING. Social living requires cordial disposition toward group members, a desire for and the enjoyment of companionship. The asocial basal mammalian legacy, presumably mediated by inborn neural mechanisms, came to be moderated in social monkeys by the evolution of a special behavioral strategy that fosters cordial relations with one's own kind. This is the comforting simian practice of mutual grooming (Altmann, 1962; Sade, 1972; Loy and Loy, 1974; Kurland, 1977; Silk et al., 1981; Fig. 7-7). Monkeys spend a considerable amount of time in grooming themselves. Self-grooming is related to the primitive scratch reflex whereby scabs, vermin or other irritants are removed from the exposed skin by a swiping movement of the paws (Fig. 4-8). In longhaired primates, self-grooming is a prophylactic necessity; indeed, some prosimians have specially adapted elongated incisor teeth or long nails for combing their hair (Boccia, 1998). As some body parts are difficult to reach, cooperation with a peer can be helpful. In addition to promoting group hygiene (Tanaka and Takefushi, 1993), mutual grooming (allogrooming) has become an important mechanism of social bonding, alliance formation and conflict resolution. As noted earlier, a monkey's first experience with being groomed starts early in life. Caressed and groomed by the mother from the time of birth, and later by siblings and kin, physical contact becomes a pleasurable experience, one that allows the individual to relax and feel secure while in the company of others. Mutual grooming is most frequent between close kin (Sade, 1972; Loy and Loy, 1974; Kurland, 1977). It may persist between mother and daughters as long as they live, and between consorting males and females during the breeding season (Carpenter, 1942; Altmann, 1962), and between unrelated males that seek to strengthen their alliances, and males that have fought with one another and seek reconciliation (de Waal, 1987).

THE CONFLICTING AFFECTS OF HOSTILITY AND AMICABILITY. Group living has many advantages. Cooperating females may help each other to jointly raise their young, and

SIMIAN GROOMING BEHAVIOR

Fig. 7-7. Grooming relationship between two macaque monkeys. (From monkey-pictures.net.)

cooperating males can better defend their territory against intruders and predators. However, social life creates conflicts among group members as individuals compete with one another for scarce or precious resources, and males compete for access to females. Monkeys are not *allosocial* animals, like ants or bees that by innate disposition selflessly work for the good of the group; monkeys are *egosocial* animals. Egotistical by primal disposition, monkeys learn to live with others of their kind because they derive benefits from that. Simian group living is based on a dynamic interplay between the inborn selfish disposition of all vertebrates to grab or appropriate whatever one desires, and the acquired social trait of foraging and hunting together and sharing goods with others. An undercurrent of mistrust and hostility—manifest in the constant bickering, fighting and shifting of alliances among individuals that characterize simian societies—is countered by affectional displays, not only by grooming one another and huddling together but also by other appeasement strategies (de Waal, 1987; Byrne and Whiten, 1988). The establishment of social order in monkey groups is either an outcome of preceding contests and fierce battles among group members, which leads to the formation of a hierarchic organization, or a persisting tradition where an established hierarchic order is passed on from one generation to the next.

The Role of Males and Females in the Organization of Monkey Societies. In a temporarily disorganized monkey troop, competition for limited resources and social status leads to fights, which may result in severe injuries and, occasionally, the death of some of the contestants. But after a period of strife, a hierarchic order tends to develop, with the strongest and most aggressive individual (the alpha male) acquiring dominance over the others, becoming the ruler of the troop (DeVore, 1965; Simonds, 1965; Holloway, 1974). In time, some females also acquire an important role by forming enduring cooperative matrilines (Kawai, 1958; Silk et al., 1981; Chapais and Gauthier, 2002).

THE ROLE OF MALE HOSTILITY IN THE FORMATION OF SOCIAL HIERARCHIES. In monkey species that live in small groups, the hierarchic order tends to be quite simple. The largest and strongest male serves as the leader of the group; the younger males and all the females readily accept their subordinate position. In larger simian troops, the hierarchic order may be quite complex, with

an alpha male and several higher and lower ranking subordinates (Koyama, 1967; Kummer, 1971; Deag, 1977; Kaplan, 1978; Watanabe, 1979; Meikle and Vessey, 1981; Berman, 1982; Tilford, 1982; de Waal, 1987, 1989; Gouzoules and Gouzoules, 1987). The alpha male acquires dominance over others by a variable combination of the display of strength, actual fights, and the ability to form and maintain political alliances. Once its position is established, it may rule as a tyrant or as the accepted patriarch of the group (Fig. 7-8). Typically, the lower ranking males get out of the way of the alpha male as he moves past them, and may signal their submission by such gestures as looking away, holding their ears tightly against their head, lip smacking, or presenting their rump in the manner of females. The alpha male terminates squabbles among group members, decides when to leave a site and where to proceed next, and he sires most of the group's offspring. When the alpha male becomes old and feeble, or when new members join the group, his status may be challenged by one or more aggressive individuals. The challenged alpha male may counter by soliciting help from its kin or allies or he may be deposed.

SIMIAN *ALPHA* MALE

Fig. 7-8. Young and older stumptail macaque monkeys look on as the alpha male is eating by itself.
(From Wikipedia, after Macaca arctoides.png.)

Particularly instructive is the aggression-based social organization of baboons, since they are adapted to a terrestrial life style that may resemble that of the early hominids that moved from the African forests into the open grasslands. A baboon troop, among the largest in subhuman primates, may have as many as 100 members. Mature baboon males may weigh over 30 kg, are very strong, and they engage in fierce fights when conflicts arise among them about access to females. They display their impressive canines, stare at one another, bark, screech, grind their teeth, and draw blood (Estes, 1991). Finally, the largest male, one distinguished by the highest testosterone concentration in its blood (Bergman et al., 2006), acquires dominance over the others and peace is restored. (Even the dominance rank of females is correlated in baboons with blood testosterone concentration; Beehner et al., 2005.) Importantly, once the alpha male has secured its position by brute force, it may switch to display such conciliatory acts as grooming subordinates or presenting its rump (Altmann, 1980; Strum, 1987; de Waal and Ren, 1988). Because fights produce excessive stress in subordinate males (as indicated by elevated glucocorticoid and reduced testosterone levels) this conciliatory behavior promotes group welfare (Virgin and Sapolsky, 1997; Bergman et al., 2005).

THE ROLE OF FEMALE AMICABILITY IN SUSTAINING THE SOCIAL ORDER. In addition to the strongest and most adroit male, an experienced female may also acquire high rank within the group. As a matriarch she not only helps close kin and other females to rear their young but also plays a role in the appeasement of the aggressive males (Silk et al., 1981; Bernstein and Ehardt, 1985). Among Japanese macaques, a troop may contain several matriarchal lines

(matrilines) in which daughters of high-ranking females inherit their mothers' social status (Kawai, 1958; Chapais and Gauthier, 2002). In general, higher-ranking females are groomed more often than lower-ranking females (Sade, 1972; Oki and Maeda, 1973; Silk, 1982) and when males groom juveniles, they are more likely to groom the offspring of higher-ranking mothers than the offspring of lower-ranking mothers (Kurland, 1977; Silk et al., 1981). Typically, grooming is reciprocated among female macaques and the alliances they form help the partners against aggressive males (Ventura et al., 2006). Grooming partners also display a greater tendency to reconcile after a conflict than unrelated monkeys (Call et al., 1999; Cooper et al., 2005). Members of high ranking matrilines tend to support their kin when conflicts arise with others, and their young may challenge lower-ranking animals, with the latter often accepting their subordinate status without a fight (Datta, 1983). High-ranking females have many advantages over low-ranking ones. They are more efficient foragers, have more progeny, and their offspring are heavier and have a better chance to survive infancy (Mori, 1979; van Noordwijk and van Schaik, 1987; de Waal, 1987). Because males often leave their matriline to join other groups, the inheritance of high rank is more common among female than male progeny (Angst, 1975). Having lost their social rank, it may take males some time before they can improve their status in the new group through aggressive displays and fighting (Sugiyama, 1976; Tilford, 1982).

The role played by females in reducing within-group aggression is illustrated by a recent report of social changes in a troop of wild baboons. Under unstable social conditions, all baboons display endocrine and behavioral indices of stress and even after a hierarchic order is established, the lower ranking members of the troop remain chronically stressed, as indicated by their elevated blood glucocorticoid levels, and, in association with reduced testosterone concentration, they consort less with females (Sapolsky, 1993; Virgin and Sapolsky, 1997). In the early 1980s, a troop of macaques occupied a site near a garbage dump where aggressive males prevented the others access to the dump. Several years later, the consumption of tainted meat in the dump led to a tuberculosis outbreak and most the aggressive males died. Once the aggressive males were gone and there was an increase in the ratio of females to males, group relations became much more peaceful (Sapolsky and Share, 2004). Significantly, the hierarchic order established within a group aids only within-group peace. Outsiders typically evoke hostility, and that xenophobia often leads to bloody fights between different groups living in close proximity (Southwick et al., 1974).

7.1.5. The Modification of Basic Affects by Experience and Learning. In lower vertebrates that mature with little or no parental support, the basic affects are the principal guiding forces of behavior throughout life. The same applies to mammals during the neonatal period and early infancy. Inborn feelings and emotions function as stimulus assessment mechanisms to aid the inexperienced animal to respond appropriately to environmental stimuli. For instance, nutrients that are beneficial to the organism (such as "sweet" carbohydrates and amino acids) are accompanied by a positive feeling tone (pleasure) and accepted; those that are harmful (such as "bitter" alkaloids) are accompanied by a negative feeling tone (displeasure) and rejected. The inborn sensory discriminations are a product of an evolutionary selection process that is genetically transmitted from generation to generation. But as species-specific mechanisms, these affective discriminations are readymade, stereotypic reactions that better

serve the survival of the species than the specific needs of the individual. To be beneficial to the individual who tries to adapt itself to its distinctive physical and social milieu, the basic emotions are modified in mammals by experience and learning. While anger is a useful response when one is maliciously struck by a foe, it is maladaptive if unintentionally hurt by a friend. Flight is an adaptive response to a ferocious dog bearing its teeth, but not to a friendly dog wagging its tail. As in all higher mammals, the basic emotions are modified in monkeys as they develop and mature by mnemonic and cognitive processes.

From Hunger to Hedonism and Greediness. Monkeys will self-administer saccharin solutions that have no nutrient properties (Carrol, 1985), presumably just for the pleasure of the sweet taste. The pleasure produced by consuming appetizing nutrients when hungry, has led in higher animals to hedonism, i.e., the consumption of highly palatable nutrients even if not hungry. If done in moderation, hedonism is probably beneficial to the individual because it reduces stress. However, if carried to excess, gluttony is not only harmful to the individual as it leads to obesity but also leads to social conflict when one's greed frustrates another's access to food. Anyone who has watched the frenzy that some species of monkeys display when they are fed in a zoo and compare that, say, with cows that peacefully line up at the trough where they are periodically fed, witnesses the profound difference in the emotional disposition of the two species. As food is thrown into their enclosure, each monkey darts forward and greedily grabs what it can, filling its mouth and cheek-pouch with favored items, and retreating to a spot where it can enjoy what it has grabbed without molestation. After the monkeys have filled themselves, food remains scattered in the enclosure indicating that the frenzy was not due to the shortage of food but gluttony and greed. This greediness is also common in the field. Baboons, for instance, never share food with one another, including a mother with her young (Strum, 1987). (Limited food sharing has been reported in species that engage in cooperative hunting, i.e., white-faced capuchin monkeys; Perry and Rose, 1994.)

Another hedonistic disposition that creates social conflict in monkey societies is hypersexuality. Females are typically promiscuous but males tend to monopolize females and tend to follow them in and out of the breeding season in the hopes of sexual gratification. That is, sexual behavior has become divorced in monkeys from serving the biological imperative of species propagation, becoming another means of emotional gratification. Anestrous females frequently present their rump to males as an appeasement signal and the solicitation of friendship, and monkeys spend much time not only in heterosexual but also homosexual and autoerotic activities (Chevalier-Skolnikoff, 1974). From the perspective of social organization, this hypersexuality has both positive and negative consequences, promoting social bonding in smaller, single male family units but creating social conflict in larger, multi-male troops.

From Fear to Anxiety and Timidity. Fear is the basic affective reaction to perceived danger. A sudden lightning or thunder, a looming mass or the approach of a predator, trigger fear and that is instantly followed by defensive reactions that may protect the individual from being hurt, injured or killed. Acute fear reaction consists of visceral and autonomic processes that foster increased vigilance and preparedness—such as the secretion of corticotropin hormone, cortisol, epinephrine and norepinephrine, and increased heart rate—and certain stereotypic overt activities, such as fleeing, hiding or freezing. Human neonates exhibit a startle response,

such as widening of the eyes and retraction of the head and clasping with the arms, when dropped from a height or upon impending collision with a real or simulated object (Landis and Hunt, 1939; Ball and Tronick, 1971; Bower, 1974). To withdraw at the slightest sign of danger has considerable survival value, particularly to a defenseless young who is the choice target of predators (Öhman, 1993). Some of these reactions persist into adulthood, such as blinking in response to a looming object. And much like humans, rhesus monkeys jump backward or duck when viewing a screen on which a shadow is rapidly expanding (Schiff et al., 1962). However, these inborn fear reactions are wasteful or maladaptive if experience reveals that the stimulus eliciting them does not pose any danger. As we noted earlier, infant vervet monkeys indiscriminately take cover when a raptor, like an eagle, or a non-raptor, like a goose, flies overhead (Seyfarth et al., 1980; Seyfarth and Cheney, 1986). As they mature, vervet monkeys become more discriminatory and ignore innocuous birds, presumably those that their elders do not respond to emotionally.

In contrast, it is highly advantageous that inexperienced animals learn to respond with fear when confronted by situations that they do not innately sense as dangerous. This may be the case when a young monkey climbs on a vine that cannot hold its weight or plays with a scorpion that is likely to bite it. The experienced mother observing such an event may emit a distress call and retrieve the young or, else, the injured young learns a painful lesson that it is not likely to forget. This is illustrated by the development of rhesus monkeys' fear of snakes. Mineka et al. (1984) presented food to naïve laboratory-raised monkeys adjacent to a transparent box containing a snake. The monkeys proceeded to consume the food without any trepidation. Subsequently, the same monkeys were allowed to observe wild-raised peers displaying intense fear in the same situation. Quickly, the laboratory-bred monkeys learned to avoid the food placed near the snake. This finding indicates that a monkey needs not to get bitten by a snake to become afraid of snakes; it acquires that phobia by merely witnessing the emotional reactions of its peers. In a modification of the experiment, some laboratory-bred monkeys were allowed to watch a spliced film in which the wild monkey's fear was seemingly elicited either by the presence of a toy snake or a crocodile, or by a rabbit or a bunch of flowers. The laboratory-bred monkeys learned to fear the former but not the latter objects (Cook and Mineka, 1989). This suggests that some innately given configurational features of predators play a role whether or not fear is acquired. Experience may also turn dislike into liking. For instance, most monkeys in the wild are reluctant to enter streams or lakes, as if they have an innate aversion to water. However, Japanese macaques have learned to bathe in geothermal hot springs (Fig. 7-9) to escape the winter cold (Suzuki, 1965) and, likewise, they may proceed to bathe in the cool sea during the hot season (Galef, 1990).

JAPANESE MONKEY BATHING IN A HOT SPRING

Fig. 7-9. A Japanese macaque monkey swimming in a geothermal hot spring. (After Will Burrard-Lucas.)

Infant monkeys begin to play with one another as soon as they become mobile, and their mother allows them to leave her. This social play takes many forms but perhaps the most prevalent is playful fighting. Play fighting is an important activity for two reasons: it promotes the development of skills that a monkey needs to defend itself when confronting adversaries or predators, and it determines the animal's future status within the social hierarchy. Through play fighting, the young learns about its physical strength, endurance, and fighting skill relative to others. Through repeated incidents of defeat, a weaker monkey learns to submit itself to stronger peers, will seek to appease them, and will become subservient to them. If that does not help to avoid repeated punishment, chronic anxiety may lead to the development of timidity as an enduring temperamental trait.

The development of anxiety and timidity as enduring temperamental traits has been studied experimentally in monkeys. Stroebel (1969) exposed rhesus monkeys to aversive stimuli that they could avoid by pressing a lever. When they were no longer punished and the lever was removed, the animals displayed a behavior suggestive of chronic anxiety and depression, such as inactivity, poor grooming habits, and compulsive hair pulling. Mineka et al. (1986) raised two groups of infant monkeys: the "masters" who could control the dispensing of food, water and delicacies, and their "yoked" partners who received the same rewards but could not control the delivery. Compared with the master group, the yoked animals showed less exploratory behavior, could not effectively deal with the threat posed by a robot toy, and became more emotionally aroused when separated from their peers. Rosenblum and Paully (1984) exposed nursing mothers to unpredictable feeding schedules, which produced stress in both mother and young, and disturbed their mutual relationship. These young became anxious and timid individuals as adults relative to their normally reared peers and became subordinate members of the group. Subordinate position within the dominance hierarchy has been found to produce elevated cortisol levels in monkeys when challenged with stressors (Abbot et al., 2003).

From Anger to Mistrust and Malevolence. Anger is readily triggered in infant monkeys by such aversive stimuli as restraining or denying access to something they desire. The young that cannot have what they wish often throw a temper tantrum. As they become more independent and join a playgroup, they (the males in particular) engage in frequent mock fights, learning about each other's strength, agility and endurance. The larger, stronger, and more skilled ones gradually come to intimidate and subdue those that are weaker, and that heralds their future status in the social hierarchy. Once they reach adolescence, the more aggressive members of the group acquire higher ranks, which become manifest in their access to favored nutrients, comfortable resting spots, and receptive females. Adult monkeys have a low threshold for anger and rage, and often engage in hostile and vicious behavior toward members of their own group and, in particular, toward outsiders that they come into contact with (Hall, 1964; Southwick, 1969; Southwick et al., 1974).

Some of the overt manifestations of simian belligerence includes such offensive displays as staring, bearing of canines, and the assumption of an offensive posture, and not rarely in biting the adversary, drawing blood and sometimes producing injuries that lead to death. Their constant bickering evinces the hostile disposition of monkeys as a temperamental trait, as does their recurrent fights with competitors for social status and access to females.

From Amicability to Trust and Benevolence. Monkeys living in a large troop have to develop amicable relationship with one another, some degree of trust among individuals that are inclined to be distrustful of one another. A strategy that has evolved in monkeys to promote that is mutual grooming. Grooming among unrelated adults is a learning-based behavioral strategy as the actor that provides the recipient with pleasure expects reciprocation. Mutual grooming has a developmental history. Its foundation is the altruistic disposition of the monkey mother to care for its young but life experience is also a factor since, as we noted earlier, female monkeys raised by abusive mothers will themselves abuse their young. In all social primates, adolescent and adult females take great interest in newborn and maturing infants, a tendency that is called "aunt behavior" (Hinde et al., 1964; Hinde and Spencer-Booth, 1967; Baldwin, 1969; Jolly, 1972). Females groom, cuddle and carry a new infant, and if the mother is too protective, they groom the mother until she relents and allows them to touch the baby. Being groomed and cuddled makes the young relax and feel secure in the family setting. When the young becomes more independent and begins to interact with peers and gradually becomes a member of the social hierarchy, it learns that grooming helps to widen its supportive social network (Silk et al., 1981; Silk, 1982; DeWaal, 1987). Inferiors groom their superiors to gain their good will; dominant males groom inferiors to encourage their allegiance; and, most importantly, monkeys that have fought with one another tend to seek reconciliation by grooming one another.

Endocrine Effects of Amicable and Hostile Social Relations. Because of the close linkage between affects and endocrine reactions, rearing conditions and traumatic events have a profound effect on the emotional development of the individual. In humans, childhood abuse and violence in daily life produce stress, which is associated with endocrine reactions, such as elevated blood cortisol levels and altered serotonergic and adrenergic metabolism (e.g., Coccaro et al., 1996; Miczek et al., 2002; Tsigos and Chrousos, 2002; Van Itallie, 2002) and the mental pathology known as posttraumatic stress disorder (Mason et al., 1988; Yehuda, 2001; de Kloet et al., 2008). Specifically, children with a history of early abuse and combat veterans with traumatic experiences have elevated corticotropin releasing hormone (CRH) levels in their cerebrospinal fluid system (CSF) and, as judged by the concentration of the monoamine metabolite, 5-hydroxyindoleacetic acid (5-HIAA), lowered serotonin levels. The same has also been observed in monkeys with a history of early abuse (Champoux et al., 1989; Higley et al., 1992; Rosenblum et al., 1994; Coplan et al., 1996; Kalin et al., 1998; Lyons et al., 1999: Howell et al., 2007) or those living in a disorganized social setting (Ray and Sapolsky, 1992; Sapolsky, 1993, 1997; Sapolsky and Spencer, 1997). The consequence of these endocrine changes are profound metabolic disturbances (Kaufman et al., 2007), immune system disorders (Lubach et al., 1995), circulatory dysfunction (Strawn et al., 1991), and, in females, in social withdrawal (Shively, 1998), the suppression of procreation (Centeno et al., 2007), and the rejection and abuse of offspring (Fairbanks, 1989; Higley et al., 1996a, 1996b). A similar pattern was found among cross-fostered females, suggesting that low serotonergic functioning produced by maternal rejection has repercussions across generations (Maestripieri, 2005; Maestripieri et al., 2006).

Innate and Acquired Factors in the Development of Amicability and Hostility. There are species differences in the amicability and hostility of different monkeys. Rhesus macaques

tend to be more aggressive than stump-tailed macaques, pigtail macaques more aggressive than bonnet macaques (Thierry, 1986). Reflecting this species difference, the concentration of corticotropin-releasing factor (associated with combativeness) is higher in the cerebrospinal fluid of pigtail macaques than in bonnet macaques, while the concentration of oxytocin (associated with amicability and gregariousness) is higher in bonnet macaques than in pigtail macaques (Rosenblum et al., 2002). Social isolation produces more aggressive behavior in rhesus macaques than in pigtail macaques (Sacket et al., 1976), and cerebrospinal fluid 5-HIAA concentration, a serotonin metabolite, is lower in rhesus than in pigtail macaques (Westergaard et al., 1999). However, the abuse of infants appears to be the result of experience rather than genetic inheritance in some families of pigtail macaques (Maestripieri, 2005). When the young of more aggressive rhesus macaques are raised by the less aggressive stump-tailed macaques, the rhesus macaques grow up to be become more conciliatory in their relations with others (de Waal and Ren, 1988). Correspondingly, a correlation was observed in capuchin monkeys between mother-infant relationship and the development of conciliatory behavior later in life (Weaver and de Waal, 2003). Monkeys that had a secure attachment relationship with their mothers during infancy developed a conciliatory style with others, whereas those with an insecure maternal attachment showed an agitated conciliatory style.

Amicability and Hostility as Our Bivalent Simian Affective Legacy. Although monkeys are extremely intelligent when compared with most other mammals, their behavior is governed by emotions to a large extent. This emotionalism has both positive (prosocial and adaptive) and negative (antisocial and maladaptive) consequences. On the positive side is the monkey mother's intense affection for her young. The strong and enduring maternal/filial affection represents a great behavioral advance for several reasons. First, the maternal care received by the vulnerable infant greatly enhances its chances of survival. Second, the bond between mother and young contributes to the trans-generational preservation of a matriarchal social support system. Third, the trust that develops between mother and young fosters the development of an amicable relationship with other members of the group. Forming maternal love and filial trust between mother and young is one of our most important simian legacies. Related to maternal love is the cordial treatment that the young receives from its siblings and the network of cooperating females. This contributes to the development of trust in others, which, in turn, greatly contributes to the development of group solidarity with all its beneficial consequences. Although hairless and clothed humans have abandoned grooming as a means of fostering togetherness, the desire for companionship is evident when we sit around the bonfire or dining room table, singing or sharing experiences with one another. The curiosity, playfulness, and exuberance of monkeys is also an important simian trait and ensures that they become knowledgeable about their world and become adept in exploiting its resources. That, too, is a positive simian legacy. However, monkeys also have many negative emotional traits, dispositions that make living with others stressful. Monkeys are restless, bickering and belligerent individuals. They tend to be hedonistic, gluttonous and oversexed. They are greedy, ever ready to grab what others have and are reluctant to share what they have with others. Looking at it from the human perspective, this is our burdensome simian inheritance: our own disposition toward restlessness and belligerence, our selfishness and greed, and our tendency to be oversexed. As we describe below, this dual legacy is largely attributable to the brain limbic system, an emotional neural mechanism, that we share with monkeys.

7.2. The Simian Limbic System: Neural Mechanisms of Affective Motivation

7.2.1. The Organization of the Limbic System. The term '*le grande lobe limbique*' was coined by Broca (1878). In Broca's morphological usage, the limbic lobe consists of the circumferential complex in the medial cerebral hemispheres, which extends from the olfactory cortex anteriorly to the midbrain posteriorly. The term later acquired a functional connotation. Papez (1937) described an ancient "emotional circuit" in the mammalian brain, consisting of the cingulate gyrus, the hippocampus, the amygdala, the hypothalamic mammillary body, and the anterior thalamus that are interconnected by way of the cingulum bundle, the fornix, and the mammillothalamic tract. Subsequent research, which implicated additional midline structures in visceral and emotional regulation, led to MacLean's (1949) proposal of the "limbic system" (or "visceral brain") as a distinct functional entity in the core of the forebrain. In time, some other structures have been assigned to the limbic system (Fig. 7-10) and it is now conceptualized that some of the newer structures serve as an interface between the phylogenetically older brainstem and the more recently evolved neocortex (White, 1965; Powell and Hines, 1974; MacLean, 1986; Kunishio and Haber, 1994; Carmichael and Price, 1995a, 1995b; Morecraft and Van Hoesen, 1998; Chiba et al., 2001; Morgane et al., 2005; Groenewegen, 2007).

AFFECTS AND THE LIMBIC SYSTEM. Among the brain mechanisms mediating emotional behavior in fishes, we have identified the paleocephalic reticular formation, the periaqueductal gray, and the hypothalamus (Section 3.2.5). The paleocephalic origination of emotional behavior seemed to be supported by studies carried out in the early 20th century, which showed

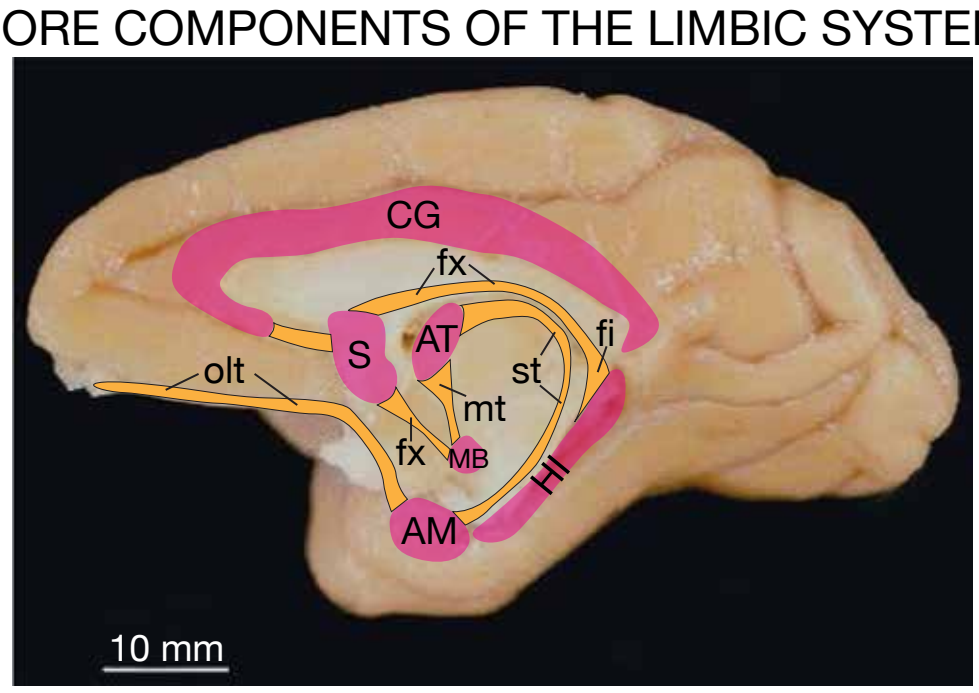


Fig. 7-10. Sagittal view of the limbic system. Abbreviations: AM, amygdala; AT, anterior thalamus; CG, cingulate gyrus; fi, fimbria; fx, fornix; HI, hippocampus; MB, mammillary body; olt, olfactory tract; S, septum; st, stria terminalis.

that decorticated cats and dogs display exaggerated anger and fear reactions when disturbed. That behavior was attributed to the release of ancient brainstem emotional mechanisms from cognitive control (Section 3.2.4). However, subsequent studies revealed that, in addition to these ancient hindbrain structures, components of the forebrain limbic system also play an important role in mammalian emotional behavior. For instance, rats with implanted electrodes in structures associated with the medial forebrain bundle engage in self-stimulation, suggesting that they experience positive (rewarding) affects (Olds, 1956; Rolls, 1975). In clinical studies of conscious human patients, stimulation of parts of the amygdala was found to produce anxiety, and stimulation of the septum pleasurable feelings (Heath et al., 1968). More recent studies revealed that patients with amygdala lesions were deficient in recognizing facial expressions of fear and anger (Adolphs et al., 1994) and scanning studies indicate that the amygdala is activated in normal human subjects when viewing facial expressions of emotions (Irwin et al., 1996; Lane et al., 1997). These new studies have also implicated some neocortical structures in emotions. For instance, patients with bilateral orbitofrontal lesions fail to appreciate the significance of such emotional expressions as fear, anger, sadness and happiness (Damasio et al., 1990; Blair et al., 1999; Adolphs et al., 2001). These neurological findings can be related to several evolutionary advances characterizing the affective life of mammals: the elaboration of ancient affects; the emergence of new ones; and the modification of basic affects by mnemonic and cognitive processes.

HIERARCHIC ORGANIZATION OF THE LIMBIC SYSTEM. We conceive of the mammalian limbic system as a hierarchically organized neural complex that consists of ancient ganglionic and more recent allocortical and neocortical components. Its ganglionic components, as modified piscine legacies, include the brainstem periaqueductal gray, raphe nuclei, and reticular formation; the diencephalic hypothalamus, preoptic area, and some anterior and midline thalamic nuclei; and the telencephalic amygdala, septum, and nucleus accumbens. Its major allocortical components are the rhinencephalon, the hippocampus and some associated structures. Its neocortical components are the insular, cingulate and orbitofrontal cortices. Among the large fiber tracts that interconnect components of the limbic system are the following: the medial forebrain bundle, which courses from the rostral forebrain, through the lateral hypothalamus, to the brain stem; the fornix, which links the hippocampus and the septum with the hypothalamus (mammillary body); the stria terminalis, which links the amygdala to other limbic structures; the cingulum bundle, which connects the orbitofrontal and cingulate cortices with caudal limbic structures; and the uncinate fasciculus, which connects the temporal pole cortex and the orbitofrontal cortex. The anterior commissure is the limbic system's analogue of the neencephalic corpus callosum.

The lower-level ganglionic components of the limbic system receive alerting ("nonspecific," "diffuse") afferent input from the interoceptive, nociceptive, visual, somesthetic, and auditory systems, and they are the source of a neuromodulatory output system, the dopaminergic and serotonergic efferents, which are widely distributed throughout the forebrain, in particular the frontal and temporal lobes. The allocortical components, particularly the rhinencephalon, are closely linked with the olfactory system, which plays a major role in feeding and sexual behavior. This component of the limbic system has not kept pace with the expansion of the neocortex in the line that led from basal mammals to prosimians and monkeys (Fig. 7-11).

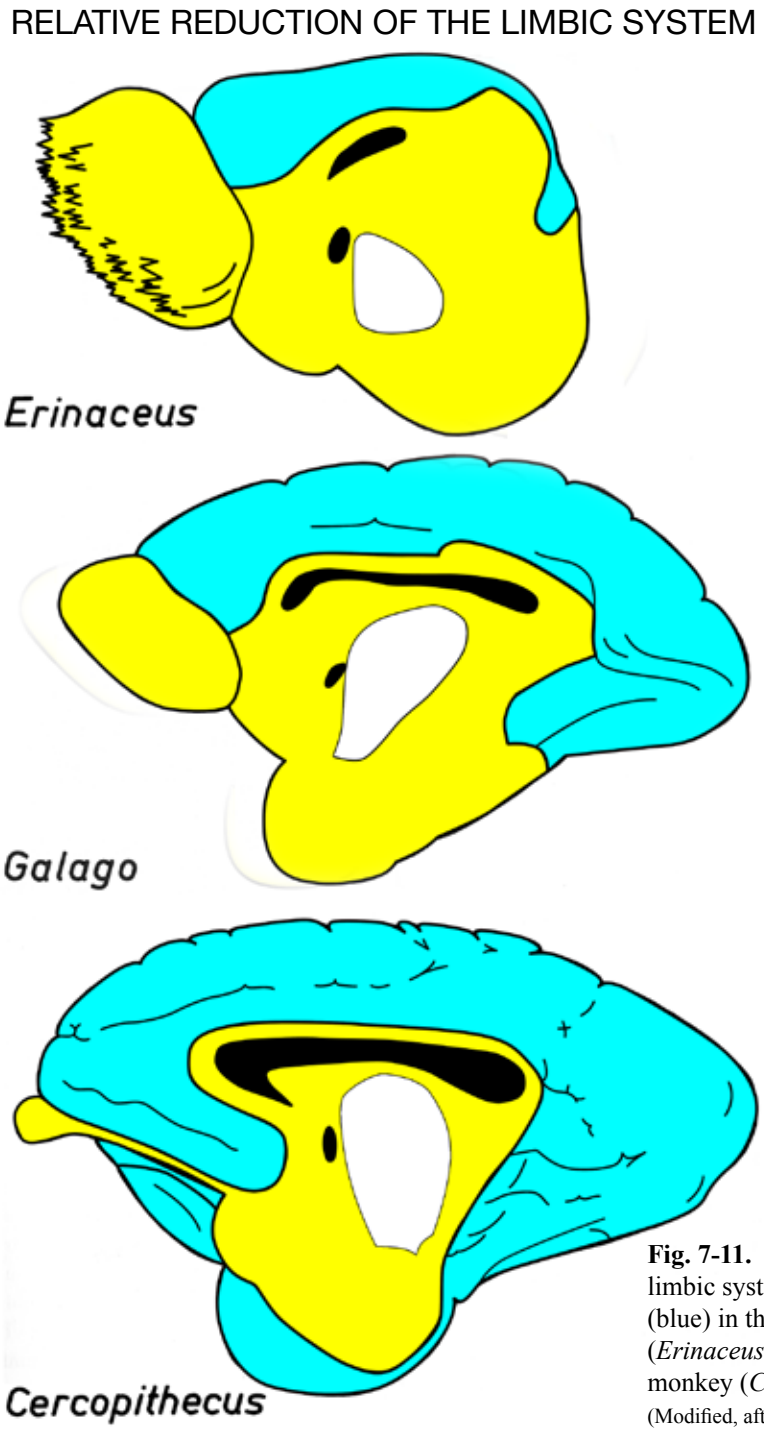


Fig. 7-11. Reduction in the relative size of the limbic system (yellow) relative to the neocortex (blue) in the forebrain of the hedgehog (*Erinaceus*), a prosimian (*Galago*), and a monkey (*Cercopithecus*).
(Modified, after Stephan and Andy, 1970.)

In contrast, the neocortical components of the limbic system—the insular, cingulate and orbitofrontal cortices—have become greatly elaborated in primates, reaching their peak in man (see below). These structures are closely linked with the prefrontal and temporal cortex and bring to bear detailed perceptual information, memory and cognitive considerations to regulate the activity of the lower level emotional mechanisms.

7.2.2. The Ganglionic Components of the Limbic System. We shall consider first the structure and functions of the ganglionic components of the simian limbic system: the serotoninergic, dopaminergic and adrenergic nuclei of the brainstem; the expanded hypothalamus and preoptic area; the amygdala; and the nucleus accumbens.

Brainstem Arousal Mechanisms of the Limbic System. In addition to CNS components whose function is to carry "specific" messages, by way of large caliber axons (typically using glutamate as a fast synaptic transmitter) and process these messages to reconstruct what transpires in the external world, the CNS also has components whose main function is "nonspecific" arousal, the behavioral activation of the individual and the mobilization of its energy resources. A high proportion of these are concentrated in what was originally described as the diffuse reticular formation in the core of the brain stem but are now distinguished as specific structures, such as the raphe nuclei, the locus coeruleus, the periaqueductal gray, and the ventral tegmental area. These structures contain neurons that are the source of monoamine neurotransmitters, serotonin, dopamine, and norepinephrine (noradrenaline).

THE RAPHE NUCLEI. Neurons that produce serotonin (5-hydroxytryptamine, 5-HT) as a transmitter are concentrated in all vertebrates in the brainstem raphe nuclei and send axons to most regions of the CNS. Serotonergic neurons are an ancient heritage: they have been identified in fish (Ekstrom and Ebbeson, 1989; Vecino and Ekstrom, 1990; Winberg et al., 1993; Senthilkumaran, 2001), amphibians (Tan and Miletic, 1990) and reptiles (Smeets and Steinbusch, 1988; Guirado et al., 1989; Martinez-Guijarro et al., 1994; Baxter et al., 2001b). They are also prominent in the brainstem of mammals, including subhuman primates and man (Wilson and Molliver, 1991; Coccaro et al., 1996; Miczek et al., 2002; Tsigos and Chrousos, 2002). As in lower vertebrates, increased serotonergic activity has been associated in mammals with vigilance, behavioral mobilization, and coping with stress (Veneema, 2009). Low serotoninergic brain activity has been correlated in female macaques with aggression, impulsivity, and a violent disposition (Westergaard et al., 1999, 2003), and with taking improper care of their young (Cleveland et al., 2004).

VENTRAL TEGMENTAL AREA. Dopamine neurons have been identified in fish (Rink and Wullimann, 2002), amphibians (González and Smeets, 1991, 1993), and reptiles (Clark et al., 2000; Henselmans and Wouterlood, 1944; Moret et al., 2004). Two main classes of dopaminergic neurons are distinguished in mammals: (*i*) those concentrated in the ventral tegmental area, which target the nucleus accumbens and orbitofrontal cortex, have been implicated in pleasure seeking; (*ii*) those concentrated in the substantia nigra, which target the striatum, have been implicated in movement induction. In primates, dopaminergic activation has been associated with maternal behavior (Champagne, et al., 2004), modulation of aggression (Miczek et al., 2002), and the assessment of the rewarding outcome of ongoing behavior (Satoh et al., 2003; Tobler et al., 2005; Bayer and Glimcher, 2005).

LOCUS COERULEUS. Outside the CNS, noradrenaline is a hormone produced by the adrenal glands and is the synaptic transmitter of the sympathetic branch of the autonomic nervous system. Within the CNS, noradrenaline neurons are concentrated in the locus coeruleus of the brainstem (González and Smeets, 1991, 1993), and their axons are widely distributed

throughout the brain (Bouret and Sara, 2009; Blier and Briley, 2011). Locus coeruleus neurons fire irregularly during quiet wakefulness, and in a sustained manner when aroused or stressed. In primates, activation of the dopamine system has been associated with reward assessment in mnemonic and cognitive functions (Satoh et al., 2003; Bayer and Glimcher, 2005; Tobler et al., 2005). Current research is directed at clarifying the ill-understood interaction among dopaminergic, adrenergic and serotonergic neuronal systems and their exact role in emotional arousal, mood, and affective disposition (Miczek et al., 2002).

The Role of the Hypothalamus in Maternal Altruistic Behavior. The hypothalamus is the "head ganglion" of the "visceral brain" and is involved in the production and release of a great variety of hormones and hormone releasing factors. These secretions regulate growth and regeneration, reproductive maturation, and gastrointestinal functions. The hypothalamus is also involved in affective functions, including the activation of the sympathetic and parasympathetic nervous systems, regulation of the pituitary gland, and the coordination of feeding, sexual activity, and maternal behavior.

THE ROLE OF THE HYPOTHALAMUS IN EMOTIONAL BEHAVIOR. We have considered earlier the imputed role of the hypothalamus in the regulation of hunger and appetite, rage and fear, and amorousness in fishes (Section 3.2.4). The pivotal role of the hypothalamus in these basic emotional functions has been retained and further elaborated in mammals. For instance, there is good evidence from lesion studies that the ventromedial hypothalamic nucleus (VMH) is the "satiety center" in the regulation of hunger in rats (e.g., Anand and Brobeck, 1951). The VMH contains a large population of neurons that respond to glucose levels in the blood (King, 2006) and the obesity of VMH-lesioned rats has been attributed not to indiscriminate overeating but to their hedonism ("finickiness"), the excessive consumption of favored food items (e.g., Teitelbaum, 1955). Hypothalamic lesions also affect the feeding behavior of monkeys (Anand et al., 1955; McHugh et al., 1975; Hamilton et al., 1976) and electric stimulation of the hypothalamus in freely moving monkeys increases food consumption (Lacan et al., 2008). Correspondingly, scanning studies indicate hypothalamic activation during eating in humans (Tataranni et al., 1999; Liu et al., 2000). Among other preserved functions of the monkey hypothalamus are the regulation of arousal, as manifested, for instance, by increases in pulse rate, blood flow, and arterial and venous pressure upon stimulation of the anterior hypothalamus (Forsyth, 1970).

THE ROLE OF THE HYPOTHALAMUS IN MATERNAL BEHAVIOR. The structural and functional organization of the hypothalamus is far more complex in monkeys (Fig. 7-12) than in lower vertebrates and it controls several added functions. We single out below one of these, the regulation of maternal behavior, which includes not only parturition and lactation but also the affective regulation of maternal caregiving. In the rat, maternal behavior is initiated by neurons of the paraventricular nucleus that cause the pituitary release of oxytocin and vasopressin, two peptide hormones that aid uterine contraction and milk ejection (Insel and Harbaugh, 1989). The subsequent affectional manifestations of maternal behavior—such as nursing, grooming and retrieval of the young—also depend on hypothalamic (Olazabal and Fereira, 1997) and medial preoptic area (Numan, 1974) mediation since lesions of either of them in rats interfere with maternal caring for offspring. There are also reports of hypothalamic

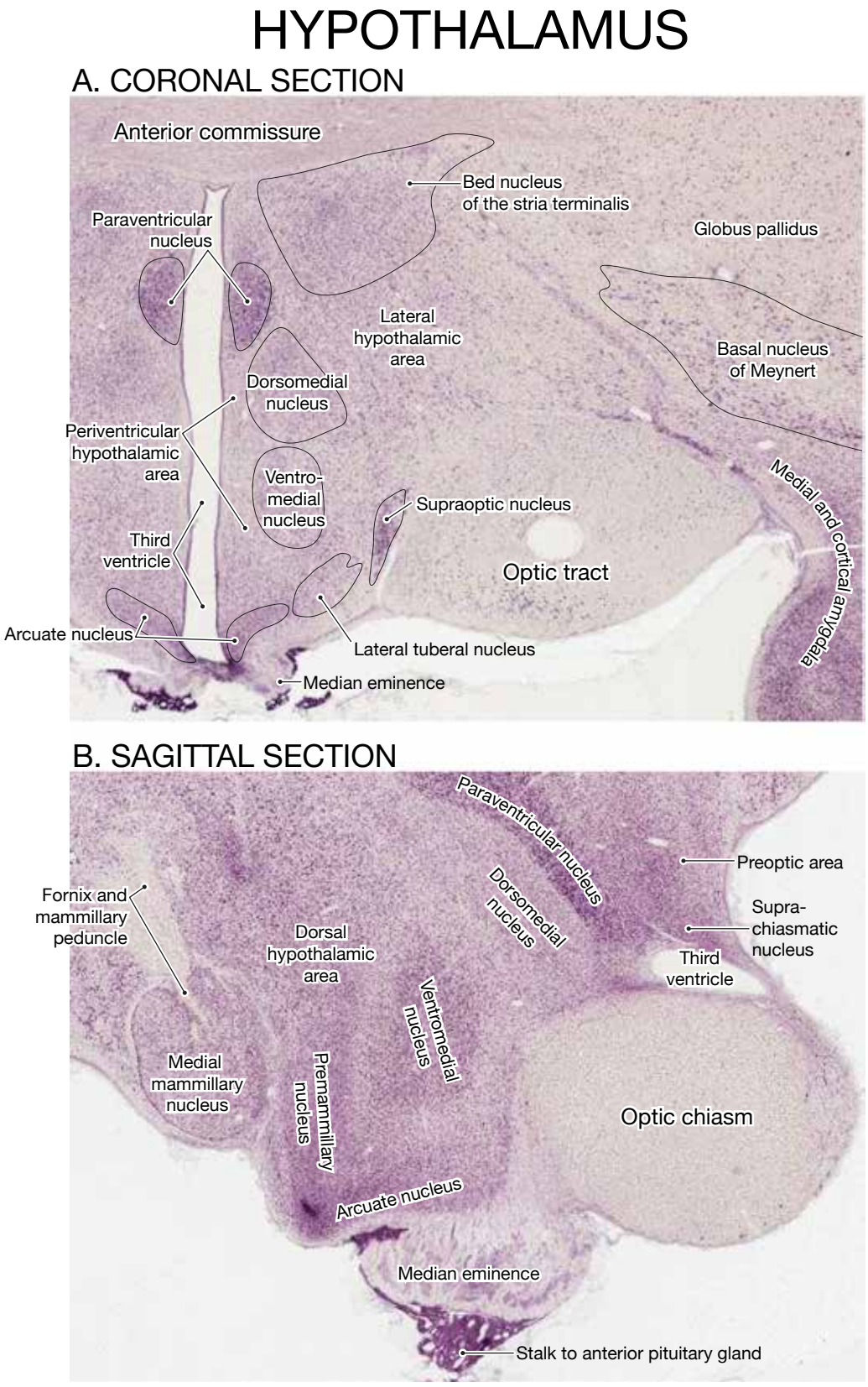


Fig. 7-12. The hypothalamus of the vervet monkey in a coronal (**A**) and sagittal (**B**) section. (From BrainMaps.org.)

involvement in reproductive processes in monkeys. For instance, hypothalamic stimulation in juvenile monkeys induces premature puberty (Plant et al., 1989), and anterior hypothalamic and preoptic lesions interfere with male sexual behavior (Slimp et al., 1978).

THE ROLE OF OXYTOCIN IN MATERNAL AND AFFILIATIVE BEHAVIOR. Peptides with nine amino acids (nonapeptides) are an ancient family of neural signaling molecules. Arginine-vasotocin (AVT) neurons have been identified in the hypothalamus, preoptic area, and septum of lizards (Bennis et al., 1995), and the blood concentration of AVT increases in reptiles when they are ready to lay eggs (Figgler et al., 1989). In mammals, oxytocin (OT) and vasopressin (VP) are synthesized by neurons of the hypothalamic paraventricular and supraoptic nuclei, transported to and stored in the posterior pituitary gland, and released during delivery and in response to suckling by the young. These peptidergic neurons play a major role in parturition and lactation in rodents, such as the rat (Fahrbach et al., 1984; van Leengoed et al., 1987; Pedersen et al., 1992; Engelmann et al., 1999; Ebner et al., 2005; Beery et al., 2008) and the vole (Insel and Shapiro, 1999a, 1992b) as well as in sheep (Kendrick et al., 1987; Keverne and Kendrick, 1992).

OT- and VP-containing neurons and fibers are also present in regions other than the hypothalamus and they have been shown to play an important role in maternal and affiliative behavior (Insel, 2010). The evidence comes mostly from rodents. Adult virgin rats tend to avoid or attack pups but when they are injected with estrogen and OT, they exhibit all facets of maternal behavior, such as licking and retrieving the altricial young (Fahrbach et al., 1984; Pedersen et al. 1992). Differences in the affiliative behavior of two species of voles—the pair-bonding (monogamous) ones that live together in burrows with their offspring, and the solitary ones that live by themselves—have been attributed to different levels of OT/VT activity (Shapiro and Insel, 1990; Wang et al., 1994; Insel, 2010). When vasopressin is administered to a male of the pair-bonding species that has not yet mated, the treatment induces it to become attached to the female it has mated with (Winslow et al., 1993). Variations in the quality of maternal behavior in rats have been correlated with oxytocin levels. "Good" mothers, those that provide high level of nursing care to their young, have higher concentration of oxytocin receptors than mothers that are less caring (Francis et al., 2000; Cameron et al., 2008). Interestingly, there may be a synergistic relationship between oxytocin and dopamine activity as individual differences in maternal behavior correlate with dopamine levels in the nucleus accumbens (Champagne et al., 2004; Shahrokh et al., 2010; Douglas, 2010).

OT/VP neurons and fibers are also present in several limbic regions of the monkey brain, including the septum, the amygdala, the hippocampus, and the bed nucleus of stria terminalis (Caffé et al., 1989; Wang et al., 1997). VP receptor sites have been identified in monkeys in the septum, amygdala and subiculum, and in the cingulate, piriform, entorhinal and prefrontal cortices (Young et al., 1999). As in rodents, oxytocin in monkeys plays a role in affiliative behavior. Pair-bonded tamarin monkeys with higher oxytocin levels cuddle and groom each other more, and are more sexually active than those with lower oxytocin levels (Snowdon et al., 2010). Cerebrospinal fluid oxytocin levels are higher in the less aggressive and more socially adept mother-reared rhesus monkeys than in their more aggressive and less socially adept nursery-raised peers (Winslow et al., 2003). Similarly, oxytocin administration in humans has

been associated with increased generosity and trust in others (e.g., Kosfeld et al., 2005; Zak, 2007). How do these peptides produce the emotions that are associated with prosocial affects? We assume that they do so by turning on and off, and facilitating or inhibiting higher-order limbic brain mechanisms that generate affects (see below).

The Role of the Amygdala in Vigilance and Defensive Behavior. The amygdala is an ancient subcortical structure that has been identified in the forebrain of fishes (Section 3.2.4), amphibians (Section 4.1.2; Figs. 4-11 to 4-13), and reptiles (Section 4.2.2; Fig. 4-24) and shown to play a central role in fear and rage reactions. The amygdala is well developed in mammals, and it is of great significance that it has evolved in primates in parallel with the neocortex, both in terms of its size and structural complexity (Stephan et al., 1987).

STRUCTURE OF THE AMYGDALA. The simian amygdala is embedded in the anterior portion of the medial temporal cortex and is composed of about a dozen nuclei with different cellular organization and connections (Fig. 7-13). Most prominent among these are the accessory basal, basal, central, cortical, lateral, and medial nuclei (Amaral et al., 1992). The lateral, basal, and accessory basal nuclei are, respectively, 32, 39 and 39 times lager in monkeys than in rats, the central and medial nuclei only 8 and 4 times so, and neuronal packing density was between 2.4 and 3.7 times lower in the monkey than in the rat (Chareyron et al., 2011). As a limbic system structure, the monkey amygdala has extensive connections with both paleocephalic structures involved in visceral regulation and neocortical areas involved in perceptual and mnemonic processes. These include the following: connections with the olfactory (Carmichael et al., 1994), gustatory (Hopkins, 1975; Mehler, 1980; Price and Amaral, 1981), visual (Herzog and Van Hoesen, 1976, 1981; Aggleton et al., 1980; Cheng et al., 1997; Iwai and Yukie, 1987; Amaral et al., 2003), and auditory (Yukie et al., 2002) sensory systems; connections with paleocephalic structures such as the periaqueductal gray, the midbrain reticular formation,

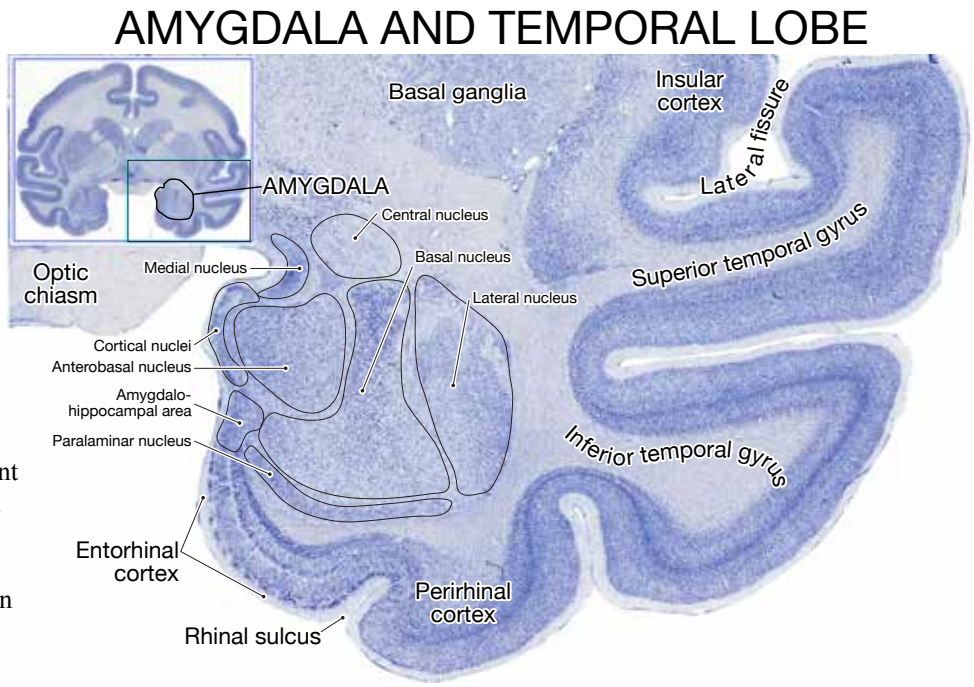


Fig. 7-13. The amygdala and adjacent entorhinal cortex and perirhinal cortex, in a coronal section of the macaque forebrain (insert). (From BrainMaps.org.)

and several hypothalamic nuclei, (Jongen-Rêlo and Amaral, 1998; Kalin et al., 2004; Ebner et al., 2005); connections with limbic structures, such as the nucleus accumbens and the ventral striatum (Russchen et al., 1985; Friedman et al., 2002; Fudge et al., 2002, 2004); and connections with the anterior insular cortex (Mufson et al., 1981), the temporal cortex (Seltzer and Pandya, 1978; Aggleton et al., 1980; Turner et al., 1980; Van Hoesen, 1981; Galaburda and Pandya, 1983; Aggleton and Mishkin, 1984; Amaral and Price, 1984; Stefanacci et al., 1996; Cheng et al. 1997; Ghashghaei and Barbas, 2002), and the prefrontal and orbitofrontal cortices (Porrino et al., 1981; Amaral and Price, 1984; Carmichael and Price, 1995a). The temporal cortical areas preferentially project to the lateral nucleus of the amygdala, the frontal cortical areas to the basal and accessory basal nuclei (Stefanacci and Amaral, 2002).

THE ROLE OF THE AMYGDALA IN DEFENSIVE BEHAVIOR. It was shown some time ago that electrical stimulation of the amygdala in anesthetized cats, dogs and monkeys triggers various visceral and autonomic reactions, including changes in blood pressure and heart rate, micturition, and gastric motility (Kaada, 1951, 1972). Another effect of amygdaloid stimulation is pupillary dilation and orienting movements of the external ear (Ursin and Kaada, 1960). Subsequent experiments carried out in wakeful animals produced similar results (Kaada et al., 1954). In line with this indirect evidence of the involvement of the amygdala in emotional arousal, early lesion studies showed that its destruction transforms aggressive laboratory monkeys into anxious, submissive animals (Rosvold et al., 1954) and also abolishes their fear of snakes and unfamiliar objects (Weiskrantz, 1956) and reduced emotionality (Aggleton and Passingham, 1981). Similar taming effects were also observed following amygdalectomy in free-ranging monkeys (Kling, 1972). Many of the operated animals were attacked by peers, became socially isolated, and eventually died of their wounds or malnutrition. Subordination to peers was also observed in monkeys subjected to amygdalectomy during infancy (Thompson et al., 1977).

More recently, the technique of selective neurotoxic lesions has been used to study the behavioral effects of amygdalectomy, and these have confirmed most of the earlier observations (Meunier et al., 1999; Kalin et al., 2001, 2004). In a study in which lesioned and normal rhesus monkeys were paired to observe their dyadic interaction, the operated animals were judged to be less aggressive than their peers and also less sociable (Emery et al., 2001). But when two operated and two normal monkeys were brought together their interrelation was somewhat different (Machado et al., 2008). The normal monkeys affiliated preferentially with their mild-mannered operated peers, enhancing the groups' amicable relationship. Another finding has been that amygdalectomized monkeys awake from sleep less often than do their normal peers (Benca et al., 2000). And, according to a developmental study, amygdalectomy does not appreciably affect the relationship of monkeys with their mother as infants, but when they get older, they do not join her when threatened or meet her in a group (Bauman et al., 2004a). The authors interpreted these findings to indicate that amygdalectomy reduced the anxiety that makes normal juveniles seek their mother's protection when uncomfortable. In summary, the observed changes in the social behavior of amygdalectomized monkeys can be interpreted to mean that the principal function of the amygdala is social vigilance, making normal animals watchful and ready to defend their self-interest. Monkeys with amygdala lesions have reduced motivation to obtain food in a social setting and reduced finickiness in food selection. Lesioned monkeys accessed preferred food items less often than their normal

peers (Bauman et al., 2004b), and readily consumed unpalatable food when both palatable and unpalatable food was available (Machado et al., 2010).

THE ROLE OF THE AMYGDALA IN FORAGING BEHAVIOR. As an ancient neural mechanism, the function of the amygdala is to allow the animal to recognize external stimuli that signal danger, and trigger such defensive reactions as freezing, hiding, fleeing, or such offensive reactions as threat displays and fighting. In lower vertebrates, offensive and defensive responses are triggered by innately recognized intense stimuli, such as the odor of a predator, the noise generated by an intruder or the shadow it casts. We presume that these discriminations are mediated by paleocephalic mechanisms. The elaborated amygdala of mammals has become a more sophisticated vigilance system. By virtue of its extensive connections with neencephalic perceptual and mnemonic mechanisms, the mammalian amygdala can use individual experience to better assess what is safe and what is dangerous in different behavioral situations. It has been known for some time that amygdala lesions in mammals interfere with fear conditioning to auditory and visual stimuli (Davis, 1992; LeDoux, 1996) and that single neurons in the monkey amygdala distinguish stimuli on the basis of their affective associations (Nishijo et al., 1988; Paton et al., 2006).

One of the learning-based functions of the monkey amygdala is the regulation of foraging behavior. Being largely omnivorous, monkeys have to carefully discriminate what they ingest. Studies using the technique of recording neuronal activity in behaving monkeys indicate that the amygdala is involved in the gustatory and visual discrimination of nutrients on the basis of their novelty and familiarity, and past experience with their palatability and hedonic quality (Nishijo et al., 1988; Wilson and Rolls, 1993; Scott et al., 1993; Yan and Scott, 1996; Karadi et al., 1998). Amygdala neurons that respond to palatable food change their discharge pattern when the food is rendered unpalatable (Ono et al., 2000). This is in line with lesion studies which showed that the operated animals become deficient in discriminating nutrients on the basis of their reward value (Murray et al., 1996) and display reduced satiation effects (Málková et al., 1997).

THE ROLE OF THE AMYGDALA IN RECOGNIZING PEERS AND THEIR EMOTIONAL EXPRESSIONS. Members of a hierarchically organized monkey troop know one another and their status within the group, and communicate their current mood, desires and intentions by vocalization, gaze direction and facial expressions. The simian amygdala contains neurons that selectively respond to a monkey or a human face (Rolls, 1984; Leonard et al., 1985; Gothard et al., 2007). It has been suggested that the lateral amygdala mediates fear conditioning and extinction to simple stimuli, whereas the basal amygdala mediates fear responses to more complex stimuli, such as faces (Parkinson et al., 2001; Yaniv et al., 2004). Some amygdala neurons discriminate the identity of a monkey face, others the particular facial expression of any monkey, particularly a threatening face (Fig. 7-14). There are also amygdala neurons that are selective for gaze direction (Hoffman et al., 2007) and those that are selective for vocal expressions, such as screaming or cooing (Kuraoka and Nakamura, 2007). Corresponding to these findings in monkeys, patients with amygdala lesions are deficient in recognizing facial expressions of fear and anger (Adolphs et al., 1994, 1995; Young et al., 1995, 1996; Calder et al., 1996). And scanning studies indicate that the amygdala is activated in normal human subjects during

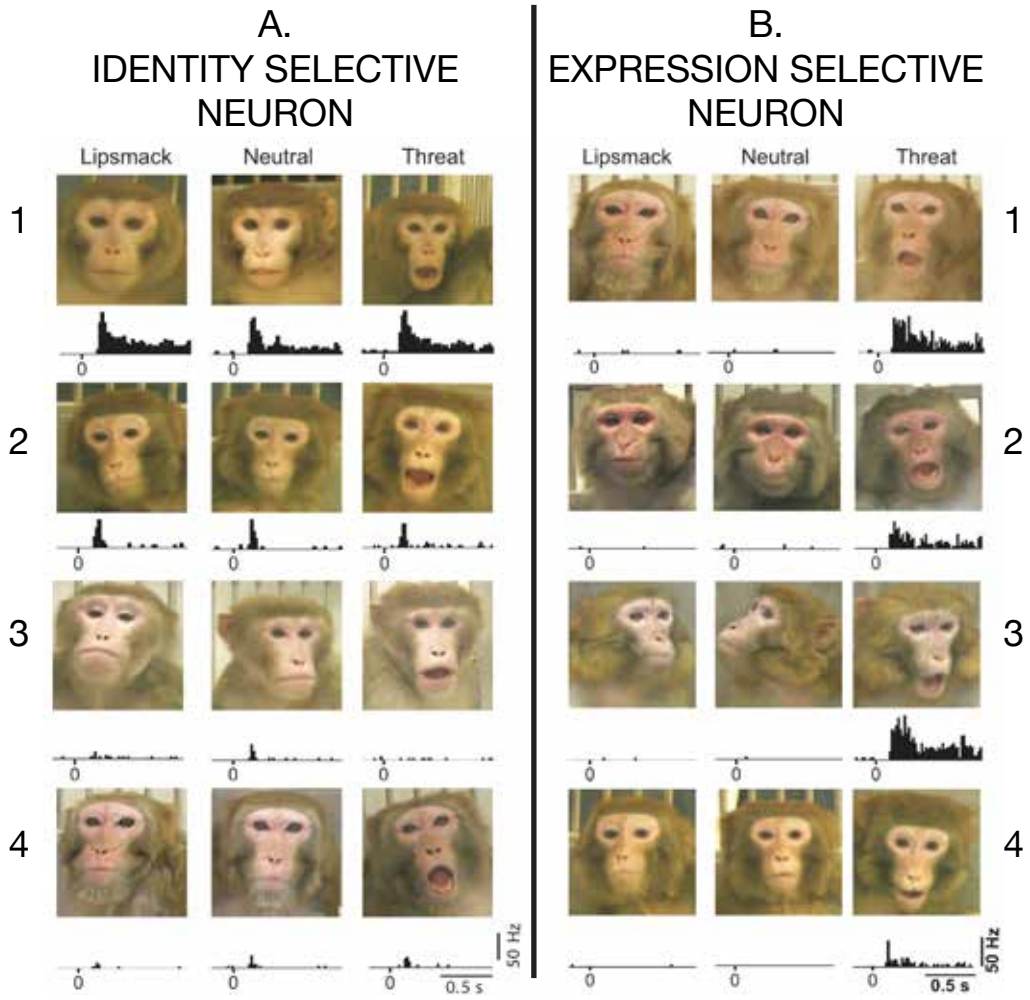


Fig. 7-14. **A**. An amygdala neuron discharging briskly in response to the image of a particular monkey face, irrespective of its facial expressions (row 1). **B**. Another amygdala neuron discharging briskly to the different facial expressions of the same monkey (right column in rows 1-4). (After Gothard et al., 2007.)

aversive conditioning and extinction (e.g., LaBar et al., 1998; Phelps et al., 2004) or when viewing facial expressions of emotions (Irwin et al., 1996; Lane et al., 1997). We may conclude that the primate amygdala, aided by its extensive paleocephalic and neencephalic connections, plays a major role in the affective-cognitive regulation of behavioral vigilance, the vital task of recognizing evident and subtle cues of danger from a variety of sources: food that is safe and unsafe to consume, the identity of individuals, visual facial expressions, and vocal emotional expressions.

The Role of the Nucleus Accumbens in Hedonistic Behavior. The nucleus accumbens is a component of the ventral striatum and experimental studies indicate that, together with other constituents of the limbic system, it plays a major role in motivating the individual to engage in activities that produce affective gratification (rewards).

STRUCTURE OF THE NUCLEUS ACCUMBENS. The mammalian nucleus accumbens is composed of two parts, a core and a shell. As studies carried out mostly in rats indicate, both core and

shell contain predominantly medium sized spiny neurons with similar physiological properties but different connections (Záborsky et al., 1985; Zahm and Heimer, 1988; Voorn et al., 1989; Sesack and Grace, 2010). Both core and shell get input from limbic structures: the shell from the hippocampal formation (subiculum), the parvocellular basal amygdala, and the dopaminergic neurons of the ventral tegmental area; the core from the magnocellular component of the basal amygdala, the insular cortex, and the substantia nigra. There are differences in the dopamine innervation of core and shell (Deutch and Cameron, 1992). The nucleus accumbens also receives glutamatergic input from the prefrontal cortex (Berendse et al., 1992; McFarland et al., 2003; Kalivas et al., 2005). Efferents of the nucleus accumbens target the ventral pallidum, which projects to the motor thalamus, and thus the nucleus accumbens appears to be the visceral component of the striatal feedback loop. The crescent shaped nucleus accumbens of monkeys (Fig. 7-15) has similar properties to those found in humans (Meredith et al., 1996).

THE ROLE OF THE NUCLEUS ACCUMBENS IN HEDONIC MOTIVATION. Since the nucleus accumbens is closely connected with the core structures of the limbic system and also the prefrontal cortex, it can modulate organized instrumental behavior to motivate rewarding ends (Goto and Grace, 2008; Gruber, 2009; Stuber, 2009). It can make hedonic motivation, the seeking and maximizing of pleasure, exert a powerful influence on what activities the animal chooses to engage in and what choices it makes when those are available. Stimulation of

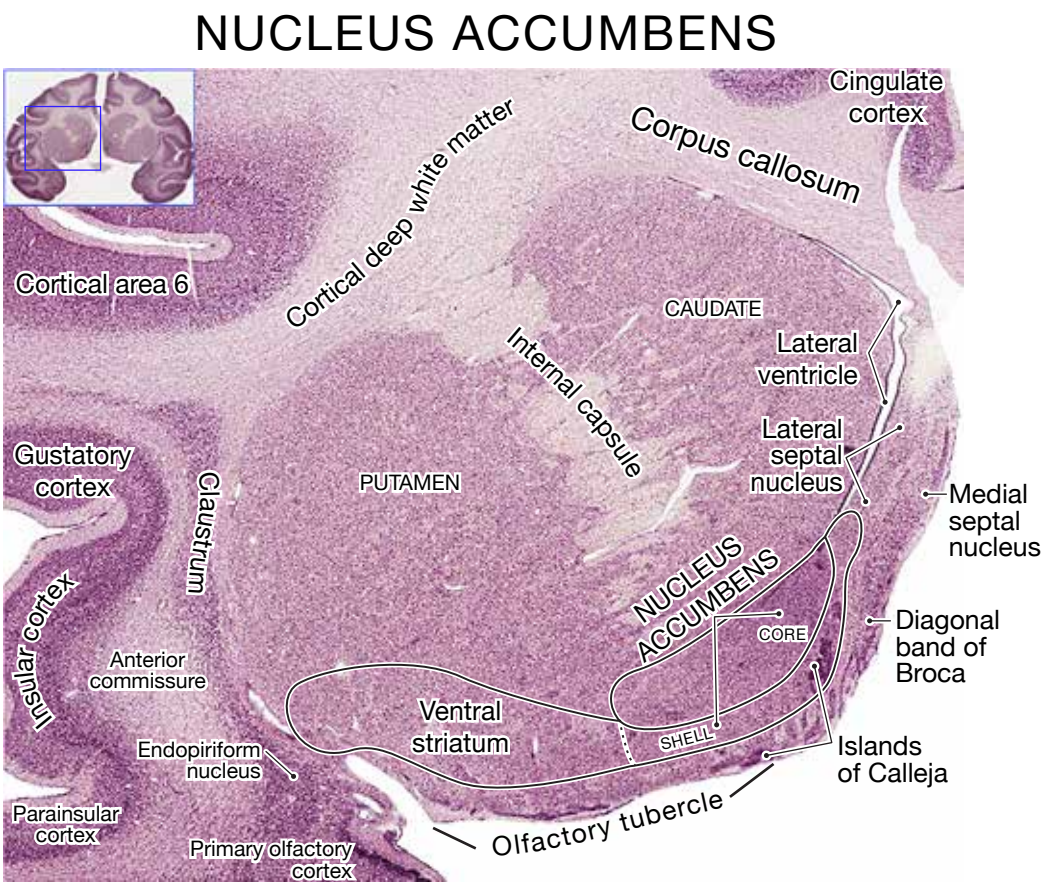


Fig. 7-15. The nucleus accumbens and the striatum in a coronal section of the macaque brain. (Modified, after BrainMaps.org.)

the nucleus accumbens in monkeys apparently produces pleasurable feelings. Monkeys with electrodes implanted into the nucleus accumbens engage in self-stimulation and will work to receive such stimulation (Bichot et al., 2011). It is currently unclear as to what role the core and shell play in triggering pleasurable affects. There is a report (Ambroggi et al., 2011) that, in the rat, selective inactivation of afferent input to the core, but not to the shell, decreases responding to a reward-predictive cue; and inactivation of the shell, but not the core, increases responding to the unrewarded cue. There is also a report that the shell and the core play different roles in tracking a rat's need for and preference for salt (Loriaux et al., 2011). It is also unclear to what extent the nucleus accumbens regulates specific behaviors or acts as a general pleasure-seeking mechanism. Its involvement in food selection is suggested by the finding that, acting on different dopamine receptors, different input channels to the nucleus accumbens generate either desire for food or its avoidance (Richard and Berridge, 2011). The formation of affectionate bonds between prairie voles has been linked to dense concentration of oxytocin receptors in the nucleus accumbens (Insel and Shapiro, 1992a). The injection of an oxytocin antagonist into the nucleus accumbens blocks mating-induced partner preference in voles (Gingrich et al., 2000; Young et al., 2001). The fostering of affectionate bonds may depend on the joint action of dopamine and oxytocin (Liu et al., 2003). In rats, heightened maternal care (licking and grooming of pups) has been associated with increased dopamine activity in the nucleus accumbens (Champagne et al., 2004; Shahrokh et al., 2010).

THE NUCLEUS ACCUMBENS AND COMPULSIVE PLEASURE SEEKING. Studies in behaving rats (Kalivas and Duffy, 1990; Kalivas et al., 2005; Willuhn et al., 2009) and monkeys (Lyons et al., 1996; Porrino et al., 2002) have shown that the administration or consumption of psychoactive drugs (alcohol, cocaine, etc.) increase the concentration of dopamine in the nucleus accumbens. The same has been found in human drug addicts, individuals with the compulsion to use legal (alcohol, nicotine) or illegal (heroin, amphetamine, etc.) mood altering drugs despite their awareness of its harmful personal and social consequences (Drevets et al., 2001; Haber and Knutson, 2010). In both animal and man, alcohol, cocaine, heroin, and amphetamine abusers have lower levels of dopamine receptor binding sites than non-abusers (Volkow et al., 1999; 2004). And low ranking monkeys have a lower concentration of striatal dopamine receptors than high-ranking monkeys (Grant et al., 1998; Nader and Czoty, 2005). Social stress may be a risk factor for developing drug dependence. According to one recent report, ablation of the nucleus accumbens in human alcoholics alleviates their craving for alcohol, and reduces their symptoms of irritability and depression (Wu et al., 2010). Finally, stimulation of the nucleus accumbens has been reported to alleviate refractory obsessive-compulsory disorder (Denys et al., 2010) and depression (Kuhn et al., 2011) in human patients.

7.2.3. The Allocortical Component of the Limbic System: The Hippocampus. In contrast to the idea that the hippocampus is fundamentally a mnemonic and cognitive mechanism, we argue below that, as a component of the limbic system, its primary function is a combined motivational and regulatory one. This interpretation is based, to begin with, on a consideration of the connections of the hippocampus with other brain structures. On the one hand, the hippocampus is closely linked with the hypothalamus and the septum, two ancient brain mechanisms involved in visceral and behavioral energy mobilization. On the other hand, it has close connections with the phylogenetically more recent perceptual and mnemonic mechanisms

of the ventromedial temporal cortex. More specifically, we will argue that the dual function of the hippocampus is the initiation of exploratory behavior, the overcoming of the fear of the unknown and venturing out into external world, and the regulation of that behavior by using experience to construct a map of the layout of the environment and readily distinguish within it what is novel and what is familiar, what has to be treated with circumspection and what can be taken for granted.

Organization of the Hippocampus. The mammalian hippocampus is a unique allocortical structure, composed of the interlocked Ammon's horn and dentate gyrus (Fig. 7-16). The principal neuronal elements of Ammon's horn are the large pyramidal cells with long axons. The principal constituents of the dentate gyrus are the densely packed smaller granule cells with shorter axons that terminate on the pyramidal cells within the hippocampus. The hippocampus has extensive connections with the septum (Lewis and Shute, 1967; Swanson, 1978) and the hypothalamic mammillary body (Wyss et al., 1979), two structures implicated in visceral and autonomic regulation. It also has connections with the diagonal band of Broca (Siegel et al., 1974; Gaykema et al., 1991), which has close connections with the olfactory bulb, and also receives a large adrenergic input from the locus coeruleus (Swanson et al., 1987). The principal reciprocal connection of the hippocampus with the cerebral cortex is by way of components of the ventromedial temporal region, including the subiculum, the parahippocampal gyrus, the perirhinal cortex, and the entorhinal cortex. By way of these structures, the hippocampus receives input from the neocortical association areas (Insausti et al., 1987; Witter, 1993; Suzuki, 1996). Hence, the hippocampus may be considered a limbic interface that has extensive connections with both subcortical visceral-autonomic mechanisms and neocortical perceptual-mnemonic mechanisms.

Theories of Hippocampal Function. Ever since a single clinical case (patient HM) indicated that the intended bilateral surgical destruction of the hippocampus produces a profound and

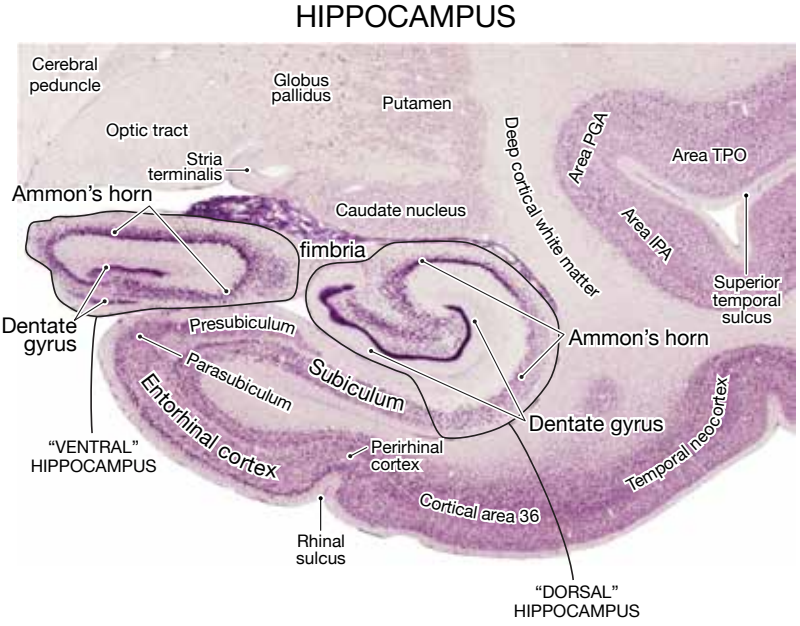


Fig. 7-16. The hippocampus in a coronal section of the macaque brain. (Its relative size and location is shown in Fig. 7-17.)
(Modified, after BrainMaps.org.)

permanent anterograde amnesia (Scoville and Milner, 1957), the hypothesis became popular that it plays a major role in memory storage. While HM could recollect what he experienced before surgery and could engage in a meaningful conversation after surgery, he could not consolidate new experiences into long-term memories.

THE ROLE OF THE HIPPOCAMPUS IN MEMORY AND LEARNING. Although it was questioned from the outset whether HM's amnesia was due to hippocampal damage *per se* (indeed, a recent magnetic resonance imaging study revealed that most of his entorhinal cortex was also destroyed; Corkin et al., 1997), the report prompted a flurry of experimental investigations, mostly in rats and monkeys, regarding the role of the hippocampus in mnemonic functions. Some studies suggested that, indeed, large hippocampal lesions produce learning deficits that could be attributed to amnesia for what has been learned before the operation but other studies failed to demonstrate such effects. For instance, normal rats placed in a T-maze randomly explore the right or left alleys on the first trial but will choose with a high degree of probability the alternate arm on their second trial, presumably because they can remember which arm they have already explored. Rats with extensive hippocampal lesions do not display this tendency for alternation (Roberts et al., 1962; Means et al., 1971). Similarly, large hippocampal lesions produce deficits in passive avoidance learning. Getting shocked when approaching a baited cup, or stepping down onto an electrified floor, normal rats will predictably withhold making that response on the next trial; but rats with large hippocampal lesions display deficits in this avoidance response (Kimura, 1958; Isaacson and Wickelgren, 1962). Both rats (Swanson and Isaacson, 1967) and monkeys (Douglas and Pribram, 1966) tend to perseverate in responding to a cue when that no longer produces a reward and fail to switch in a two-choice situation when the cues are reversed (Kimble and Kimble, 1965). On the other hand, it has also been found that rats with hippocampal lesions readily learn simultaneous two-choice discrimination tasks (Kimble, 1963). Likewise, monkeys suffer little deficit in such tasks following ablation of the hippocampus (Douglas and Pribram, 1966). Differences in the size and location of lesions, and the involvement of other brain structures made an interpretation of these findings difficult.

More recently, the role of the hippocampus in memory processes has been reinvestigated in monkeys with isolated (excitotoxic) hippocampal lesions. These studies indicate that destruction of the hippocampus that spares adjacent structures produce little or no deficits in a simple learning tasks, such as object and place associations (Meunier et al., 1993, 1996; Baxter and Murray, 2001). That suggests little role for the hippocampus in memory consolidation. Nor does isolated hippocampal lesions produce deficits in such tasks as delayed non-matching to sample (Murray and Mishkin, 1998) or one-trial learning (Málková and Mishkin, 2003). These findings rule out a major role for the hippocampus in working memory. However, isolated hippocampal lesions do produce mild to severe learning deficits in more complex choice-based tasks that require the animal to play attention to a series of learned cues. These tasks include: (*i*) the conditional selection of one of two visual cues depending on the pattern of the background (Ridley et al., 2001); (*ii*) mastering a delayed nonmatching-to-sample task where the monkey has to recollect a rule (nonmatching) as well as heed cues that serve as instructions of what choices it has to make in a particular trial (Beason-Held et al., 1999; Zola et al., 2000; Alvarado et al., 2002; Nemanic et al., 2004); and (*iii*) learning to respond

with different movements to different cues (Brasted et al., 2003). Moreover, severe learning deficits were obtained in monkeys in which hippocampal lesions were combined with lesions of the adjacent perirhinal and entorhinal cortices (e.g., Meunier et al., 1993, 1996; Eacott et al., 1994; Buckley and Gaffan, 1998a, 1998b; Murray and Bussey, 1999; Chavoix et al., 2002; Buckmaster et al., 2004). These findings suggest that temporal lobe structures with which the hippocampus is intimately connected play a more important role in mnemonic functions than does the hippocampus itself. (We discuss in detail the involvement of the temporal cortex in mnemonic functions in Section 7.3.2.)

THE ROLE OF THE HIPPOCAMPUS IN BEHAVIORAL INHIBITION. Based on a series of experimental results, we proposed some time ago that the function of the postnatally-developing hippocampus is to inhibit the hyperactivity of juveniles and turn them into less exuberant and more attentive and discriminative adults (Altman et al., 1973; Bayer et al., 1973). In these studies we exposed rat pups to low-level X-irradiation during the formation of the postnatally-generated dentate granule cells, and prevented 85 percent of them to form. X-irradiation selectively kills the radiosensitive precursors of dentate granule cells. These rats with a miniscule dentate gyrus behaved much like rats do following ablation of the entire hippocampus. They were hyperactive, showed random behavior in a T-maze (revisiting the maze alley that they have already explored before), and displayed deficits in passive avoidance learning (stepping down from a pedestal to the floor where they previously got shocked). In a subsequent study we found that the X-irradiated rats showed no deficits in the acquisition and reversal of easy visual and tactile discrimination tasks but were handicapped when the discriminations were made more difficult (Gazarra and Altman, 1981). Based on these mixed findings we suggested that hippocampus does not function as a memory consolidator *per se* but rather as an attention facilitator. During its postnatal development, the hippocampus inhibits juvenile hyperactivity and turns maturing animals into more attentive and less active adults. We suggested that adult rats with granule cell hypoplasia behave like humans do with attention deficit disorder; their deficits in one-trial learning and difficult discrimination tasks are due to their inattentiveness. This presumed attentional deficit of the experimental animals was supported by reports that these rats do not become distracted by novel stimuli while engaged in an experimental tasks (Wickelgren and Isaacson, 1963; Hendrickson et al., 1969; Cohen and Swenson, 1970; Gustafson, 1975). Likewise, hyperactive gerbils with hippocampal lesions examine novel objects placed in their cages less than do normal animals (Glickman et al., 1970).

THE ROLE OF THE HIPPOCAMPUS IN SPATIAL ORIENTATION. Opposing the theory of attentional deficits, Nadel et al. (1975) and O'Keefe and Nadel (1978) proposed that the principal function of the hippocampus is spatial learning, i.e., the construction of "cognitive maps" of the layout of the environment. O'Keefe and Dostrovsky (1971) made the important discovery that some hippocampal neurons, called "place cells," increased their firing rate when a freely moving rat reached a particular spot in the testing arena. Later it was found that different hippocampal place cells became active as the rat moved to different locations (Wilson and McNaughton, 1993) and that some place cells fired in relation to the animal's distance from the target that it was trying to reach (Gothard et al., 1996; Redish, 1999). Place cells have also been identified in the hippocampus of monkeys (Ono et al., 1991; Hori et al., 2003) and man (Ekstrom et al. 2003). These hippocampal neurons were also characterized as "spatial view cells" because

they become selectively active either when a monkey orients itself toward a target or moves toward it (Robertson et al., 1998; Georges-François, et al., 1999; Rolls, 1999). However, the idea that the hippocampus was specifically a "cognitive" mechanism was difficult to reconcile with other findings. For instance, when rats are passively moved about in a testing area, the selectivity of place cells is attenuated or abolished (Foster et al., 1989). The same has been observed in monkeys: whereas place cells became active when restrained monkeys moved themselves in a cab from one location to another, that activation did not occur when the experimenter moved the monkeys over the same locations (Nishijo et al., 1997; Ono and Nishijo, 1999). The same has been observed when spatial translocation took place in a virtual rather than a real environment (Hori et al., 2003). That is, hippocampal neuronal activation appears to be associated with self-motivated locomotion in space rather than the perception of one's location in a particular region (Vanderwolf, 2001). Indeed, it has been found that maximal place cell activation occurs when monkeys freely move about in a three-dimensional environment (Ludvig et al., 2004).

The Role of the Hippocampus in the Motivation and Regulation of Exploratory Behavior. We propose that while hippocampal functioning requires memory and learning—i.e., the ability to distinguish between familiar and unfamiliar objects in the environment and their spatial location—the specific function of the hippocampus is not memory consolidation or cognitive processing but the instigation and coordination of exploratory and investigative behavior. We offer (*i*) phylogenetic, (*ii*) ontogenetic, (*iii*) anatomical, and (*iv*) behavioral support for this interpretation.

PHYLOGENETIC CONSIDERATIONS. A homologue of the hippocampus has been described in lower vertebrates, and we illustrated that in reptiles (Fig. 4-26). However, the presumptive reptilian hippocampus does not have the morphological features of the mammalian hippocampus. In contrast, the distinctive cellular organization of the mammalian hippocampus is fully developed in basal mammals, such as the common shrew (Fig. 7-17A). But here is a paradox. The hippocampus of the shrew extends from dorsal to ventral alongside the entire extent of the neocortex. The hippocampus of primates shifts to a smaller medial position in a prosimian (Fig. 7-17B), and an even smaller ventromedial position in a simian (Fig. 7-17C). The relative diminution of hippocampal size (which continues in apes and man) is associated with the great dorsal and lateral expansion of the neocortex that shifts the rhinencephalon from lateral, to ventrolateral, to ventromedial positions. As a result, the hippocampus becomes embedded in the ventromedial temporal cortex in higher primates. Since the advance in mnemonic and cognitive processing power of primates is correlated with neocortical expansion but the hippocampus does not expand in parallel with it (as, parenthetically, the neostriatum and the neocerebellum do), it seems unlikely that it could be a principal mechanism for the increased mnemonic and cognitive abilities of higher primates.

ONTOGENETIC CONSIDERATIONS. The hippocampus is one of the few mammalian brain regions in which the bulk of granule cells, what we have called microneurons, are generated postnatally (Altman and Das, 1965). Another important brain region is the cerebellum where the production of microneurons (granule, basket and stellate cells) continues through infancy, exactly until the time that rats become competent runners and climbers and are ready to be

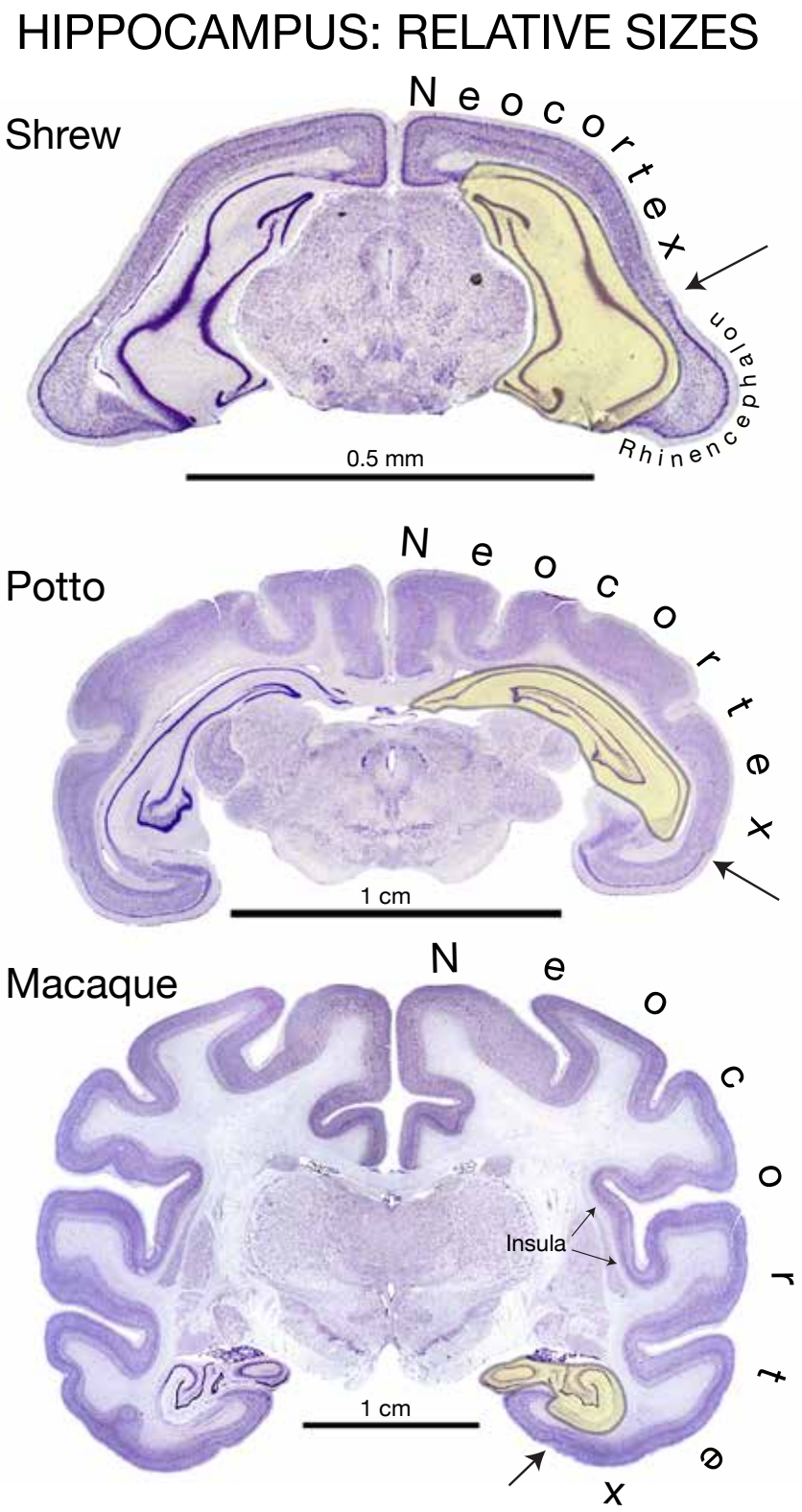


Fig. 7-17. The hippocampus (*yellow*) in a basal mammal (Shrew), a prosimian (Potto), and a monkey (Macaque). Note the decrease in the relative size of the hippocampus, and its displacement with the rhinencephalon ventromedially, in the macaque. *Arrows* indicates the rhinal sulcus, border of the rhinencephalon. (Shrew and potto, after BrainMuseum.org; macaque, after Brainmaps.org.)

weaned (Altman and Bayer, 1997). Microneurons are cortical cells with locally arborizing short axons that connect with the prenatally-generated macroneurons with long axons. They function as excitatory or inhibitory components of feedback loops and play a major role in the normal functioning of the brain structure in which they are embedded. As we noted earlier, adult rats with hippocampal granule cell hypoplasia behave much like animals do without a hippocampus. There is some evidence that preweanling rats devoid of the full complement of granule cells, likewise, behave as if they lack a functional hippocampus. Preweanling rats display little evidence of spontaneous alternation, passive avoidance learning or attention to novel stimuli (Amsel and Stanton, 1980; Lobaugh et al., 1985). If, as we argue, the functioning of the hippocampus is the instigation of exploratory behavior, delaying hippocampal maturation until the nestlings can feed and defend themselves is an adaptive feature of behavioral maturation. (Lactating rats are known to retrieve their young when they stray from the nest.)

ANATOMICAL CONSIDERATIONS. In basal mammals with a small neocortex, there is a close linkage between the hippocampus and the olfactory apparatus. Indeed, it was assumed by the early anatomists that the hippocampus is a component of the olfactory system (Ariëns Kappers et al., 1936). While that assumption was justly criticized by Brodal (1947), it remains a fact that olfactory stimulation triggers short-latency evoked potentials in the hippocampus of rats, cats and monkeys (Cragg, 1960; Yokota et al., 1970; Wilson and Steward, 1978), and odors and sniffing elicit beta and gamma waves in the rat dentate gyrus (Vanderwolf, 1992, 2001). The exploration of novel objects is principally characterized in rats by sniffing and whisker movements (Berlyne, 1955; Welker, 1964). However, cognition also requires visual perception and the consolidation of what is perceived in memory. The expansion of the visual and haptic projection and association areas in monkeys is of great importance because of their role in the extraction of information about the detailed and multifarious properties of the objects they encounter in their environment. But the hippocampus is not at the hub of these information-processing channels and stations, and it becomes progressively distanced from them in the ascending order of primates as it is translocated from the entire medial convexity of the cerebral hemispheres to the ventromedial temporal cortex (Fig. 7-17). In dexterous primates, the exploration of the detailed visuo-haptic properties of objects is the function of the neocortex.

BEHAVIORAL CONSIDERATIONS. Venturing into outside world is an extremely hazardous undertaking, particularly for small mammals that are easy targets of raptors and carnivores. Because their high rate of metabolism forces small mammals to feed constantly, they have to be on the move to find safe routes from one foraging site to another, know how to avoid dangerous areas, find escape routes and hiding places when threatened, and do that swiftly and effectively. When a rat is placed into a novel environment, it becomes extremely anxious, as indicated by its freezing, urinating and defecating. As time passes, the rat becomes gradually habituated to the new environment and then starts to explore it (Berlyne, 1963). We suggest that the principal function of the hippocampus, as a limbic activating mechanism, is to overcome fear by motivating the animal to explore its environment. To do that economically and safely, the rat has to have a good internal map of the layout of its environment and be able to readily distinguish what it is familiar and novel. With regard to the role of the hippocampus in that function, we hypothesize that the pyramidal cells of Ammon's horn, which interconnect the

hippocampus with the septum and the hypothalamus, play a major role in the regulation of behavioral activation with reference to the vital needs of the organism. Indeed, there is some evidence that food deprivation enhances the hyperactivity of rats with hippocampal lesions (Tracy et al., 2001). The granule cells of dentate gyrus, which receive input from the entorhinal cortex (embedded in the medial temporal cortex), in turn, regulate hippocampal activation on the basis of perceptual and mnemonic information.

In summary, because the monkey hippocampus has only indirect connections with the high-resolution neencephalic sensory systems, it is not suited to be a mechanism for the appreciation of the detailed features and properties of the environment and the objects it contains. Rather, the hippocampus appears to be a first-responding orienting mechanism and novelty detector, enabling an animal to swiftly recognize the layout of the place it explores and distinguish the objects it contains whether familiar or unfamiliar, dangerous or safe, rewarding or uninteresting. Moreover, we postulate that the hippocampus plays a greater role in the behavior of furtive basal mammals than it does in higher primates furnished with more advanced perceptual, mnemonic and cognitive mechanisms.

7.2.4. The Neocortical Components of the Limbic System. We shall consider here three neocortical components of the limbic system: the insular, cingulate, and orbitofrontal cortices. While their function is not well understood, the available evidence suggests they relate affective assessment of bodily needs and wants with the cognitive assessment of environmental situations. For example, selecting behavior in terms of its experienced harm or benefit, the magnitude of obtainable rewards, and the risks involved.

The Insular Cortex: Its Role in Visceral Regulation and Benefit Assessment. The insula (island of Reil) is a buried component of the primate cerebral cortex (Fig. 7-18). Dissections reveal that is convolutions are continuous anteriorly with the orbitofrontal and frontal cortices, and posteriorly with the paracentral, superior temporal, and inferior parietal cortices (Crosby et al., 1962). This widespread cortical connection is supported by tract-tracing studies (Mesulam and Mufson, 1982; Augustine, 1996). The anterior insular cortex is the target of olfactory and gustatory input from the adjoining orbitofrontal cortex (Kobayashi et al., 2002; Ifuku et al., 2003) and the posterior insula is associated with the somatosensory cortex (Burton and Jones, 1976; Robinson and Burton, 1980). In particular, the posterior insular cortex receives afferents from a thalamic region that relays high threshold nociceptive (painful) and thermal input conveyed by the spinothalamic tract (Burton and Jones, 1976; Mufson and Mesulam, 1982; Schneider et al., 1993). Correspondingly, many neurons in the posterior insula selectively respond to nociceptive stimuli (Robinson and Burton, 1980). The involvement of the insula in visceral functions is indicated by the older finding that its stimulation in anesthetized mammals, including primates, triggers salivation, piloerection, respiratory and blood pressure changes, and gastric motility (Kaada et al., 1949; Hoffman and Rasmussen, 1953; Frontera, 1956; Showers and Lauer, 1961). Correspondingly, stimulation of the insular cortex in conscious human patients triggers alimentary visceromotor and autonomic reactions (Penfield and Rasmussen, 1950; Penfield and Faulk, 1955) and the anterior insula is activated by breathlessness (Banzett et al., 2000), disgusting smells (Heining et al., 2003) and observing expressions of disgust (Krolak-Salmon, 2003).

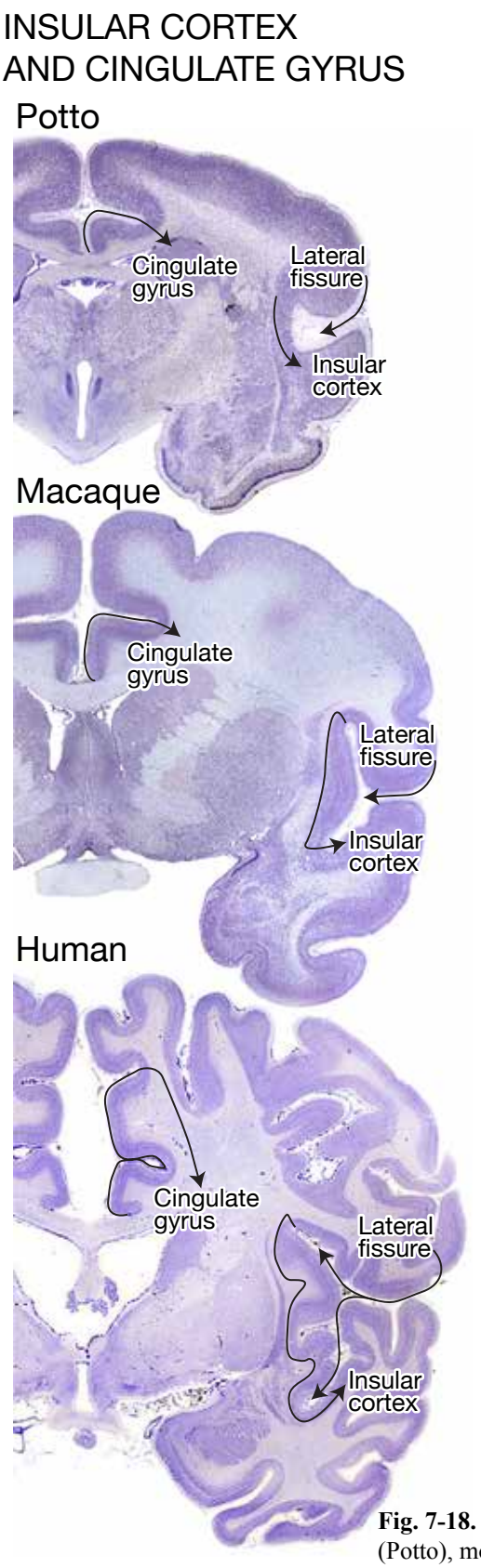


Fig. 7-18. The insular cortex and cingulate gyrus in a prosimian (Potto), monkey (Macaque), and Human brain. Note its expansion and increased foliation in parallel with the neocortex. (After BrainMuseum.org.)

THE ROLE OF THE ANTERIOR INSULAR CORTEX IN THE REGULATION OF NUTRITION. Most monkeys are omnivores, which makes the selection of nutrients a challenging task in the wild. They have to learn how to select food items in different seasons in terms of their caloric content, hedonic properties, beneficial and harmful properties, as well as expense in terms of effort and risk involved. Nutrition is regulated by sensory information of internal and external origin. Internal sensors signal the need to provide the body's caloric reserves, as well as minerals and vitamins necessary for growth, tissue repair and other vital processes. Chemical interoceptors gauge the concentration of different metabolites and nutrition-related signaling molecules, and mechanical interoceptors signal volume changes in the nutrient stores of the gastrointestinal tract and fatty tissues. The task of external sensors is to locate feeding sites and how best exploit available resources. The latter requires olfactory, gustatory, visual and tactile discrimination. It has been found that neurons in the simian insula selectively respond to different taste qualities, such as sucrose, salt, or quinine (Yaxley et al., 1990) and insular stimulation in awake monkeys triggers the facial expression of disgust, such as grimaces and lip smacking, as well as refusal to eat (Caruana et al., 2011).

THE ROLE OF THE POSTERIOR INSULAR CORTEX IN CORPOREAL SENSATIONS AND AFFECTS. Whereas food-related reactions are elicited from the more anterior parts of the insula, the posterior insula has been implicated in responding to nociceptive and thermal stimuli (Stephani et al., 2011). In man, stimulation of the insular cortex elicits both painful and painless somatotopically localized sensations (Ostrowsky et al., 2002). According to a recent evaluation of a large data bank, there are only two areas in the human cerebral cortex

stimulation of which evokes somatic pain, the posterior insula and the adjacent medial parietal operculum (Mazzola et al., 2011). Correspondingly, scanning studies indicate that the insular cortex is activated during painful stimulation of the skin, muscles or the trigeminal nerve (Bromm and Chen, 1995; Kakigi et al., 1994, 1995; Oshiro et al., 1998; Valeriani et al., 2000; Frot and Mauguière, 2003; Henderson et al., 2007). Insular activation also occurs in response to sensations of warmth (Paulson et al., 1998; Gelnar et al., 1999; Casey et al., 2000; Craig et al., 2000; Brooks et al., 2002; Olausson et al., 2005), heartbeat changes (Critchley et al., 2004), breathlessness (Banzett et al., 2000), and non-painful esophageal (Phillips et al., 2003) and gastric distension (Stephan et al., 2003).

COMPARISON OF INSULAR FUNCTIONS IN MONKEY AND MAN. The insula—unlike the hippocampus but much like the rest of the neocortex—has expanded greatly in the primate line, reaching it zenith in man. In prosimians, the insula is a simple invagination (Fig. 7-18A); it is a buried, two-pronged convolution in monkeys (Fig. 7-18B); and a highly convoluted structure in man (Fig. 7-18C). To what extent are the findings about insular functions in man applicable to monkeys? It has been suggested that the human insular cortex has a cognitive function: changing implicit feelings about one's internal state into explicit conscious experiences and sources of deliberate behavior (Craig, 2009). This idea is supported not only by the findings already referred to but also by the report that engaging one's body in voluntary activities (Tsakiris et al., 2007) and observing the reflection of one's body image (De Vue et al., 2007) activates the insular cortex. If so, the human insula is one of the cortical mechanisms that contributes to our explicit awareness of what we are feeling and doing at any give time. This may not be the function of the simpler simian insular cortex because we do not currently have evidence for self-awareness in monkeys. (As we describe below, monkeys do not recognize themselves in a mirror.) It is more likely that the function of the simian insular cortex is to let feelings influence behavioral choices, but that is done without explicit awareness.

The Cingulate Cortex: Interfacing Affect and Cognition in Avoiding Suffering and Maximizing Benefit. The cingulate cortex is a midline cortical structure that extends from the frontal lobe anteriorly to the parietal lobe posteriorly, consisting of an anterior (areas 32, 24) and a posterior (areas 23, 31) component. Much like the insular cortex, the cingulate gyrus has expanded greatly in the line of primates from prosimians to man (Fig. 7-18). There is emerging evidence that anterior cingulate cortex is involved in the joint affective-cognitive regulation of the avoidance of suffering and the maximization of pleasure.

STRUCTURE OF THE CINGULATE CORTEX. The simian cingulate cortex is targeted by afferents of the limbic thalamus, the anterior, intralaminar and midline nuclei (Crosby et al., 1962; Baleydier and Mauguière, 1980; Vogt and Pandya, 1987; Hatanaka et al., 2003), and it is interconnected with the adjacent premotor and prefrontal areas (Ghosh et al., 1987; Morecraft and Van Hoesen, 1992, 1993; Arikuni et al., 1994; Nimchinsky et al., 1996; Wang et al., 2001; Luppino et al., 2003; Petrides and Pandya, 2007). The anterior cingulate cortex (areas 25, 24) contains sensory and motor representations of the hand and the body, as well as motor representation of the body, with the forelimb located caudally and the hindlimb rostrally (Luppino et al., 1991; Cadoret and Smith, 1995). The posterior cingulate cortex (areas 23, 31) is also connected with the parietal cortex (Baleydier and Mauguière, 1980; Battaglia-Mayer et

al., 2001; Kobayashi and Amaral, 2003; Morecraft et al., 2004) and visual structures concerned with gaze control (Pandya et al., 1981; Huerta and Kaas, 1990). There is an outflow from the cingulate cortex, by way of the external capsule, to the basal ganglia, the hypothalamus, the subthalamic nucleus, and the tegmentum (Crosby et al., 1962; Takada et al., 2001), and there is also a direct efferent pathway to the spinal cord (Biber et al., 1978; Murray and Coulter, 1981; Hutchins et al., 1988; Galea and Darian-Smith, 1994; He et al., 1995; Dum and Strick, 1996; Morecraft et al., 1997; Hutchins et al., 1998).

THE ROLE OF THE CINGULATE CORTEX IN VISCERAL AND AFFECTIVE REGULATION. The role of the cingulate cortex in visceral regulation has been known for some time. Much like in the case of the insular cortex, stimulation of different anterior cingulate loci in different mammalian species, including monkeys, augments or arrests such visceral processes as salivation, shivering, piloerection, heart rate, and gastrointestinal motility (Smith, 1945; Ward, 1948; Kaada, 1951; Showers and Crosby, 1958; Showers, 1959; Luppino et al., 1991; Godschalk et al., 1995; Morecraft and Van Hoesen, 1998). Ablation of the anterior cingulate cortex in monkeys has been associated with blunting of emotional responses (Hadland et al., 2003a; Rudebeck et al., 2006). The operated monkeys display less fear of snakes than control animals, stare at each other less, and take little interest in films displaying monkeys in action. A role of the human cingulate cortex in visceral and emotional processes is indicated by the findings that it is activated by pleasant or painful tactile stimulation (Rolls et al, 2003a), cardiovascular mobilization (Critchley et al. 2003), distention of the gastrointestinal tract (Stephan et al., 2003; Hamaguchi et al., 2004), and gastric pain (Lu et al., 2004). Cingulate cortex activation was also noted in humans when a decision had to be made whether a substance is safe to swallow (Watanabe, et al., 2004) or when the subject had to heed an instructional cue to swallow or not swallow (Toogood et al., 2005).

THE ROLE OF THE ANTERIOR CINGULATE CORTEX IN REWARD ASSESSMENT. The involvement of the simian anterior cingulate cortex in the appreciation of the rewarding outcomes of behavior is indicated by several experimental studies. Following inactivation or ablation of the cingulate cortex, monkeys fail to refrain from responding to cues when those no longer signal reward (Shima and Tanji, 1998; Rushworth et al., 2003). Although the operated animals are not handicapped in learning visual discriminations, they are handicapped in performing different actions to obtain different rewards (Hadland et al., 2003b). According to another study, monkeys with anterior cingulate lesions can modify their behavior when the cues for correct response are reversed but, unlike normal monkeys, they cannot integrate that experience into another behavioral pattern and revert to their old choice (Kennerley et al., 2006). Single-cell recording studies indicate that cingulate cortex neurons code for the degree of reward expectancy, and monitor behavioral performance in relation to the success or failure to obtain a reward, and the hedonic quality or magnitude of the reward (Akkal et al., 2002; Russo et al., 2002; Shidara and Richmond, 2002; Seo and Lee, 2007; Hayden and Platt, 2010). In one of these studies (Russo et al., 2002), monkeys were trained (a) to use a joystick to align and hold a light beam in the center of the computer screen to initiate a trial, and (b) receive a food reward by correctly executing a complex hand and arm movement (Russo et al., 2002). Thereafter, (c) several peripherally located circles appeared briefly on the screen with one of them being brighter than the others. That cue disappeared and, after a short delay, the monkey

had to move the joystick to the location of the previously displayed brighter circle. This task required the learning and recollection of several actions: the retention in working memory of the changing location of the correct target in any given trial; refraining from responding during the delay period; and the translation of a remembered visual cue into coordinated arm and hand movements. Concurrent recordings from anterior cingulate neurons showed that some of them were active during the preparatory phase of the trial, others during the delay period, and the vast majority when the monkey moved the joystick toward the correct target. It has been suggested that the anterior cingulate cortex, as a limbic interface, has an "affective" (visceral) and a "cognitive" (volitional) component (Devinsky et al., 1995). The affective component would play a role in assigning emotional valence to what is sensed or perceived whereas the cognitive division would monitor behavioral performance to insure and maximize rewarding outcomes. Brain scanning studies in humans suggest an increasing cognitive control exerted by the anterior cingulate cortex, by being implicated in risk assessment and conflict monitoring (Botvinick et al., 2004; Brown and Braver, 2007; Carter and van Veen, 2007).

THE ROLE OF THE POSTERIOR CINGULATE CORTEX IN BENEFIT MAXIMIZATION. At the foundational level, basic affects trigger simple dichotomous responses: approach whatever evokes pleasure, relief or comfort; avoid whatever evokes displeasure, pain or discomfort. In the case of nutrition, positive sensations trigger ingestion, negative feelings trigger rejection. But living in a rich environment, like a bountiful forest that offers multiple and varied choices, the task becomes what to choose among the available alternatives, and do that on the basis of knowledge about their respective advantages and disadvantages. There is some evidence that the posterior cingulate cortex plays an important role in this process by bringing to bear previous positive or negative affective outcomes. Two facets of this affective assessment have been studied experimentally, reward maximization and risk assessment.

As noted before, in contrast to the anterior cingulate cortex, which is closely connected with the interoceptive sensory system, the posterior cingulate cortex is also connected with the exteroceptive system. While there are several brain regions involved in gaze control—including the frontal eye field, the supplementary eye field, areas in the parietal and occipital lobes, and the superior colliculus—there is evidence that the posterior cingulate cortex is a component of that system (Vogt et al., 1992; Dean and Platt, 2004, 2006). In a study by Hayden et al. (2008), the discharge pattern of single posterior cingulate neurons was studied in monkeys engaged in a gambling task. Monkeys sitting in front of a monitor had to shift their gaze from a central square to one of two peripherally appearing cues to receive a reward. If they turned their gaze to one of the cues, they consistently obtained a mid-size amount of juice; if they turned their gaze to the other cue, they variably obtained a smaller or a larger amount of juice. Analysis of the data indicated that the monkeys turned their gaze toward the risky cue more often following a preceding large reward than following a preceding small reward. Concurrent recordings identified single posterior cingulate neurons that discharged in relation to the magnitude of the reward obtained, suggesting that these neurons contributed to the coding of this affectively motivated choice behavior. Monkeys take risks when there is an opportunity to get a greater reward, and some posterior cingulate neurons fire at the highest rate when they opt for a risky choice (Heilbronner et al., 2011). Similar findings have been found with functional imaging studies in human subjects. They had to respond to a small visual target that

was either correctly or incorrectly cued by the direction of an arrow (Mesulam, et al., 2001). Correct cueing tended to improve the speed of target detection, and that was associated with activation of the posterior cingulate cortex. In a related study (Small et al., 2003), subjects had to respond to visual targets preceded by helpful or misleading cues. Response to the valid cue tended to reduce reaction time, and that was associated with activation of the posterior cingulate and medial prefrontal cortices.

The Orbitofrontal Cortex: Its Role in Affective-Cognitive Integration. The simian frontal lobe is the region of the anterior cerebral hemisphere situated anterior to the frontal eye field (Figs. 6-10 to 6-13). It consists of two large subdivisions, the narrower orbitofrontal cortex rostrally and the broader dorsolateral prefrontal cortex caudally. The orbitofrontal and dorsolateral prefrontal cortices differ in several respects, including cytoarchitecture, neurotransmitter organization, and connections (Walker, 1940a; Barbas, 1988; Barbas and Pandya, 1989; Petrides and Pandya, 1999; Cavada et al., 2000; Dombrowski et al., 2001). Here we are concerned with the orbitofrontal cortex, which in contrast to the dorsolateral prefrontal cortex, may be considered a division of the limbic system. (We shall deal separately with the dorsolateral prefrontal cortex in Section 7.4.)

STRUCTURE AND CONNECTIONS OF THE ORBITOFRONTAL CORTEX. The monkey orbitofrontal cortex consists of areas 10-12 ventrolaterally, and areas 14 and 25 ventromedially (Fig. 6-18). It differs from the dorsolateral prefrontal cortex (areas 9, 45 and 46), first, in terms of its connections with other brain regions. While both receive a large input from the thalamic mediodorsal nucleus (MD), the two are targeted by different components of MD. MD has three components: the medial magnocellular region; the lateral parvicellular region; and the far-lateral multiform region (Walker, 1940b; Olszewski, 1952; Pribram et al., 1953). Whereas the parvicellular and multiform regions target the dorsolateral prefrontal cortex, the orbitofrontal cortex is preferentially targeted by the magnocellular MD (Tobias, 1975; Tanaka, 1976; Barbas et al., 1991; Ray and Price, 1993; Bachevalier et al., 1997). There is a similar pattern in the reciprocal projections of the prefrontal areas to MD (Siwek and Pandya, 1991). Second, like the magnocellular MD, which has olfactory (Benjamin and Jackson, 1974), amygdaloid (Aggleton and Mishkin, 1984) and limbic-cortical connections (Russchen et al., 1987), so also the orbitofrontal cortex receives indirect olfactory (Carmichael et al., 1994; Critchley and Rolls, 1996a) and gustatory (Yarita et al., 1980; Carmichael and Price, 1995b; Yarita et al., 1980) inputs. It has been suggested that the lateral orbitofrontal region is principally the target of sensory input and the medial region the source of an output system (Price, 2007).

As a component of the limbic system, the orbitofrontal cortex has extensive connections with the ventral striatum (Haber et al., 1995; Öngür and Price, 2000), the amygdala (Porrino et al., 1981; Aggleton and Mishkin, 1984; Barbas and De Olmos, 1990; Carmichael and Price, 1955a; Ghashghaei and Barbas, 2002), the hippocampus (Barbas and Blatt, 1995), the hypothalamus (Öngür et al., 1998; Öngür et al., 1998; Rempel-Clower and Barbas, 1998; Öngür and Price, 2000), and the periaqueductal gray (An et al., 1998), all of them structures implicated in affective processes. With reference to neocortical connections, the orbitofrontal cortex is linked with the insular cortex (Pritchard et al., 1986; Baylis et al., 1995), the cingulate cortex (Carmichael and Price, 1995a), the sensory and motor areas (Carmichael and Price, 1995b),

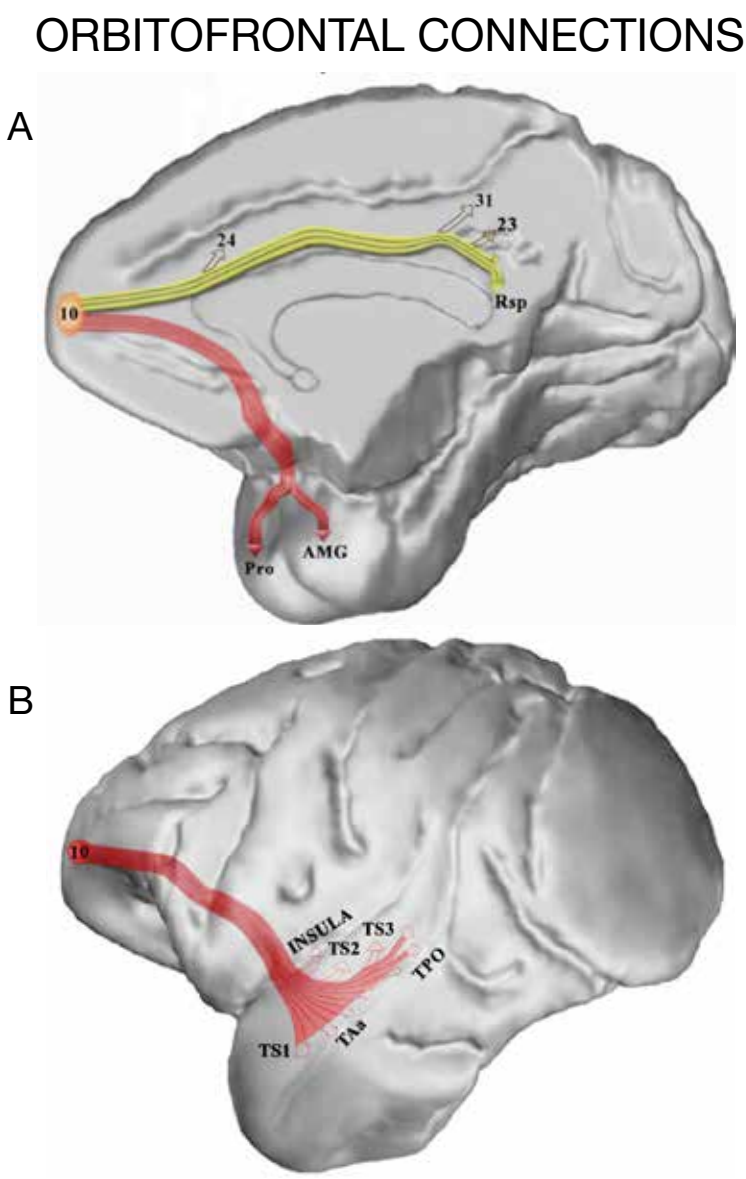


Fig. 7-19. A. Efferent bundles that connect the pole of the prefrontal cortex with the cingulate gyrus, temporal pole and amygdala medially. B. Efferent bundles that connect the pole of the prefrontal cortex with the superior temporal gyrus and the insula. (From Petrides and Pandya, 2007.)

and the temporal cortex (Seltzer and Pandya, 1989; Barbas, 1993; Carmichael and Price, 1995a, b; Barbas et al., 1999; Kondo et al., 2003; Cavada et al., 2000; Rempel-Clower and Barbas, 2000). Petrides and Pandya (2007) recently identified in macaques three large pathways from area 10 of the orbitofrontal cortex: (*i*) the ventromedial uncinate fasciculus that targets the amygdala; (*ii*) the medial cingulate fasciculus that targets the cingulate gyrus; and (*iii*) a lateral fasciculus within the external capsule that targets the superior temporal multisensory areas (Fig. 7-19). Of these, (*i*) and (*ii*) may be thought of as affective/motivational connections, and (*iii*) as mnemonic/cognitive connections. By virtue of these connections, the orbitofrontal cortex is a position to integrate affective and cognitive functions.

More specifically, it has been hypothesized that the lateral orbitofrontal cortex is involved in processing sensory information related to food procurement and selection, whereas the medial orbitofrontal cortex is more concerned with the autonomic and endocrine regulation of alimentary processes (Neafsey, 1990; Morecraft et al., 1992; Carmichael and Price, 1994;

Price, 1999). Supporting this dichotomy is the evidence that the lateral orbitofrontal cortex is the target of converging input from olfactory, gustatory, somatosensory, auditory, and visual cortical areas (Jones and Powell, 1970b; Chavis and Pandya, 1976; Petrides and Pandya, 1984; Barbas, 1988, 1993; Seltzer and Pandya, 1989; Hackett et al., 1999; Romanski et al., 1999; Cavada et al., 2000), whereas the medial orbitofrontal areas are a major source of cortical output to visceromotor and autonomic structures, including the hypothalamus and the brainstem (An et al., 1998; Öngür et al., 1998; Rempel-Clower and Barbas, 1998; Cavada et al., 2000; Öngür and Price, 2000; Chiba et al., 2001).

FUNCTIONS OF THE ORBITOFRONTAL CORTEX. The involvement of the orbitofrontal cortex in reward assessment is suggested by clinical studies of patients with frontal lobe lesions. Bechara et al. (1994) tested subjects with a card game where some high risk cards could be selected with large gains, other low-risk cards could be selected with small gains. Normal subjects opted for a low risk strategy. Patients with orbitofrontal lesions (but not with dorsolateral prefrontal lesions) kept on gambling as if oblivious of the risks. In a visual matching task, orbitofrontal patients tended to respond more rapidly than normal subjects (Berlin et al., 2004) but displayed deficits in reversal learning tasks (Hornak et al., 2004). These observations suggest that orbitofrontal cortex is involved in impulse control. Patients with orbitofrontal lesions also display deficits in the appreciation of emotional stimuli, including emotional expressions (Ishai, 2006; Heberlein et al., 2008).

The selection of actions that maximize rewards characterizes the behavior of monkeys both in the wild and in the laboratory. That involves a consideration of the hedonic quality and quantity of the anticipated reward, the time and effort required to obtain it, and the likelihood of succeeding or failing. Early lesion studies disclosed that monkeys with frontal lesions display deficits in assessing the attractive or aversive quality of stimuli (e.g., Butter et al., 1970; Jones and Mishkin, 1970). That has been confirmed in recent investigations: orbitofrontal lesions in monkeys interfere with making choices on the basis of reward value and reward contingency (Thorpe et al., 1983; Baylis and Gaffan, 1991; Watanabe, 1996; Pears et al., 2003; Izquierdo et al., 2004). Among other brain regions implicated in reward assessment are structures closely connected with the orbitofrontal cortex: the cingulate cortex (Cadoret and Smith, 1995; Shima and Tanji, 1998; Akkal et al., 2002; Shidara and Richmond, 2002; Hadland et al., 2003b; Hayden and Platt, 2010); the premotor cortex (Wallis and Miler, 2003b); the temporal (Liu and Richmond, 2000) and parietal cortices (Platt and Glimcher, 1999; McCoy and Platt, 2005a; Bendiksby and Platt, 2006); and several brain regions with a high concentration of dopamine-containing neurons (Schultz et al., 1997; Satoh et al., 2003; Bayer and Glimcher, 2005; Tobler et al., 2005).

Most of the experimental studies concerning the role of orbitofrontal neurons in reward assessment have dealt with diet selection. In behaving monkeys, some orbitofrontal neurons are selectively activated by either unimodal or multimodal olfactory, gustatory or visual stimuli (Rolls and Baylis, 1994; Critchley and Rolls, 1996a; Rolls et al., 1996b, 1999; 2003a; Rolls, 2001; Rolls et al., 1999, 2003a; Verhagen et al., 2003). For instance, some neurons are activated differentially in response to fruit juices with different odors, tastes and colors (Fig. 7-20). Hence, the orbitofrontal cortex may be the site where information is integrated not

only on the basis of their odor and taste but also their appearance. Orbitofrontal neurons also differentiate food items in relation to the animal's changing nutritional needs and appetite, as some of them cease responding to glucose or fruit juice when the animal has become satiated with them (Rolls et al., 1989; Critchley and Rolls, 1996b; Fig. 7-20).

Evidence is accumulating that the activity of some prefrontal and orbitofrontal neurons is correlated with the following variables: the hedonic value of the expected reward (Thorpe et al., 1983; Critchley and Rolls, 1996b; Tremblay and Schultz, 1999; Kobayashi et al., 2002; Watanabe et al., 2002; Rolls et al., 2000; Padoa-Schioppa and Assad, 2008); its quantity (Leon and Shadlen, 1999; Wallis and Miller, 2003a; Roesch and Olson, 2005); the probability of getting the reward (Tremblay and Schultz, 1999); and the elapsed time before the reward is delivered (Hikosaka and Watanabe, 2000; Roesch and Olson, 2005). Orbitofrontal neurons may increase their rate of discharge in response to cues predicting reward, while waiting for the delivery of the reward, and as the reward is consumed. As an illustration of these studies, Thorpe et al. (1983) trained monkeys to discriminate appetizing or aversive stimuli by sight or by taste. Orbitofrontal neurons were identified that were selectively activated by one or the other stimuli. Some neurons responded specifically to the sight of the food item, others responded differentially to the same syringe that was used previously either to deliver a solution of aversive saline or appetizing glucose. When the solution delivered was reversed, the response of the same neuron was also reversed.

There is some evidence for a role of the orbitofrontal cortex in learning about the palatability of nutrients (Rosenkilde et al., 1981; Thorpe et al., 1983; Watanabe, 1996; Watanabe et al., 2002; Rolls, 2000; Rolls, 2001; Ito et al., 2001). In an experiment in which particular odors were arbitrarily associated with the delivery of either glucose or saline, some orbitofrontal neurons selectively responded to the odors that were associated with glucose but not those associated with saline, or vice versa (Critchley and Rolls, 1966a). In a study by Wallis and Miller (2003b), monkeys had to choose between pictures associated with different amounts of juice as a reward. In both the prefrontal cortex and the orbitofrontal cortex, neuronal activity was correlated with reward magnitude. But there were some differences in the two regions and the authors suggested that the orbitofrontal cortex assesses reward magnitude and the prefrontal cortex is responsible for ensuing response selection. In line with these findings, macaques with medial orbitofrontal lesions make abnormal choices when presented with certain food items; for instance, they opt for meat over fruit, although normal macaques are reluctant to eat meat (Baylis and Gaffan, 1991). Learning-based diet selection may be aided by the extensive connections of the orbitofrontal cortex with the hippocampus and the entorhinal cortex (Insausti et al., 1987; Barbas and Blatt, 1995; Cavada et al., 2000; Rempel-Clower and Barbas, 2000).

In summary, there is emerging experimental evidence that the limbic system plays a dual role in behavior: engaging cognitive processes to serve vital affective ends, and modifying affective processes by realistic cognitive considerations. The limbic system consists of a core of paleocephalic mechanisms that tag sensations and perceptions with dichotomous affective qualia—such as, like-dislike, pleasure-pain, and fear-anger—and a superstructure of allocortical and neocortical mechanisms that supply realistic information about challenges

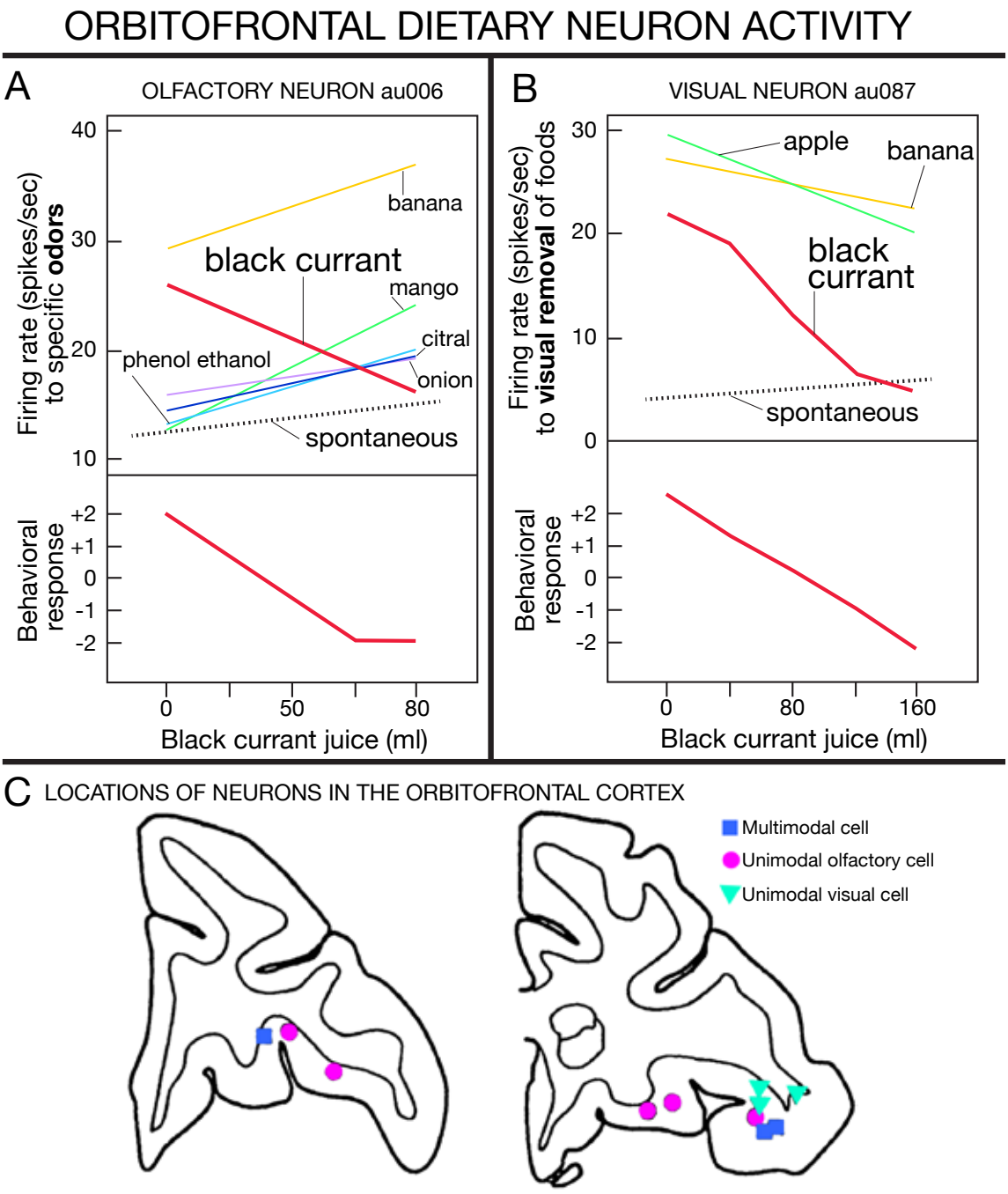


Fig. 7-20. **A**. Changing firing rate of an orbitofrontal olfactory neuron to different odorants relative to its spontaneous level of discharge (top). When satiated with the consumption of black currant (bottom) the neuron's firing rate diminishes to that stimulus. **B.** Changing firing rate of an orbitofrontal visual neuron to the sight of different fruits (top) and to black currant to which it is getting satiated (bottom). **C**. Location of olfactory, visual and multimodal neurons in the orbitofrontal cortex of a macaque.
(Modified, after Critchley and Rolls, 1996.)

and opportunities, and changing conditions and circumstances in the external world. Due to the expansion of the neocortical components of the limbic system in monkeys, their behavior is governed by a set of complex emotions, and they have a rich affective life. That richness is shown in the great affection of mothers for their infants, the adventurousness and playfulness of juveniles, the complex ambivalent social relationship of adults, alternating fighting each other for gain and subsequently seeking reconciliation. As we describe below, monkeys are unique in the animal world in terms of their mnemonic and cognitive abilities—heralding an advance toward human intelligence, but they are also distinguished by impulsivity, greed, hatred, and proneness to violence—traits that are another aspect of our simian legacy.

7.3. Simian Mnemonic Advances and the Temporal Cortex

7.3.1. Mnemonic Advances: Learning Based on Memory Images. Learning plays a minor role in the behavior of lower vertebrates when compared with mammals. Lower vertebrates respond adaptively to survival-promoting objects, events, and beings (food, danger, conspecifics, predators) by relying mostly on "preprogrammed" or "hard-wired" stimuli and responses, or what has been called "inborn releasers" and "fixed action patterns" (Lorenz, 1950; Tinbergen, 1951). If reared in isolation from birth and deprived of any opportunity to learn from daily experience, lower vertebrates react to environmental stimuli much the same way as do normally reared conspecifics (Thorpe, 1963; Eibl-Eibesfeldt, 1970). But lower vertebrates are handicapped relative to mammals because the variety and specificity of stimuli that they can discriminate by genetically transmitted sensory templates is necessarily limited, and so is the repertoire of their motor actions and reactions. Lower vertebrates can benefit from individual experience but their mode of learning—such as association-based conditioning—lack the rapidity and flexibility of behavioral modification displayed by mammals. We hypothesize that a major contributor to the advanced learning ability of mammals is their possession of *imagery* as a mental faculty. We know imagery as a subjective experience when we retain in our mind a quasi-perceptual representation of what we have recently experienced (short-term working memory) and can recollect what we have experienced in the more distant past (long-term recollection memory). These memory images provide us with a wealth of added information to what we directly sense or perceive, which greatly enriches our knowledge of what transpires in the world around us. But how can we *objectively* test the proposition that the cat or dog that we live with, and the monkeys we observe or test in the laboratory rely on subjective imagery when they display behavioral modification on the basis of individual experience? We propose that we are justified in inferring mediation by memory imagery when an animal manifests rapid rather than slow learning, as is the case with conditioning and trial-and-error learning. We assume that the animal learns fast, ideally after a single exposure or trial, because it mentally recollects what it has previously perceived.

Memory Images: From Slow to Fast Learning. Slow learning, much of it occurring without awareness, includes habituation, sensitization, associative learning, and habit formation. All animals tend to respond to sudden and intense stimuli (lighting, thunder, etc.) and ignore recurring and weak stimuli (the rustling of leaves, the sound of ocean waves, etc.). This is a useful disposition because explosive events often signal danger or harm and background happenings have no significance. However, repeated experience may reveal that an intense stimulus

originates from an innocuous source whereas a weak stimulus has disastrous consequences. Adaptive mechanisms have accordingly evolved that, using accumulated experience, enables an animal to ignore previously heeded strong but innocuous stimuli, called habituation, and respond to previously unheeded stimuli that signal harm, called sensitization. As we have described it earlier, habituation and sensitization have been demonstrated in protozoans without a nervous system, and in primitive metazoans with an elementary nervous system. A more complex process than sensitization or habituation is learning by association. Several types of associative learning have been demonstrated in a great variety of species: appetitive conditioning, salivating in response to a cue that has been repeatedly followed by feeding; aversive conditioning, trembling in response to a cue that has been coupled with an electric shock; avoidance conditioning, leaving a dangerous or toxic site; instrumental conditioning, learning what movements or actions to perform to receive a reward. These different types of learning obey different principles but they are alike in that they all require many repeated stimulus-response associations. This gradualness is usually attributed to the slow process of modifying synaptic connections and it is a functionally useful trait because it assures that fortuitous associations do not lead to behavioral modification.

In contrast to these slow learning processes, there are several fast learning processes. One of them, imprinting, was originally discovered in birds but has been demonstrated in all vertebrates, including mammals. For instance, neonatal mice learn after a single association of an arbitrary odor with milk delivery to select that odor in a choice situation (Armstrong et al., 2006). But imprinting, as defined, is limited to a critical period of early development. Another instance of rapid behavioral modification is one that we are all familiar with, i.e., verbal instruction. If I am told by my employer only once "go to the market and buy a sack of potatoes," I will do that, and being told "but don't waste your time chatting with people," I will refrain from doing that. This type of verbally mediated rapid learning is, of course, outside the scope of nonverbal animals. But there are many instances of rapid learning in animals. Mice refrain from stepping down from a pedestal to a floor on their second trial if they previously received an electric shock for having doing so (Jarvik and Essman, 1960). Wild animals become bait shy after a single instance of poisoning (Garcia et al., 1966; Milgram et al., 1977). Vervet monkeys learn in a single trial to avoid poisoned food cued by a distinctive color (Johnson et al., 1975) or shape (Domjan et al., 1982), and squirrel monkeys and marmosets learn in a single trial to discriminate cookies sweetened with sugar or adulterated with quinine by their the color or shape, and remember that discrimination for several months (Laska and Metzker, 1998). Likewise, capuchin monkeys can learn to recognize after a single trial a feeding station containing edible rather than plastic bananas by a visual cue (Garber and Paciulli, 1997). What mechanisms may mediate one-trial learning in these nonverbal animals? Our hypothesis is that it is mediated by a mechanism familiar to all of us, i.e., evoked memory images. Salient experiences are retained in memory, or are stored and retrieved as quasi-perceptual images after a single exposure or trial.

The Subjective Properties of Memory Imagery. Introspectively, memory imagery refers to the recollection of past experiences in a pictorial form rather than verbally. Memory images share some features with perceptual images but the two can be distinguished in most instances both by subjective and objective criteria. Subjectively, we can tell much of the time

(though not in the case of dreams and illusions) whether the visual image we behold represents something that is actually "out there" (a bottom-up process) or something that takes place "in our head" (a top-down process) because perceptual images tend to be vivid and persistent (as long as the evoking stimuli are present) whereas memory images tend to be fainter and ephemeral. Objectively, *imaging* (seeing) and *imagery* (recollecting) can be distinguished by such simple maneuvers as closing one's eyes or turning off the light: perceptual images will disappear in the dark, recollected imagery may actually become intensified. We can also use another sensory channel, such as touch, to verify whether what we seem to see is actually there or just remembered or imagined. While, strictly speaking, imagery refers to vision, it has its counterparts in other sensory modalities. We may "re*call*" a voice or a melody, and re-experience tactile, olfactory or gustatory sensations. The fact that we do not have separate terms for the latter suggests that in our mental life (but not necessarily in that of other species) the prevalence of visual imagery outranks other modalities both qualitatively and quantitatively.

STUDIES OF IMAGERY. The nature and psychological importance of imagery in humans has been a controversial topic for a long time. The empirical philosophers, like Locke (1690) and Hume (1748), believed that perception itself consists of an amalgamation of sense impressions with recollected images. The psychologist, Galton (1883) found in a pioneering empirical study that there are individual differences in the extent to which human subjects rely on imagery, as opposed to verbal reconstruction, when they try to recall a past scene or episode. Although some psychologists, like Külpe (1895), believed in "imageless thought," others argued that there are two representational systems involved in human cognition—a language-based *discursive* one and an image-based *pictorial* one—and that we rely to different degrees on one or the other depending on the psychological tasks involved (Paivio, 1971; Sheehan, 1972). The function of imagery has been the topic of experimental investigations (Kosslyn, 1980, 1994). Subjects were given the task to determine whether pairs of rotated geometric drawings were the same or different (Shepard and Metzler, 1971; Shepard, 1982). The investigators found that reaction time increased linearly as the rotation increased from 0º to 180º. This suggested that the subjects rotated mental images in their "head," and took them longer to make long rotations than short rotations. Kosslyn et al. (1978) had subjects memorize a sketch of a nature scene and then asked the subjects to describe the distance between different items that it contained. The results showed that the response time was a linear function of the distances between two objects on the map. This again suggested that scanning of a recollected mental image is similar to visual scanning of a map.

This type of experimental findings suggested the existence of two different types of cognitive processes: (a) pictorial, graphic and holistic imagery, and (b) verbally mediated conceptual and analytical ideation. Opposing this theory of dual mechanisms, some writers have argued in favor of a single discursive process, maintaining that mental images do not exist at all or are epiphenomena of little importance (e.g., Dennett, 1981; Pylyshyn, 1981, 2003). The argument was that if mental images existed, they would have to be scanned by a "mental eye," which would require another eye, and so on, *ad infinitum*. We maintain that we do not have to invoke a mediating "mental eye" to recollect what we have perceived. The same immediate subjective process that provides imaging as a central representation of peripheral input (perception), may also be the one that makes possible imagery as a central representation

of either a persisting reverberation (short term memory) or the retrieval of a consolidated trace (long term memory) of what we recollect. Rather than to conceive of subjective experience as a "ghost in the machine" (Ryle, 1949), it is more helpful to think of it as a direct manifestation of neural activation. Much as perceptual images can be evoked by peripheral stimulation of the eye, they can also be evoked by stimulating the temporal cortex, (Penfield, 1958; Farah, 1989; Bartolomeo, 2002; Dulin et al., 2008; Moro et al., 2008), a region (as we describe below) strongly implicated in certain types of memory functions.

When we turn from verbal humans to nonverbal animals we are left with only one possible candidate for memory-guided behavior, i.e., that of imagery. When we get thirsty while working outside in the garden on a warm day and decide to get a cold drink, we may follow a combination of a verbal "script" and "imagery" how to get into the house, find the refrigerator in the kitchen, open its door and find a bottle of water. How does a nonverbal animal solve a similar problem? Anyone owning a dog may have witnessed how the panting dog will carry out a similar series of acts by going into the house, locating its water dish, and proceed to drink. Since it cannot rely on verbal guidance, we must assume that it uses a series of memory images. These may include a general spatial image how to get into the house; a more specific spatial image how to locate the kitchen; and a target image where to look for its water bottle. A house-trained dexterous (but nonverbal) capuchin monkey might be able to carry out virtually all the steps that a person does, relying entirely on guidance by imagery. In all these instances, the solution of the multi-step task requires long-term memory as to what the serial order of the steps are and how to perform each one of them, and short-term memory, also called working memory (Baddeley and Hitch, 1974) to recollect what has already been done and what remains to be carried out.

Varieties and Different Facets of Memory. There is accumulating evidence that, instead of being a unitary process, there are several mnemonic processes and, at least some of them, are mediated by different brain mechanisms. We begin with the important distinction between factual and procedural memory.

FACTUAL AND PROCEDURAL MEMORY. *Factual* learning is the perception-based acquisition of familiarity with the endless variety of objects, beings and events in the environment that have a bearing on a subject's needs and wants. *Procedural* learning is the mastery of instrumental activities to effectively deal with environmental challenges and achieve desired ends. Procedural learning in primates involves mostly the acquisition of the skills needed to locomote through space with agility and, in particular, to conjointly use the attentive eyes and the dexterous fingers to manipulate objects. Factual learning, which is the subject matter of this chapter, furnishes the individual with the ability to recognize and identify as distinct entities the multitude of specific objects in its habitat by their distinctive configurational features and substantive properties, as well as become familiar with their location and movement in space, and the dynamic transformations they undergo over time.

RECOGNITION AND RECOLLECTION MEMORY. There is an important distinction between *recognition* memory, perceiving something as familiar or known, and *recollection* memory, seeing with "the mind's eye" something that is not perceptually present. Learning to recognize

objects, beings and events in the external world is based on a hierarchic perceptual process that we have described in the previous chapter. Considering only the role of vision in object recognition and identification, the process begins in the striate cortex by the elementary perception of points and oriented lines in the visual field. This is followed in successive order, as the information passes through further processing in the adjacent occipital and posterior temporal association areas, by the perception of angles, contours and, finally, particular patterns as figures against a background. The next step in the process is the identification of the perceived figures not as mental pictures but as real distinctive objects in the external world. The final step, which takes place in the anterior and medial temporal cortex, is the storage of the objects' images as a mnemonic trace. The engrams formed can subsequently be used in two ways, as matching templates to aid perceptual recognition and as recollection memory. Recognition is a simpler, bottom-up process; recollection is a more complex top-down process.

MEMORY IN DIFFERENT SENSORY DOMAINS. There are differences in the contributions made to factual learning by the different senses. The olfactory and gustatory senses aid the subject to recognize the varied properties of different nutrients; the somesthetic senses support vision in learning about the substantive properties of objects; and the auditory sense provides information about the sounds accompanying certain events in the natural world and the calls made by different animals. Unimodal brain stations process the information gathered by the different senses and different brain mechanisms may be involved in their storage. As an indication of that difference, recollection memory is far better developed in primates (but not in other mammals) in the visual and auditory domains—seeing mental pictures and hearing mental voices—than is the mental ability to recollect olfactory, gustatory and somesthetic experiences. Comprehensive object recognition, of course, requires multimodal integration and cortical areas have been identified where this may take place.

SHORT-TERM IMAGERY. There is an important difference between short-term memory and long-term memory, remembering something for a few seconds or minutes while engaged in some enterprise, and recollecting something that has been experienced hours, days, months and years ago. The evidence for this comes from daily experience as well as clinical studies of brain-damaged patients and experimental studies in animals with selective cortical lesions. As we describe below, some cortical lesions prevent the subject to consolidate in memory any new experience—*anterograde amnesia*—while retaining the ability to remember whatever has transpired before the insult. Other cortical lesions erase whatever the subject has experienced in the past—*retrograde amnesia*—but spare the ability to relearn what has been forgotten. Without short-term memory we cannot possibly carry out any task that requires several steps performed in a serial order over a period of seconds or minutes. We usually accomplish that by a combination of pictorially recollecting what we have already done and what we still have to do, and using a verbal script, "first turn to the right, then look for the church on the left, then turn right, etc." Monkeys cannot use language to keep in mind what they have already done and what they have to do next; nonetheless, as we describe later, they are very efficient in carrying out multi-step serial tasks.

LONG-TERM IMAGERY. Long-term imagery is indicated in two situations: (*i*) when a previously encountered object, being, scene or event is recognized as familiar or known; and

(*ii*) when some past experience is recollected in a quasi-perceptual form. A distinctive subjective feature of factual recognition imagery—often referred to as declarative memory (e.g., Squire et al., 2004), a term that is not applicable to nonverbal animals—is that its contribution to perception coalesces so thoroughly with what is directly given by the senses that we usually cannot distinguish between what is based on external input and what mnemonic processes add to it. It is due to recognition imagery that when we look at a food item, for instance, we also appreciate whether we like it or not, whether it easy or difficult to digest, and when we see a person, we also recognize who he is, whether he is a friend, a stranger, or a foe. A special case of recognition imagery is the phenomenon known as perceptual completion. When we see a familiar item so briefly that we cannot get sufficient information about its features, or if it is partially occluded, we often fully recognize it because the missing elements are filled in by information retrieved from memory. That is, much of what we perceive is, in fact, partly a product of added memory.

Experimental Studies of Short-Term and Long-Term Imagery in Monkeys. The ability of monkeys to perform well on delayed matching-to-sample (Fig. 6-20B) and delayed nonmatching-to-sample tests, as we described earlier (Section 6.2.5), indicates that they rely on a persisting memory image of the sample. Short-term memory is an advanced mnemonic trait and, according to one study, it develops slowly; young capuchin monkeys that can master simple learning tasks, fail on delayed reaction tests (Resende et al., 2003). Using videos of objects, faces, natural scenes or computer-generated images, monkeys can recollect a high proportion of the pictures that they are exposed to once, matching the picture-memory capacity of human subjects (e.g., Sands and Wright, 1980; Gaffan, 1992). That capacity is enhanced if the stimulus is associated with a rewarding outcome. In an experimental study, macaques were given instruction cues that informed them whether or not they will receive a reward and what particular liquid reward they will obtain by performing a required action (Watanabe et al., 2001). The results showed that the monkeys moved faster and engaged in longer anticipatory lickings when, based on the preceding cue, they anticipated preferred rewards.

In some recent studies, the short-tem memory capacity of monkeys was directly compared with that of humans (Basile and Hampton, 2011; Crystal, 2001; Elmore et al., 2011). In one of these studies, the subjects facing a video screen were first shown an array of four or six clip-art icons as samples and, after a delay, were shown two test icons, one of which was displayed in the preceding arrays and one of which was new; their task was to touch the new icon (Fig. 7-21A). The ability of monkeys to recall what they already have seen previously was only slightly inferior to that of humans (Fig. 7-21B). Although humans can recollect what they have seen in two ways, pictorially or by assigning some verbal label to them, nonetheless the nonverbal monkeys performed well on this short-term memory task. While in most such tests the delay has been in the range of a few seconds, some studies have shown that monkeys may succeed in solving problems with delays as long as 10 minutes (e.g., Tavares and Tomaz, 2002). They must rely on mental imagery, or what has been called "picture memory" (Bruner et al., 1976; Roberts and Kraemer, 1984) to accomplish such feats. This ability to recall images seen only once suggests a mechanism analogous to what copying machines do.

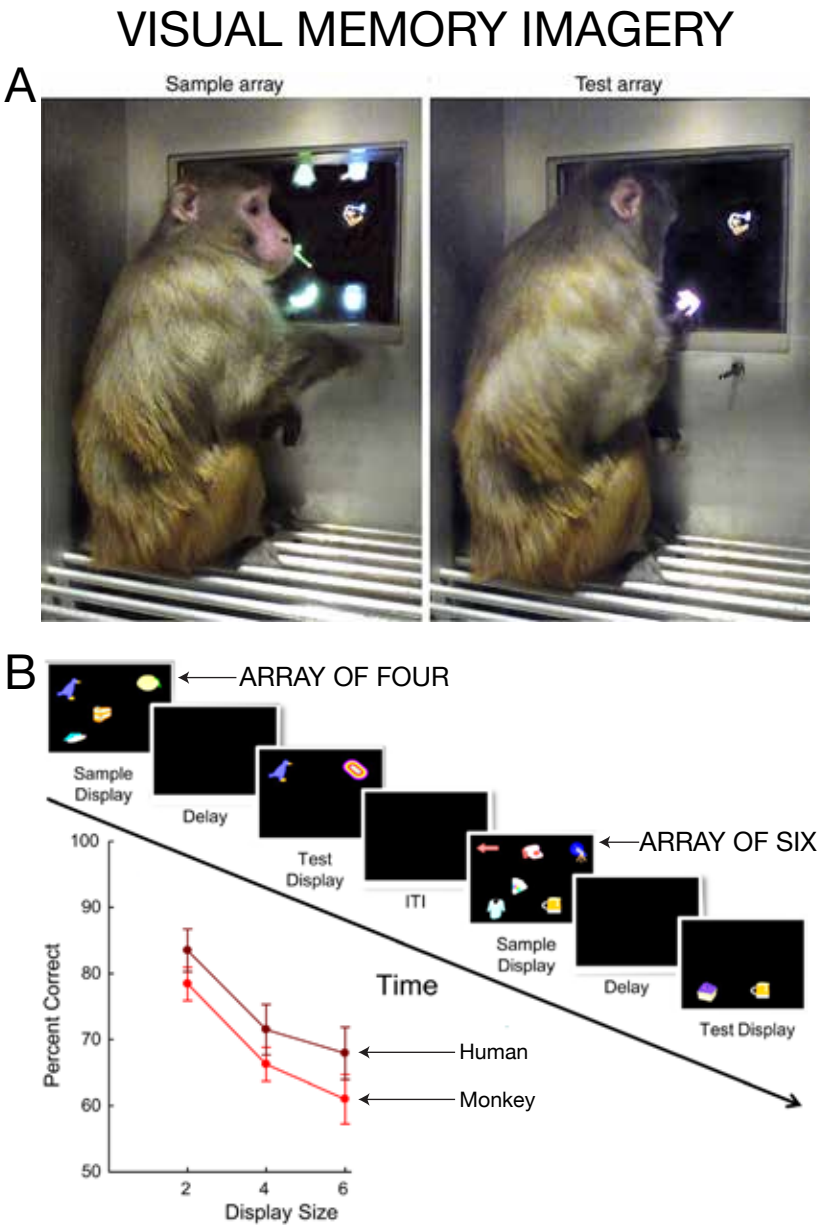


Fig. 7-21. A test of the ability of monkeys and humans to discriminate between novel and previously seen pictures. **A**. The monkey looks at a sample of four pictures and subsequently tested whether it can select, in a two-choice situation, the novel picture to obtain a reward. **B**. The percentage of correct choices made by humans and monkeys with samples of two, four and six pictures. (Modified, after Elmore et al., 2011.)

There is indirect evidence both from field observations and experimental studies for long-term imagery for monkeys; they can remember salient stimuli that they have seen only once for days, weeks and months. Field experiments have shown that capuchin monkeys (Garber and Paciulli, 1997) and squirrel monkeys (Ludvig et al., 2004) remember after a single observation where feeding sites have been established. In the wild, monkeys range widely in search of food, and those that rely on fruits and nuts in their diet appear to know not only when the trees bearing them ripen but also the shortest and safest route to reach them. For instance, baboons move rapidly and by a direct route to sites containing favored nutrients in different seasons (Pochron, 2001, 2005).

CAN IMAGERY SUPPORT EPISODIC MEMORY IN MONKEYS? If I try to reconstruct in my mind what a particular building looks like in a city that I have visited in the past, I may start out with a "snapshot" of the building's overall appearance, then try to reconstruct the architectural style of the building, where the entrance is, how many floors it has, the shape of its windows, and so on, going back and forth using this dual process of pictorial recollection and discursive verbalization. Although nonverbal animals cannot use this dual process, there is ample evidence that they can recollect what they have previously seen, often after a single exposure; hence they must rely on memory imagery. If this conclusion is correct, it follows that imagery is a distinct mental faculty, one that is independent of verbal mediation and one that has phylogenetically antedated the use of verbal mediation. If monkeys can recall as snapshots single experiences, can they arrange a series of snapshots in a temporal order to reproduce an episode, something like a narrative, from a beginning to its end? This ability—episodic and autobiographical memory—plays an important role in our lives not only in drawing lessons from past experience but also as the basis of sharing stories with others. In light of what we currently know about the conceptual abilities of monkeys (see below) we have no reason to grant them this cognitive power.

7.3.2. The Role of the Temporal Cortex in Memory and Learning. Hughlings Jackson (Jackson, 1931), and other clinical investigators of the late 19th century, reported that epileptic patients with discharges presumed to be originating in the temporal lobe experienced auras and hallucinations. The temporal cortical origin of these experiences in epileptic patients has been confirmed in recent investigations (e.g., Gloor, 1990; Bancaud, et al. 1994). The clinical work of Penfield and his associates (Penfield and Rasmussen, 1950; Penfield and Perrot, 1963) with awake patients undergoing brain operations, and more recent clinical investigations (Spatt, 2002; Bartolomei et al., 2004), have established that electrical stimulation of the temporal cortex triggers vivid sensations, hallucinations, *déjà vu* experiences and 'tape recorder recall' of past memories. The suspected role of the temporal cortex, in particular its medial component, in mnemonic processes is also indicated by psychological studies of patients with temporal cortex lesions; they show deficits in both short-term and long-term memory tasks (e.g., Buffalo et al., 1998; Squire et al., 2004), particularly if the task is made difficult (Barense et al., 2005). Finally, functional MRI studies in normal people have shown elevated medial temporal cortex metabolic activity during learning and a decrease as the task is mastered (Tulving et al., 1994; Vandenberghe et al., 1995; Henson et al., 2003).

Early Experimental Studies of Temporal Lobe Functions in Monkeys. In a pioneering study, Klüver and Bucy (1938) found that bilateral ablation of the monkey temporal lobe (temporal lobectomy) produced two profound mental changes. One of them was that while the animal continued to attend to visual stimuli, it could not respond to them meaningfully; they referred to that syndrome as "psychic blindness." The other change was an emotional one, such as abstaining to respond with fear or anger to provocations. We now know, as described earlier (Section 7.2.2), that the emotional changes of temporal lobectomy could be attributed to removal of the amygdala. Beginning in the 1950s, investigators began to use more circumscribed lesions, beginning with Mishkin and Pribram's (1954a, 1954b) studies of comparing the effects of ablation of the lateral versus the medial sectors of the temporal lobe. In the following decades investigators began to analyze temporal lobe functions in monkeys

by selective ablations of the inferotemporal cortex (Mishkin and Hall, 1955; Pribram and Mishkin, 1955; Dean, 1976). These studies suggested deficits in visual discrimination learning and object recognition tasks. No deficits were observed following these lesions in the retention or learning of auditory (Weiskrantz and Mishkin, 1958; Dewson et al., 1969), tactile (Iversen, 1967) and olfactory (Brown et al., 1963) discriminations. Investigators have more recently begun to analyze the behavioral abnormalities of monkeys following selective temporal cortex lesions. We review that below, after a consideration of our current understanding of the structural organization of the temporal lobe.

Subdivisions of the Temporal Lobe. The temporal lobe extends from the lower bank of the lateral sulcus laterally, ventrally and medially. The areal components of is lateral convexity are shown in a side view of the intact macaque brain in Chapter 6 (Figs. 6-10A, B), and its cytology can be seen in a stained horizontal section (Fig. 6-12B) and in two coronal sections (Figs. 6-14, 6-15). The ventral aspect of the temporal lobe is illustrated in Fig. 6-18C. Based on recent structural and functional investigations, we present here a parcellation of the temporal lobe into five sectors (Fig. 7-22). Starting at the top is sector 1. Much of it, the transverse gyrus of Heschl, is buried along the lower bank of the lateral fissure. This *superior* region has been identified as the auditory cortex and, as we discussed earlier (Section 6-3.5), it is implicated in vocal communication. Proceeding clockwise, sector 2, is the posterior region of the lateral temporal lobe (convexity). It consists of three areas abutting the occipital lobe, MST in the caudal superior temporal gyrus, TEO in the caudal inferior temporal gyrus, and MT between the two. We have considered this *posterolateral* region in the preceding chapter as a higher-order visual association complex implicated in visual pattern perception (Section 6.3.2). Rostral to

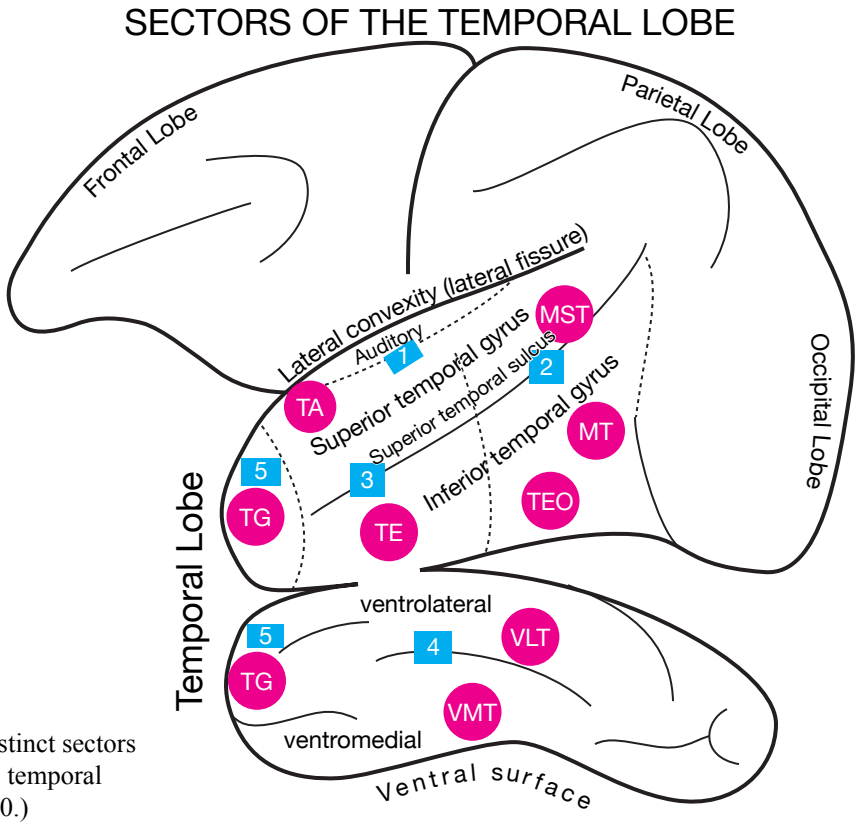


Fig. 7-22. Five functionally distinct sectors (*numbered blue squares*) of the temporal cortex. (Compare with Fig. 6-10.)

an imaginary line, forming the bulk of the *anterolateral* region is sector 3. This region has two components, the superotemporal TA and the inferotemporal TE. The evidence that we review below indicates that this region contains the principal neocortical mechanisms responsible for long-term memory consolidation. This region is closely affiliated with sector 4. Sector 4 consists ventrolaterally of the perirhinal and entorhinal cortices, designated as VLT, and ventromedially of the parahippocampal area, VMT. This sector plays a major role in short-term memory retention and, perhaps, in the transformation of ephemeral working memory into enduring long-term memory. This sector is generally referred to as the *medial* temporal cortex. The *temporal pole* is sector 5; little is currently known about that region.

The Structure and Functions of the Anterolateral Temporal Cortex. In monkeys, the anterolateral temporal region is the target of input from the visual (Rockland and Pandya, 1981) and haptic association areas (Zhong and Rockland, 2003; Beck and Kaas, 1999). It also has connections with the perirhinal and entorhinal cortices (Martin-Elkins and Horel, 1992; Saleem and Tanaka, 1996), the frontal cortex (Petrides and Pandya, 2007), the amygdala, and the basal ganglia (Cheng et al., 1997; Middleton and Strick, 1996). The frontal pole has connections with TE and TA (Seltzer and Pandya, 1978) and, by way of the uncinate fasciculus, with the orbitofrontal cortex (Markowitsch et al., 1985; Kondo et al., 2003; Olson et al., 2007). These connections suggest that the anterolateral temporal cortex is a target of input from the association areas of the perceptual system, and it is also closely connected with paralimbic structures implicated in affective functions.

TE lesions in monkeys produce short-term memory deficits. In one experiment, monkeys were first shown two identical pictures, then, after a variable interval ranging from seconds to minutes, were presented with the old picture and a new one (Buffalo, 1999). Normal monkeys tend to look at the new picture rather the one they have already seen, presumably because they are familiar with it. Monkeys with TE lesions display no preference for the new picture, presumably because they do not remember that they have already seen the other. Recordings of the activity of single anterolateral temporal neurons in monkeys engaged in various learning tasks indicate their involvement in short-term and long-term memory based object recognition. Nakamura and Kubota (1995) trained monkeys in a delayed visual recognition task. They identified TG neurons that fired continuously during the delay period but stopped firing thereafter. Naya et al. (2003) trained monkeys in a paired-associate recollection task while recordings were made from TE neurons. Sitting in front of a monitor, the animals were trained first to recognize a set of different visual displays as paired associates. Thereafter, the monkeys were briefly presented with one of the patterns as the sample and after a delay period had to choose whether the sample displayed was or was not a paired associate. The results suggested that some TE neurons became active while comparing the pairs (which requires long-term memory) while others are active in recollecting the sample (which requires short-term memory). Xiang and Brown (1998) reported that different anterior temporal lobe neurons selectively respond to visual stimuli that are novel, recently seen, or familiar. Other investigators reported similar findings (Miyashita et al, 1988; Sakai and Miyashita, 1991; Miller et al., 1993; Miyashita et al., 1993; Li et al., 1993; Fahy et al., 1993; Liu and Richmond, 2000; Messinger et al., 2001). Baker et al. (2001) recorded the activity of single neurons in the banks of the superior temporal cortex while the monkey watched a person walking along a path

where a screen made him invisible for a short period (Fig. 7-23). The discharge rate of some neurons increased appreciably as the person began to disappear behind the screen, reached its peak as he became invisible, and returned to baseline level when he became visible again. Both lesion and cell recording studies support the inference that the anterolateral temporal cortex plays an important role in mnemonic processes.

The Structure and Functions of the Medial Temporal Cortex. In monkeys, this complex consists of several distinct components. Abutting the rhinal fissure is the perirhinal cortex, situated more medially is the entorhinal cortex, and next to it is the parahippocampal region. All these structures are reciprocally connected with one another (Suzuki and Amaral, 1994a,b) and have extensive connections with other components of the temporal lobe and with the parietal, frontal, cingulate, and insular cortices (Van Hoesen, 1982; Insausti et al., 1987; Webster et al., 1991; Martin-Elkins and Horel, 1992; Distler et al., 1993; Saleem and Tanaka, 1996; Suzuki, 1996; Lavenex et al., 2002). Little is currently known about the distinctive functions of the different components of the medial temporal cortex, with possible exception of the entorhinal cortex (see below), but its contribution *de toto* is beginning to be understood.

Monkeys with medial temporal cortical lesions fail on preoperatively learned simple discrimination tasks but can relearn them (Thornton et al., 1997) as well as learn new simple discrimination tasks (Eacott et al., 1994). However, the operated monkeys exhibit mild to severe learning deficits on complex recognition or object identification tests. These include paired associate learning (Higuchi and Miyashita, 1996; Buckley and Gaffan, 1998a), recognizing familiar objects in unfamiliar contexts (Buckley and Gaffan 1998b), discriminating ambiguous stimuli (Bussey et al., 2002), oddity learning (Buckley et al., 2001), matching-to-sample or nonmatching-to-sample (Buffalo et al., 2000; Málková and Mishkin, 2003), and other complex learning tasks (Meunier et al., 1993; Chavoix et al., 2002; Buckmaster et al., 2004; Bachevalier and Nemanic, 2008). These lesion studies suggest that the medial temporal cortex is essential for mastering difficult learning tasks, although they leave open the question whether that is due to short-term or long-term memory failure. Some light has been shed on this issue by single-cell recordings in monkeys with intact temporal cortex. Xiang and Brown (1999) had monkeys learn a conditional discrimination task by responding differently to the different arrangement of three geometric figures on a screen. A high proportion of the visually responsive perirhinal and entorhinal neurons became selectively active during different phases of the learning process. Evidence has also been presented of increased perirhinal neuron activity in response to cues that signal forthcoming reward (Liu and Richmond, 2000; Liu et al., 2000).

While the specific role of different components of the medial temporal cortex in different aspects of the learning process remains to be determined, there is some evidence for the involvement of the entorhinal cortex in spatial learning. The entorhinal cortex has a distinctive laminar organization (Amaral et al., 1987) and is intimately associated with the hippocampus (Witter et al., 1989; Witter and Amaral, 1991; Witter, 1993; Blatt and Rosene, 1998; Yukie, 2000; Insausti et al., 2002). According to a new finding the entorhinal cortex contains “grid cells” that map geometric boundaries and landmarks in allocentric coordinates as the animal explores its environment and becomes familiar with it (Fyhn et al., 2004; Moser et al., 2008). This contrasts with hippocampal “place cells” that signal the animal’s position in the

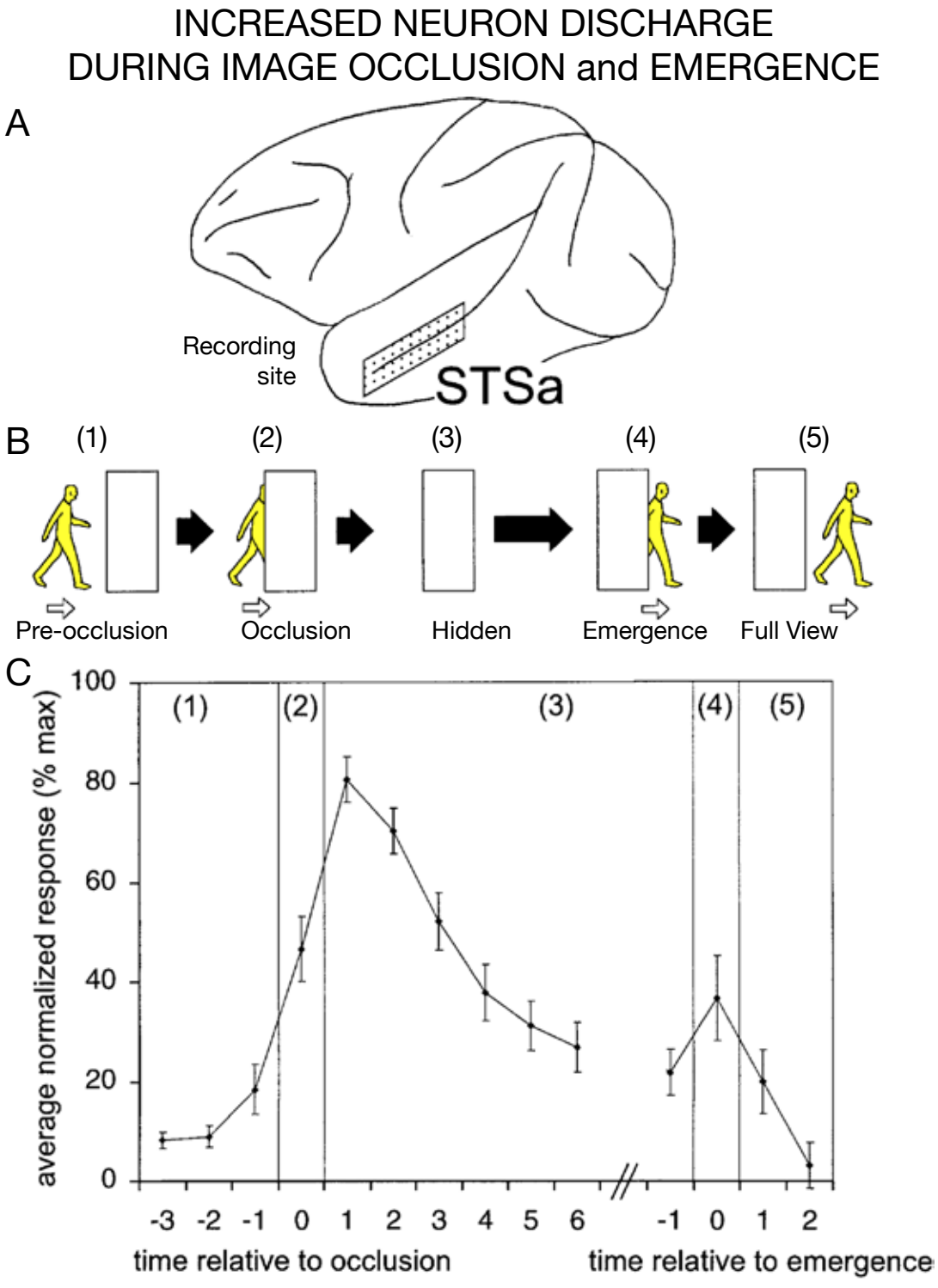


Fig 7-23. Discharge pattern of anterior temporal neurons in a "short-term memory" test. **A**. Location of the neurons recorded from. **B**. Monkeys watch a person approaching a screen (1), becoming partially occluded (2) and fully hidden (3), and then emerging (4) and getting in full view again (5). **C**. The neurons increase their discharge as the person becomes invisible and return to their baseline level as he becomes visible again. (Modified, after Baker et al., 2001.)

environment in egocentric coordinates. As we have argued earlier (Section 7.2.3), the function of the hippocampus is a motivational one, instigating the animal to explore its environment, paying particular attention to things that are unfamiliar in its habitat. The memory system of the entorhinal cortex may be the source of information for what is already familiar during exploratory behavior.

In summary, much has been discovered since the pioneering investigation of Klüver and Bucy (1938) regarding the functions of the simian temporal lobe. The mixed emotional, perceptual and cognitive alterations that they observed following temporal lobectomy may now be attributed to removal of different components of the temporal lobe as well as the amygdala, and perhaps some other structures and fibers of passage. Current investigations indicate that different sectors of the frontal lobe serve different functions. Excluding the auditory cortex, the posterolateral sector plays a crucial role in higher-order visual perception, the recognition of the varied objects of one's habitat and the events that transpire in it on the basis of object configuration, texture and color, movement and its speed, and other characteristics. But perception is an ephemeral event. To become knowledgeable about the outside world requires short-term working memory and the consolidation of what has been experienced in enduring memory stores. This apparently is the function of components of the anterolateral and medial sectors of the temporal cortex. The medial sector, which is closely associated with limbic structures, may be the more dynamic component of this system, concerned more with information acquisition; the anterolateral sector might be the system's more static component, concerned with conserving what has been learned for long-term use.

7.4 Simian Cognitive and Volitional Advances and the Dorsolateral Prefrontal Cortex

7.4.1. From Perception and Recollection to the Emergence of Cognition and Volition. The perception of objects, beings and events in the world, and the ability to recollect past experiences are two important aspects of acquiring familiarity with the world we live in. But more is needed to get a comprehensive view of what transpires in the world around us, i.e., comprehension or understanding, what is broadly subsumed under the term cognition. Cognition consists of three related processes: insight, foresight and hindsight. Insight refers to the ability to comprehend what one perceives through conceptualization and interpretation. Foresight refers to the ability to deliberate before making a choice and planning the action one undertakes. Hindsight refers to the ability to reconstruct what has transpired in the past and thus seek to explain why things turned out one way rather than another. These three processes participate in various combinations when a cognitive actor behaves rationally rather than emotionally or habitually.

THE APPERCEPTION OF RELATIONSHIPS. Objects, beings and events are not isolated entities, they are interrelated and interact with one another. Insight, foresight and hindsight are the cognitive processes concerned with the appreciation of the temporal, spatial and causal relationships that prevail among phenomena. The detection of relationships among diverse entities requires cognitive processing power, and more and more cognitive power is required when the nexus among the interrelated entities becomes less obvious. There are evident and

hidden relationships among phenomena, simple and complex relationships, and relationships that are necessary and those that are conditional or contingent on other things. Evident relationships are those that are perceptibly linked with one another by their contemporaneity and necessity. Inferring that staying in the rain will make one become wet requires minimal cognitive processing power. Complex relationships are those where the nexus between two observations are not contemporaneous or necessary, and they are even more complex where the nexus is contingent on particular conditions or circumstances. Seeing some distant rain clouds and drawing the inference that it will rain is not a necessary relationship. The rain clouds may be moving in another direction or they may pass over without producing any rain. To establish a more certain relationship requires more cognitive processing, like tracking the direction of the clouds, detecting a drop in temperature, and noticing an increase in wind speed. If a macaque monkey sees a tree heavily laden with ripe fruit, it is likely that it will climb up the tree in expectation of having a rewarding meal. That behavior requires perception not insight. If it passes by a tree without any visible fruit on it but notices discarded seeds on the ground, it could infer that the tree is bearing ripe fruit, and proceed to climb up the tree to explore if there are any fruit left there. This presumes minimal insight and foresight. Let us assume that the tree is occupied by a group of hostile baboons, but with some hindsight the macaque recalls the baboons' habit of visiting the tree in the morning and then leaving. Based on all that cognitive processing, the macaque might plan to delay its visit until later in the day and so avoid getting into a fight with the baboons. The appreciation of contingent relationships becomes more and more difficult as the number of variables increases. Below we review the available scientific evidence to what extent monkeys rely on cognitive processes in their behavior. We will consider reports of monkeys' spontaneous reliance on cognition in the wild or in semi-natural settings as well as laboratory studies in which the limits of monkeys' cognitive powers have been explored through intensive training and the use of various artificial aids. We will follow that with a consideration of what is currently known about the role of the simian dorsolateral cortex in the mediation of cognitive processes.

7.4.2. Simian Insight: Monkeys' Ability to Form Sketchy Concepts. The available evidence suggests that beyond the ability to recognize particular objects and beings, monkeys can form categories into which those objects can be placed. This ability—the transformation of what perception and imagery directly provide about particular entities by condensing and rendering them into prototypic representations—we shall call *sketchy concept formation*. We further argue that while monkeys can form imagery-based prototypic sketchy concepts, they lack the cognitive ability to form abstract concepts, ideas that cannot be represented as images but require verbal tokens and linguistic ability for referencing.

Categorization and Concept Formation. When a monkey ignores unripe green and bitter fruits on the tree but picks the ripe, sweet ones, it exhibits its ability to discriminate objects on the basis of their sensory qualities. Although *green* and *red* may be considered in some contexts as categories, as when a child is asked to sort various items into separate piles in terms of their named colors, reacting one way to green stimuli and in another way to red stimuli is not categorization but stimulus generalization, a primordial sensory ability. Categorization is a more complex process. It refers to treating different objects as equivalent in a given context because they share some important structural feature or functional property.

MONKEYS' ABILITY TO FORM SKETCHY CATEGORIES. As we noted earlier, monkeys readily learn in a three-choice oddity test (Fig. 6-20A) to treat the "odd" shaped object, irrespective of its specific configuration from one trial to the next, as belonging to the same category (correct choice) and the two "similar" objects as belonging to another category (false choice). Or, else, learn to ignore the shape of the objects and treat the odd colored object as belonging to one category, and the two similarly colored objects as belonging to another category. Markowitsch (1987) had squirrel monkeys view a sample picture and then, in a two-choice discrimination task, had them choose between two new pictures, one belonged to the same natural category as the sample, and another did not. After a single trial, the monkeys learned to classify the pictures into "natural" categories, such as cats, monkeys and people. They could also learn to disregard what the pictures portrayed and instead pay attention to their number (one, two or three items of any sort). Other studies have shown that monkeys readily learn to discriminate pictures of their own species from other species of monkeys, monkeys of any kind from people of any kind; different types of trees from non-trees, and so forth (Sands et al., 1982; Burdyn and Thomas, 1984; Schrier et al., 1984; Schrier et al., 1987; D'Amato and Van Sant, 1988). Indeed, the categorization of pictures as animals, furniture or vehicles, has been demonstrated in infant macaques without specific training (Murai et al., 2004). In the wild, as we described earlier (Section 6.1.2), a macaque may treat the same available stick as a "probe" when trying to extract a worm from a crevice, as a "spoon" when trying to remove honey from a beehive, and as a "spear" when trying to gore a gazelle. Conversely, a capuchin monkey may use a stick, a stone, or a chunk of oysters as a "hammer" to crack a nut and get its kernel or, else, lift and drop a boulder on the nut for the same purpose. Categorization provides some insight into the properties of objects by assigning different objects sharing a salient property to the same functional category, or vice versa, in accordance with the animal's current desire or preoccupation.

THE DISTINCTION BETWEEN SKETCHY ENTITY CONCEPTS AND ABSTRACT RELATIONAL CONCEPTS. Entities can be represented in awareness in the form of condensed and morphed mental images, what Rosch (1978) called prototypes. "Animals" are furry things running on four legs; "dogs" are animals with one sort of facial feature or posture, "monkeys" with another sort; "people" are upright creatures with two long legs and clad in clothing; "vehicles" are shiny metallic contraptions with four wheels, and so forth. Monkeys trained to touch the icon of a particular dog on a computer screen to get a reward, and refrain from touching the icon of a particular monkey, tend to make the correct categorical choice when, in subsequent trials, they are presented with images of a different breed of dog and a different species of monkey. The simplest way to explain that ability is to assume that, having been exposed to different exemplars of the two species in the past, sketches of dogs and monkeys are generated that can be used as templates to distinguish any exemplar of them as either a dog or a monkey. We may consider these generalized quasi-pictorial mental representations as sketchy concepts. But can monkeys form concepts that cannot be pictorially represented? Can they generate concepts such as "yesterday" or "tomorrow"; "before" or "after"; "ahead or behind"; "right" or "left," "north" or "south"; "brave" or "vicious"; "honest" or "dishonest"; "possibly" or "necessarily"? These concepts do not refer to visible or tangible entities but to their invisible temporal, contingent and causal relationships. These abstract concepts, or ideas, are based on cognitive assessments of elapsed or anticipated time; egocentric spatial directions not manifest

through discernible, fixed landmarks; personal preferences and value judgments; conjectures, inferences and interpretations about veiled powers and obscure interactions among different entities, and so forth. Humans can refer to these thought-based relational ideas by using verbal labels as tokens to designate them; hence the question: can nonverbal monkeys entertain abstract concepts?

CAN MONKEYS FORM THE ABSTRACT IDEAS OF "SAME" AND "DIFFERENT"? Nonverbal primates, such as chimpanzees, can be tested for their ability to form abstract ideas by using a series of differently shaped plastic chips. One chip is arbitrarily assigned to serve as the token for the concept "same," the other for "different." The animal is then successively shown sets of two identical or two different chips and, to obtain a reward, it has to pick the token standing for "same" or different," as the case may be. It has been assumed in the past that monkeys cannot master this task (Premack, 1986; Tomasello and Call, 1997; Thompson and Oden, 2000. However, there are a few recent reports that monkeys can form these two abstract concepts and we examine the merits of these claims. Bovet and Vauclair (2001) successfully trained olive baboons to respond to the display of a pair of apples ("same") by pulling one rope, and to the display of an apple and a padlock ("different") by pulling another rope. In the subsequent test, the baboons had to respond to the display of an apple and a banana by pulling the rope that was to be the token for "same" (both being food items), and respond by pulling the other rope, which was to stand for "different," when a cup and a banana was displayed (one being a food item, the other a nonfood item). After this was mastered, the baboons were given a long series of tests with novel food and nonfood items. The researchers found that, on the average, after exposure to 36 different object pairs, the baboons could correctly identify a novel set of stimuli as the "same" or "different" at about an 80% probability level. Because the monkeys could appreciate whether the novel pairs belonged to the same category (food+food) or a different category (food+nonfood), the authors concluded that the monkeys acquired the abstract concept of "same" and "different." However, considering the long training involved, the argument can be made that the animals mastered a difficult perceptual (rather than conceptual) discrimination, i.e., pull one rope when *two* food items are displayed, and the other rope when only a *single* food item is displayed.

In another study with a different design, Fagot et al. (2001) trained two test-sophisticated baboons on a relational-matching-to-sample task where the sample was either a matrix consisting of 16 tightly packed "same" icons or a matrix of 16 tightly packed "different" icons (Fig. 7-24). After a delay, both displays appeared on the screen and the animal had to move the joystick to the one that matched the sample. After the baboons mastered this task, they were tested with novel sets of similar and diverse icons. It took one baboon close to 5,000 trials before it could match with an 80% probability the sample with the correct novel display; the other baboon needed over 7,000 trials. As a comparison, two human subjects reached near 100% level of performance after 96 trials. The authors concluded that, albeit difficult for the baboons, they possess the ability to form the relational concept of *same* and *different*. However, an inspection of the samples indicates that the baboons may have learned by trial-and-error to distinguish them on a perceptual (sketchy concept) basis. The matrix consisting of the same icons, irrespective what they were, gives the overall impression of a homogeneous (reiterated) texture, whereas the matrix consisting of different icons gives the impression of a

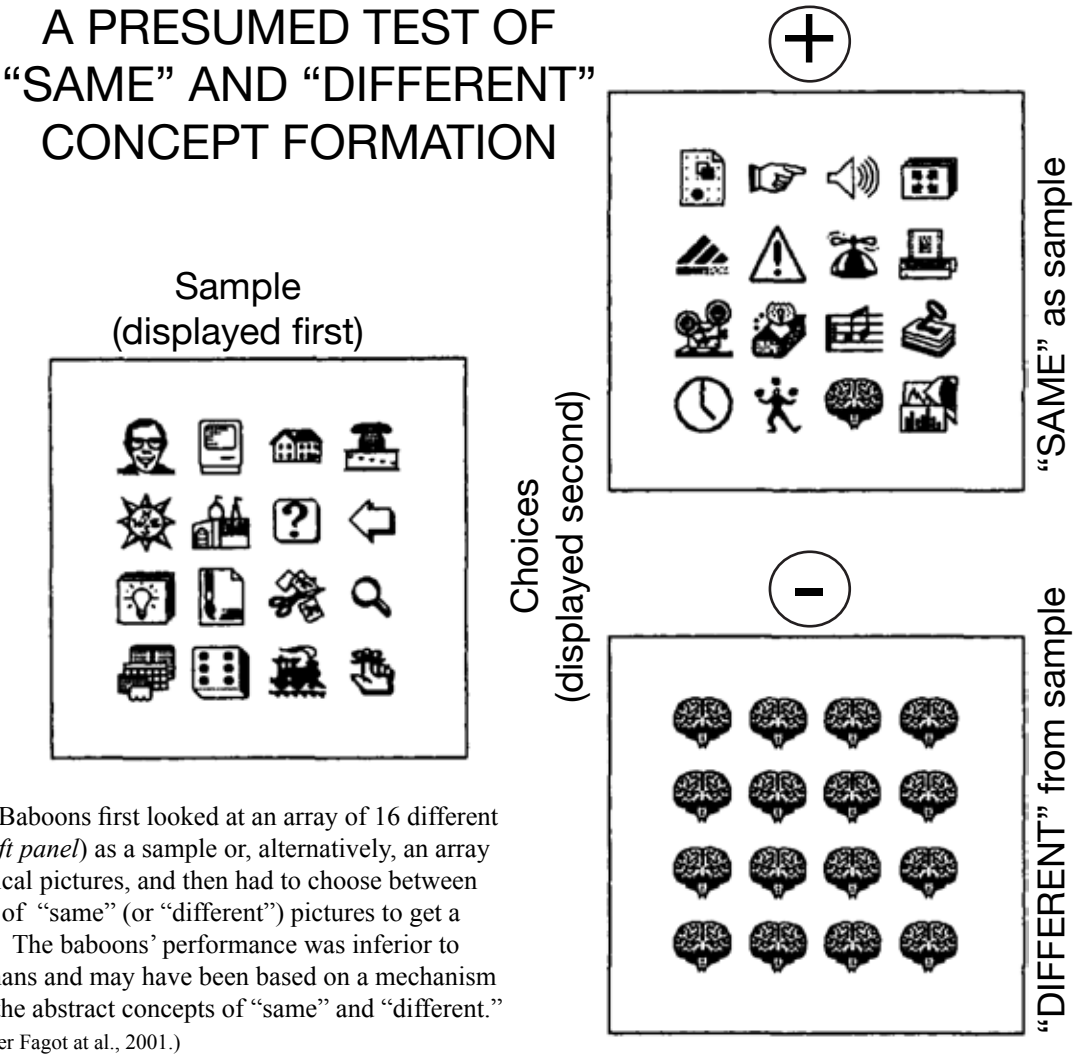


Fig. 7-24. Baboons first looked at an array of 16 different pictures (*left panel*) as a sample or, alternatively, an array of 16 identical pictures, and then had to choose between new arrays of “same” (or “different”) pictures to get a reward (+). The baboons’ performance was inferior to that of humans and may have been based on a mechanism other than the abstract concepts of “same” and “different.” (Modified, after Fagot at al., 2001.)

heterogeneous (mottled) texture. Indeed, as the authors reported, when the number of icons in the matrix was reduced from 16 to 4 and 2, the monkeys’ choice fell to a chance (about 50%) level. Presumably, the reduction of the icons in the matrix eliminated the textural effect that the animals used in matching novel samples. (The human subjects performance remained, irrespective of icon size, over 90%.) A similar effect of improved ability with large sets of items in solving same-different tasks was reported in rhesus monkeys (Katz et al., 2002). While monkeys readily learn to discriminate the “odd” from the “similar” stimuli in a perceptual discrimination tsk, there is currently no unambiguous evidence that they can entertain the abstract idea of *same* and *different*.

CAN MONKEYS ENGAGE IN ANALOGICAL REASONING? When verbally competent young children are given the following analogy test: *the dog is related to the doghouse, as the bird is related to (?)*, many of them appropriately come up with correct answer, *nest* (Goswami and Brown, 1989). Although there is nothing pictorially similar between a doghouse and a bird’s nest, children realize that both are “similar” in the sense that they serve a corresponding

function. The abstract idea of "home" and the designation of these two pictorially different items as *homes,* allow children to detect an analogous relationship between the two. Likewise, there is no pictorial similarity between pouring a glass of milk on the carpet and crossing the street by oneself but they are analogous because both are *"no-no"* actions subject to parental disapproval or punishment. Analogical reasoning is of great help in solving novel problems because it allows the application of what is already known in one situation to a comparable unknown situation. Can monkeys form the idea that pictorially dissimilar objects belong to the same category because they are *analogous* in some sense, e.g., serve the same function, obey the same rules, or share some abstract property? Kennedy and Fragaszy (2008) tested four tool-using capuchin monkeys in the following relational-matching-to-sample task (Fig. 7-25). The experimenter and a caged monkey set facing one another, each having within reach a set of three cups differing in size, shape and color. A food item was surreptitiously hidden under one of the cups in the monkey's collection and thereafter experimenter pointed with her finger to a different but analogous cup (comparable in size, shape, or color) in her own collection to inform the monkey under which analogous cup in its collection the food item was hidden. After many months of training (over 600 trials), 3 out of the four monkeys failed to solve this problem, but one of the monkeys reached criterion level of performance after 143 trials by selecting among a novel collection of cups the analogous one to which the experimenter pointed. The authors concluded that, contrary to previously held views, capuchin monkeys might be able to solve analogical problems. Considering that only one test-wise capuchin monkeys could solve the problem with all the support provided by the experimenter it is unwarranted to conclude that capuchin monkeys, perhaps the most intelligent of all simians, engage in analogical reasoning in their daily life.

"ANALOGICAL REASONING" BY A CAPUCHIN MONKEY

Fig. 7-25. Food is hidden under one of three yellow cups within the monkey's reach and the experimenter points to an analogous cup in her array (same relative size but different color and shape) as an aid to identify the correct cup. After the monkeys master this task, they are tested with novel sets of cups to determine whether they can engage in analogical reasoning. (After Kennedy and Fragaszy, 2008.)

7.4.3. Volitional Behavior: Planning, Deliberation, Collaboration, and Learning by Imitation. A facet of deliberate behavior is the awareness of what one is trying to accomplish and what action one has to take to achieve the end sought. Deliberation becomes particularly crucial when trying to solve novel problems. A monkey challenged by a two-choice discrimination task, can solve that problem by simply recollecting which of the two cues has delivered the anticipated reward in preceding trials. No planning or deliberation is needed in that situation. Planning becomes necessary if the animal has to initiate an action to achieve a desired end

state, for instance, proceed to the dispensing machine and activate it by pressing a button or inserting a token. Some deliberation is needed if there are two discrimination apparatuses available—one the source of some food item, the other of some liquid—particularly if the two are in different locations and require different tokens or different actions. Depending whether the animal feels hungry or thirsty, it will have to plan where to go and deliberate what action to carry out upon getting there. Under natural conditions, volitional behavior is exhibited when monkeys start out in the morning to proceed to a feeding site, separate there into smaller groups, and then gather in the evening at the water hole to refresh themselves and socialize. Because the availability of desired nutrients is periodic and site-specific, effective foraging may require familiarity with and consideration of the seasonal cycles of plant growth, recollection of where fruits ripen in a particular location, as well as recollection of routes to those sites, avoidance of lurking predators at particular locations and different times of the day, and so forth. This involves the planning of a series of successive moves, keeping in mind the distant goal and the intermediate steps required to reach it.

DO MONKEYS DELIBERATE BEFORE ACTING? One study addressed the question whether or not monkeys are aware that they know or do not know what their choice ought to be in a discrimination task (Hampton et al., 2004). Rhesus monkeys had to choose between four opaque tubes, only one of which contained a food reward. In some trials, the monkeys could look on while the food was put into one of the tubes, in other trials they could not. Before making a choice, the monkeys were allowed to look down the tubes to see if it contained food but were only permitted a single choice. It was found, that when they knew the location of the food, most monkeys chose the correct tube without looking into it. But when they did not know which tube was baited, they often looked down the tubes before making the choice. Another study with a matching-to-sample task (Hampton and Hampstead, 2006) indicated that when the monkeys could remember the sample, they touched the screen gently. However, they hit the screen hard, as a sign of their frustration, when they could not remember the sample. These findings suggest that monkeys are aware whether they know or do not know what they have to do, suggesting that, when necessary, they deliberate before acting.

CAN MONKEYS COLLABORATE TO ACHIEVE A GOAL? According to one study, Tonkean monkeys (but less so rhesus macaques) can solve a cooperative task by jointly pushing a heavy stone to reach a covered food source (Petit et al., 1992). Another study found that, in a task that required the pulling of two handles, one capuchin monkey successfully pulled one handle as its companion pulled the other to get a reward (Chalmeau et al., 1997). It was suggested that they lacked insight into the mechanics of what they were doing and merely learned to perform the same action concurrently. But according to more recent reports, pairs of capuchin monkeys (Mendres and de Waal, 2000; de Waal and Davis, 2003) and tamarins (Cronin et al., 2005) displayed some degree of division of labor while cooperating in pulling handles to obtain rewards, and did so even when only one of them was rewarded at each trial (Hattori et al., 2005).

CAN MONKEYS LEARN TO SOLVE PROBLEMS BY OBSERVATION? Animals reared in a social setting learn from their more experienced elders how to respond to unfamiliar objects, events, and beings. However, much of that is made possible by a simple mechanism, called social

facilitation (Zajonc, 1965). Because the young tend to follow their mother, and inexperienced adults follow experienced companions, they are likely to learn what places to visit or avoid, how to locate feeding and watering sites, shelter, escape routes, and so forth (Thorpe, 1963). The inexperienced young, for instance, can learn to select food substances by nibbling on what the mother drops or what she shares with him. Likewise, the young may learn to abstain from ingesting substances that his mother rejects or to which she displays a negative emotional reaction. But can monkeys learn to master skills by observation, by imitating the other's behavior? Observational learning presumes the insightful ability to proceed from seeing to doing, the transformation of a perceived act into a novel motor ability.

That monkeys may learn by imitation comes from accounts of the spread of a new custom among members of a troop after its initiation by a particular individual. A well-known instance of this is the report about the spread of potato washing among free-living Japanese macaques (Imanishi, 1957; Kawamura, 1963). About one year after the establishment of a feeding station on the beach of a sea island, a young female was observed to clean the sand clinging to the sweet potatoes by washing them in a stream. After 4 years, about half of the monkeys acquired the habit of washing the sweet potatoes, and after 10 years up to 90 per cent of the animals did so. Another custom adopted by the troop was the separation of the mixture of wheat and sand on the beach by dropping a handful into a pool and letting the sand sink to the bottom. Still another custom adopted by a group of monkeys was swimming. Initially the monkeys rarely entered the sea, then a few started to swim, and a few years later all but some of the older animals regularly went to swim to cool themselves or just to frolic (Fig. 7-9). Were these behavioral modifications due to imitation by observational learning or were the animals following one another and acquiring these habits by social facilitation? Several experimental studies have addressed this issue. In one experiment, a group of marmosets were allowed to observe how a trained monkey pulled and held a swinging door, rather than push it, to gain access to a food reward. Two of the marmosets displayed clear evidence of imitating the demonstrator's effective procedure; the others did not (Bugnyar and Huber, 1997). In another study, some macaques were trained to use a wooden pole as a climbing device to reach a food reward (Ducoing and Thierry, 2005). Some untrained peers that could observe that behavior benefited from the demonstration, others failed to learn to use the pole to obtain the reward. Imitation is a well-developed trait of human children and (as we shall see) of chimpanzees raised by human caretakers. However, the evidence concerning monkeys is less clear. There are considerable individual differences even within the same species and much depends on task difficulty (Fragaszy and Visalberghi, 1989).

7.4.4. Volitional Advances: Tool-Using Monkeys' Limited Reliance on Insight and Foresight. While some monkeys do not use natural objects, like a stick or a stone, as tools in the wild to crack nuts, others, like capuchin monkeys, do. To be able to do that requires prolonged learning as seen in the report of Pouydebat et al. (2006). When given a choice to select among different substrates on which to crack nuts, adult capuchins opted for such hard substances as concrete or stone whereas inexperienced juvenile capuchins selected substrates randomly. The question is: do monkeys comprehend the relationship between the tool's utility and the goal to be achieved, or is their tool-using skill merely due to a combination of great dexterity and learning ability?

TOOL USING: EVIDENCE FOR LIMITED INSIGHT. Monkeys rarely use stones as tools in the wild. An exception is a population of wild capuchin monkeys in Brazil that regularly use stones as hammers, dropping them on logs or rocks that serve as anvils (Visalberghi et al., 2007; Liu et al., 2009; Spagnoletti et al., 2011). Males are more frequent stone users than females and lift the stones higher than females do (Fig. 7-26A, B). There is also some evidence that the monkeys can gauge how heavy a stone to use, depending whether they are trying to crack nuts of low or high resistance (Fig. 7-26C). This suggests some insight into the mechanics of nut cracking.

The issue of insight into tool use was directly investigated in capuchin monkeys that were challenged in the laboratory with the task of removing a peanut from the middle of a transparent tube (Visalberghi and Trinca, 1989; Visalberghi, 1990). The animals had access to rigid and flexible sticks, long and short sticks, sticks that were too thick to fit into the tube, and sticks with extruding pegs that had to be removed before they could be inserted into the tube. Most monkeys (but not all of them) did manage to get the reward after a series of trials. However, their comprehension of what they were doing appeared to be limited; for instance, a monkey would struggle with a short stick when a better-suited long stick was readily available. In a test specially designed to test the comprehension of means-end relationships in tool use, capuchin monkeys were presented with a tube that also had a small hole as a trap (Visalberghi and Limongelli, 1994). Depending where the stick was inserted, the reward was either successfully pushed away from the trap out of the tube, or into the trap, thereby rendering it inaccessible (Fig. 7-27). After a long series of trials, only one out of four monkeys could solve this problem and it, too, gave evidence of not fully comprehending the causal relationship. For instance, when the tube was turned so that the trap no longer served as an obstacle, the monkey persisted in pushing the reward away from the trap. Some chimpanzees (Limongelli et al., 1995), and two- to three-year old children appear to comprehend the causal principles involved in these tests and behave far more intelligently from the outset of the trials.

EVIDENCE FOR LIMITED FORESIGHT. The cognitive limitation of capuchin monkeys was further illustrated in a two-step procedural task that required them to leave a covered box containing nuts and stones to collect a rock to open the box (Jalles-Filho et al., 2001). Although capuchin monkeys readily learned to use an available rock to remove the cover of the box to get to its contents, they failed if they had to leave the box, pick a rock from a familiar nearby pile and return with it. Holding on mentally, as a foresight, to the intended goal as well as the means to achieve it appears to be beyond their ability. As we shall see, chimpanzees readily solve such a two-step task both in the wild and in the laboratory. Another experiment indicated that capuchin monkeys readily learn which of two similar tools with different hooks is effective in getting a food reward, irrespective of the color or shape of the tool, but failed when the tool had to be moved to the site over traps or obstacles (Fujita et al., 2003). In another study (Santos et al., 2005), tamarins were trained to use a pulling tool to obtain a food reward. Subsequently, they were required to use that tool in combination with another one, to accomplish the same end. The animals had great difficulty in solving that problem. Finally, there is no evidence available that even the brightest of monkeys can modify an object to turn it into a suitable tool. These findings suggest that monkeys can apprehend simple means-ends relationships but fail if confounding variables are added.

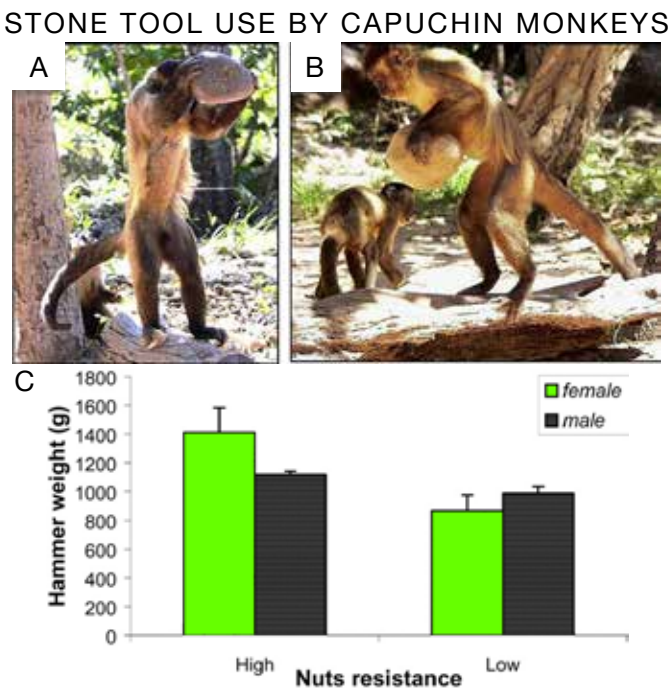


Fig. 7-26. Capuchin monkeys use stones to crack nuts (**A**, **B**), with a tendency to use heavier rocks to crack nuts that offer greater resistance (**C**). (After Spegnoletti et al., 2011.)

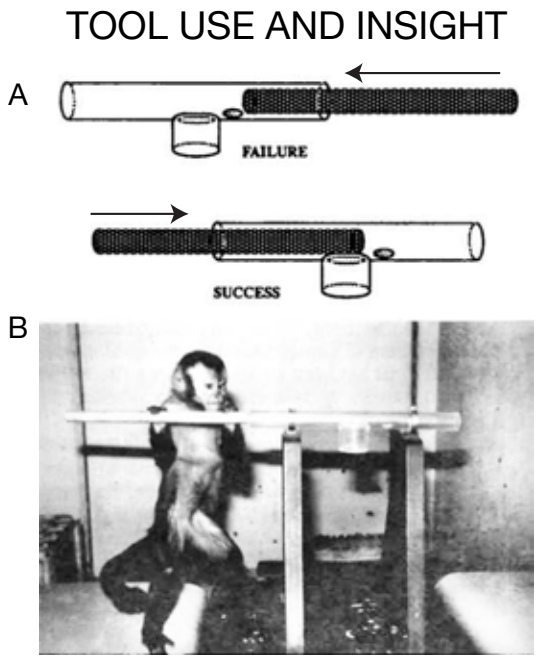


Fig. 7-27. In this test of insight into tool use, a probe has to be inserted from one end to prevent the reward falling into a trap. (From Visalberghi and Limongelli, 1994.)

7.4.5. Monkey's Limited Ability to Think and Absence of Self-Awareness. Monkeys are inquisitive animals, motivated from early infancy to acquaint themselves with everything and everybody in their habitat. They are agile and, thanks to their manual dexterity and long apprenticeship, have the potential to master complex skills before embarking on their career as procreative mature adults. And, in addition to possessing superior memory and learning abilities, they have a complex social life and long life expectancy, which allows them to continue to add to their fund of knowledge during adulthood. However, when compared with humans, monkeys have serious intellectual limitations. Although they can deliberate, as we saw, when circumstances demand it, they are fundamentally emotional and impulsive creatures rather than rational ones. They live mainly in the here and the now, tacitly aware of what goes on around them but not explicitly conscious of it. Although they have strong wills and are power hungry, they are not aware of themselves as acting individuals responsible for their deeds. Nor can they contemplate or reflect upon what goes on in the world around them because that requires two faculties they lack: the formation of abstract relational concepts and the use of words as symbols to communicate with others what they have experienced and what they know.

THE LIMITED THINKING ABILITY OF MONKEYS. Experimental studies have established that monkeys can learn to solve difficult multistep practical

problems, and they apparently do that with the aid of a mental process that may be called thinking. They seem to hold in their awareness the end sought as a goal image, and keep track of what has been accomplished and what still needs to be done by attending to prompting and guiding perceptual cues and feedback information. But that does not mean that they can entertain a meaningful stream of thought while sitting relaxed on a tree branch. To generate a meaningful inference or explanation, or produce a coherent narrative of what has transpired in the past, requires that the available perceptual images and the recollected memory images be tied together by abstract relational concepts. But as we noted, nonverbal monkeys cannot entertain abstract ideas. Although they must be tacitly aware of the difference between morning (when they wake up and embark on their foraging expedition) and evening (when they prepare themselves to climb up a tree and go to sleep), there is no reason to believe that they can entertain the simple idea of a "day" as a unit of time. Hence, they cannot possibly form the more complex temporal concept of "today," "yesterday," and "last summer" to organize snapshots of memory into a narrative of what transpired in their past. They may be tacitly aware that the sun rises at the river bend in the morning and sets behind the mountain in the evening, but since the sun does not appear to be moving, they cannot possibly infer that the sun follows an arc over the sky during the day and must be moving in an arc underneath the ground at night to reappear near the river bend next morning.

MONKEYS' LIMITED ABILITY TO EXERCISE SELF-CONTROL TO INHIBIT IMPULSIVE TENDENCIES. There is ample experimental evidence that when challenged with difficult tasks, monkeys can deliberate and behave intentionally. However, considering the pronounced impulsivity of monkeys, the question arises how much volitional control do they exert in inhibiting their emotional tendencies? Santos et al. (1999) presented one group of tamarins with food inside a transparent box, which could be reached through an opening on the side. The tamarins kept trying to get the food from the front through the solid surface instead of reaching for it from the open end of the box. Once the wall of the box was made opaque, they readily learned to reach for the food from the side. The interpretation was that the animals could not inhibit their natural disposition to reach for the desired visible target. Kralik et al. (2002) carried out several experiments with tamarins with a task in which it was economically advantageous to inhibit their impulsive tendency. One group of tamarins could choose to reach either for a smaller or a larger quantity of food when, in fact, what they got was the opposite of what they chose. The tamarins failed to learn to reach for the smaller sample in order to receive the bigger reward. The same result was obtained with another group of tamarins that received nothing if they reached for the larger quantity; they persisted in reaching for the larger quantity and ended up getting nothing. While the animals could obviously discriminate the magnitude of the sample, they could not inhibit their disposition to grab the optimal reward. On the other hand, capuchin monkeys did learn to exchange lower quality food items with an experimenter to obtain higher quality items, particularly when the difference between the two was considerable (Drapier et al., 2005). But most of the monkeys could not resist nibbling when they could exchange a smaller quantity for a larger quantity of favored items. In another experiment, capuchin monkeys were given a rod-shaped food item that they could either consume immediately or use as a tool with which to extract a preferred delicacy (Evans and Westergaard, 2006). Monkeys with little tool-use experience immediately consumed the potential tool. However, some monkeys with extensive tool-use experience displayed more self-control by delaying

gratification for the opportunity to obtain the more favored item. As a variation on this theme, the ability of capuchin and squirrel monkeys was tested to delay gratification and receive a larger reward (Anderson et al., 2010). The experimenter had six pieces of food out of reach of the monkeys, and he put them within their reach one by one. The monkeys could reach for the food whenever they wished but, once they did so, the trial was terminated. It was therefore in the animals' interest to wait until all six items were transferred. After several phases of testing, the animals finally learned to refrain from reaching for the food items until all six was available.

ARE MONKEYS AWARE OF THEMSELVES? Gallup (1970, 1982) pioneered an approach to this problem by examining what chimpanzees and monkeys might see when presented with a mirror. When first sighting their visage in a mirror, both behave as if they are facing another animal and try to interact with it. But after a few hours of exploring the mirror's properties, the chimpanzees engage in a behavior that suggests that they are beginning to realize that they are looking at themselves. The chimpanzee may start picking its teeth while looking into the mirror, look at its mouth while blowing bubbles, or turn its body to inspect its rear. In contrast, monkeys do not display this self-exploratory behavior, and after a while they just ignore their reflection. Using an experimental approach, Gallup anesthetized chimpanzees and monkeys, and marked their ear and forehead with an odorless paint. Before seeing themselves in a mirror, the awakened chimpanzees paid no attention to the painted area. However, those chimpanzees that had previous experience with the mirror (but not those that had no such experience) touched the painted areas with their fingers as they looked at themselves in the mirror. In contrast, none of the monkeys tested have passed this test. In one test, the mirror was removed for a few days from a cage where two monkeys lived together for years (Gallup and Suarez, 1991). For a short while they again tried to interact with their reflection, as if seeing other monkeys, then they stopped. Most subsequent studies confirmed Gallup's reports, including one that tested mirror self-recognition in capuchin monkeys (Roma et al., 2007). Modifying a proposal made by de Waal et al. (2005), the evidence seems to suggests that monkeys initially treat their mirror image as a "stranger," then as a "puzzling other," and finally as "no one there." We may tentatively conclude that the self-knowledge of monkeys, as determined by the self-recognition test is, at best, poorly developed.

7.4.6. Simian Advances in Social Cognition and Communication. The recognition of one's own species is widespread among vertebrates as seen, for instance, by the aggregation of fish in schools and birds in flocks. However, in most cases lower vertebrates do not seem to recognize members of the group as unique individuals. For instance, there are no "leaders" and "followers" in the school of minnows; the identity of those in the forefront constantly changes as the school suddenly turns this way or that in an attempt to avoid a predator (Section 3.3.5). There is some indication of individual recognition when, following a fight in an aquarium, two Siamese fighting fish establish a dominance relationship. However, the conspicuous physiological and behavioral differences displayed by the victor and the vanquished may be the determinant in sustaining that dyadic relationship rather than individual recognition. Among herbivores, recognition of one's own young is widespread, and that is attributed to early imprinting based on olfactory or visual cues. But there is little evidence that individual recognition plays an important role in the interrelationship of members of a herd. In contrast,

individual recognition is very important among carnivores, such as canines, that undertake coordinated hunting expeditions. The same applies to many species of monkeys that live in complex societies.

RECOGNITION OF INDIVIDUAL TRAITS AND SOCIAL STATUS IN MONKEY TROOPS. In a hierarchically organized social order it is essential that each member is familiar with the strength, agility and temperament of all the others as individuals, and of their social position. As we noted earlier, the ability of monkeys to recognize each other as individuals is based on a unique perceptual process. In contrast to object recognition, where it is advantageous to recognize a multitude of exemplars as members of the same category, the ability to recognize individual members of a large group requires discrimination of subtle differences in their physiognomy, distinctive facial features and expressions, vocal characteristics, and the like. There are several reports that monkeys within a group recognize each other as individuals with particular attributes and, when interacting with one another, take into consideration kinship, social status, and previous friendly or hostile encounters (Byrne and Whiten, 1988; Tomasello and Call, 1997; Aureli and de Waal, 1998; Call et al., 1999). When engaged in social grooming, kin is favored over non-kin, and a higher-ranking non-kin over a lower-ranking kin. Among females, the mother's social status is passed on to her daughters, which may lead to the formation of enduring matrilines. Males who leave their mothers have to fight to gain high social status and form political alliances with other males to preserve social status. The monkey that is threatened by another is likely to seek the support of a kin rather than a non-kin, or a non-kin that is dominant over the attacker rather than one that is subordinate to it. Keeping track of family relations and social position in such a third-party setting is obviously a complex cognitive process. A facet of recognizing the social consequences of one's behavior is the widespread practice of seeking reconciliation after a fight (de Waal, 1989; Kappeler and van Schaik, 1992). Peacemaking may consist of joining the opponent, touching it, clasping it, and grooming it. Another indication of the appreciation of the harmful social consequences of conflict between two monkeys is when a third-party member seeks either to pacify the aggressor or console the victim (Das et al., 1997; Call et al., 2002). Social cognition is evidently a well-developed characteristic of monkeys living in larger troops.

SIMIAN VOCALIZATION AS THE COMMUNICATION OF EMOTIONS. A prerequisite of maintaining the cohesiveness of a large group is effective communication. Monkeys extensively use eye movements, facial expressions and vocalization to share with conspecifics their feelings, desires, and moods. There is evidence for a positive correlation among primates between group size and the range of their vocal repertoire (McComb and Semple, 2005). Baboons that live in large groups, use over ten different calls and as many different facial expressions (Estes, 1991). When emitting different calls, are monkeys engaged in impulsive emotional expression? Or do their calls have referential content, denoting what they want to obtain, how to go about getting it, who will do what in a cooperative effort, and so forth, much like words do in human communication? Favoring the view that some monkey calls have referential content comes from the finding that, sighting different predators, vervet monkeys emit different calls and conspecifics react to them discriminatively (Struhsaker, 1967; Seyfarth et al., 1980). Likewise, juvenile rhesus monkeys scream when frightened by another monkey but the call has its distinctive acoustic feature, which informs the mother who threatens the juvenile. Mothers

are less likely to respond to screams when a kin rather than a non-kin threatens the young, or a dominant rather than a subordinate monkey is the source of threat (Gouzoules et al., 1984). There is also some evidence for context in simian vocalization. When a vervet monkey is separated from its group in the wild, it does not emit an alarm call when it sees a predator; it runs for cover instead (Cheney and Seyfarth (1990). And in the laboratory setting, female vervets give alarm calls at a higher rate when they are with their own offspring than when they are with unrelated juveniles (Cheney and Seyfarth, 1985). Moreover, Diana monkeys (Zuberbuhler, 2002) and putty-nosed monkeys (Arnold and Zuberbuhler, 2003) may use something similar to the syntax-governed sentences of humans when they emit two calls in combination.

THE DIFFERENCE BETWEEN SIMIAN VOCALIZATION AND HUMAN LANGUAGE. The evidence that simian vocalization is a more nuanced means of communication than was hitherto assumed, does not imply that it is an incipient form of linguistic communication. To begin with, monkeys do not have to learn to emit the repertoire of calls made by their conspecifics, and what they convey, the way humans have to learn the emission and comprehension of the conventional words and phrases of their culture. Without prior learning, squirrel monkeys emit the entire vocal repertoire of the species when 6 days old (Winter et al., 1973) and, if raised in isolation, they respond appropriately to the different alarm calls of conspecifics (Herzog and Hopf, 1984). Furthermore, no abnormalities are produced in the vocalization of vervet monkeys if they are deafened soon after birth or raised with mute mothers (Talmadge-Riggs et al., 1972). What these studies indicate is that the vocal communication of monkeys is an inborn disposition and ability (Seyfarth and Cheney, 1986). In sharp contrast, human children acquire the vast vocabulary of the particular language of their culture through imitation, training and practice: they have to learn how to pronounce the words, their precise meaning, and how to combine words by learning the grammar and syntax of their particular language. And, most importantly, once able to speak, children learn not only to express their wishes, fears and wants but also to ask questions, give answers, talk about their past experiences, converse about current concerns, and discuss future plans.

Even though both simian vocalization and human verbalization are generated by the same basic mechanism of sound generation, the two are very different. In both species, vocalization is produced by forcing air through the vocal tract using bellow-like respiratory muscles, but the acoustic features of vocalizations differ in how they are modulated (Bastian, 1965; Lieberman, 1984). The laryngeal and sublaryngeal subsystems, the *lower* vocal tract, produce barks, grunts, growls, hoots, coos, trills, etc. In contrast, the vowels and consonants that form the phonemes of human words are mainly produced by glottal pulsations of the *upper* vocal tract through intricate placements of the tip of the tongue on the palate, teeth, and lips. Spectrograms of simian calls indicate that they vary in pitch, intensity, and duration but not in the spectral complexity of human words. That is, simian vocalization is a coarse *power* production when compared with the finely tuned *precision* orchestration of human speech. The calls of monkeys, and associated facial expressions, are more like the crying, screaming, frowning, cooing, smiling and laughing of nonverbal infants, and the yelling and cussing by adults when emotionally aroused, rather than the sharing of cognitive information with others by way of a combination of a large vocabulary of words into an endless number of phrases that convey propositions, instructions, questions, arguments, narratives, and so forth.

ABSENCE OF A SIMIAN NEOCORTICAL NETWORK FOR VOCAL COMMUNICATION? While there is extensive literature on the brain mechanisms of language comprehension and speech production in humans, there are few studies on the brain mechanisms of simian communication. Single-cell recordings have revealed the presence of neurons in the auditory cortex of monkeys that selectively respond to species-specific calls (Newman and Wollberg, 1973; Winter and Funkenstein, 1977; Rauschecker et al., 1995; Wang et al., 1995; Rauschecker and Tian, 2000; Tian et al., 2001; Wang and Kadia, 2001), and imaging studies have identified superotemporal regions that are activated by species-specific vocalizations, and are selective for calls emitted by familiar monkeys relative to the calls of other animals (Petkov et al., 2009). Correspondingly, superotemporal lesions severely interfere with the ability of monkeys to respond to the calls of conspecifics (Heffner and Heffner, 1989; Harrington et al., 2001). On the other hand, there may be no simian neocortical mechanism for volitional vocalization. According to Jürgens (1979), stimulation of many brainstem sites in the squirrel monkey produce vocalization expressing fear or anger but such vocalization is not triggered by neocortical stimulation. In rhesus monkeys an apparent absence of volitional control of the vocal apparatus is suggested by the reported lack of a direct projection from the cortical tongue region to the hypoglossal nucleus, the subcortical structure that controls vocalization, although there is such a projection to the nucleus ambiguus, which controls mastication (Simonyan and Jürgens, 2003). Using a different approach, Rilling et al. (2008) reported that the component of arcuate fasciculus, which interconnects the temporal lobes, an essential element of the circuit responsible for speech production in humans, is absent in macaques. These findings may partly explain why monkeys that can master extremely complex cognitive and instrumental tasks but cannot learn to speak. Regrettably, there are no specific studies currently available regarding the cortical control of the other media of simian communication, in particular that of facial expression and gesturing.

In summary, monkeys are incapable of linguistic communication, first, because of their inability to articulate words. Second, and more importantly, without words monkeys lack the ability to form ideas and engage in thinking. Ideas and thoughts are higher-order mental processes than perceiving and remembering. They are conjectures, inferences, explanations, questions, beliefs, musings, fantasies, etc., about what we experience. Words are essential vehicles for the ideas we form. Humans have evolved a language, and all normally developing children are self-motivated to learn to speak, because of our cognitive need to comprehend what we experience. Monkeys lack that motivation.

7.4.7. The Role of the Simian Dorsolateral Prefrontal Cortex in Cognition and Volition. The simian dorsolateral prefrontal cortex is an extended region of the frontal lobe, traditionally divided into areas 9, 45 and 46 (Fig. 6-10A). In the rhesus monkey, it is convoluted, composed of the superior, medial and inferior temporal gyri (Fig. 6-13B). The prefrontal cortex is distinguished from the orbitofrontal cortex, which we considered earlier as a component of the affective system (Section 7.2.4), as principally a cognitive mechanism concerned with the intelligent management of behavior. Clinical studies have established that patients with extensive frontal lobe lesions, including those who have undergone frontal lobotomies, undergo profound personality changes. The symptoms include deficits in the ability to carry out daily activities that require mental concentration and deliberation, impulsivity and irresponsibility,

failure to delay gratification, saying and doing things that are considered socially and morally inappropriate, and ignoring the consequence of one's actions (Brickner, 1936; Damasio et al., 1990; Passingham, 1993; Bechara et al., 1994; Fuster, 1997; Anderson et al., 1999; Stuss and Knight, 2002; Hornak et al., 2003; Chamberlain and Sahakian, 2007; Torregrossa et al., 2008). Accordingly, it is widely believed that the frontal lobe is the highest-order integrative center of the human brain. Since the simian prefrontal cortex resembles cytoarchitectonically its human counterpart (Walker, 1940a; Pribram et al., 1953; Petrides and Pandya, 1999, 2002), its functions have been experimentally investigated from that perspective.

Organization and Functions of the Simian Prefrontal Cortex. Unlike the cortical sensory, motor and premotor areas, the prefrontal cortex is not targeted by the large thalamic relay nuclei that directly convey peripheral sensory input from the visual, auditory and haptic systems. The major source of thalamic input to the prefrontal cortex is the mediodorsal nucleus (MD; Walker, 1940b; Olszewski, 1952; Tobias, 1975; Goldman-Rakic and Porrino 1985; Ray and Price, 1993). This is a reciprocal connection, as a large complement of prefrontal efferents targets the MD (Kievit and Kuypers 1977; Siwek and Pandya, 1991). There are also connections with the premotor and motor areas (Morecraft and Van Hoesen, 1993; Carmichael and Price, 1995b; Muakkasa and Strick, 1979), but most of the cortical connections of the prefrontal cortex are with higher-order association areas, including the parietal cortex (Petrides and Pandya, 1984; Caminiti et al., 1996; Gallese et al., 1997), the temporal cortex (Seltzer and Pandya, 1989; Bachevalier et al., 1997; Barbas et al., 1999; Rempel-Clower and Barbas, 2000; Luppino et al., 2001; Marconi et al., 2001), and the cingulate cortex (Morecraft and Van Hoesen, 1993; Arikuni et al., 1993). There are also connections with the striatum (Alexander et al. 1986; Yeterian and Pandya, 1994; Ferry et al., 2000; Middleton and Strick, 2002; McFarland and Haber, 2003) and the cerebellum (Middleton and Strick, 2001; Kelly and Strick, 2003). That is, the MD and the prefrontal cortex are key components of the internal cortico-basal ganglia-thalamo-cortical loop.

EXTRINSIC AND INTRINSIC PROCESSOR SYSTEMS IN THE SIMIAN CEREBRAL CORTEX. In his classical study of the monkey thalamus, Walker (1938) distinguished three regions in the macaque cerebral cortex: regions receiving very dense thalamic projections, those receiving light thalamic projections, and those receiving no thalamic projections (Fig. 7-28). (*i*) The dense-projection areas, with one exception, are the primary projection areas (A1, V1, S1, and M1). (*ii*) The light-projection regions are the association areas of the occipital (visual), parietal (haptic) and frontal (premotor) cortices, the posterior sector of the temporal cortex, and the orbitofrontal cortex. (*iii*) The region without thalamic projection is the anterior temporal cortex that we now know to play a major role in memory storage and retrieval. The exception to this generalization is the prefrontal cortex, which has a dense thalamic projection but, as we noted, is targeted by the internally connected mediodorsal nucleus rather than the externally connected relay nuclei of the thalamus.

An incomplete series of coronal sections of the monkey forebrain immunostained with parvalbumin (prepared by E. G. Jones) supports the division of the cerebral cortex into different regions with reference to their apparent connections with the peripheral senses by way of the thalamic relay nuclei. The method used stains intensely the optic tract fibers (Fig. 7-29B)

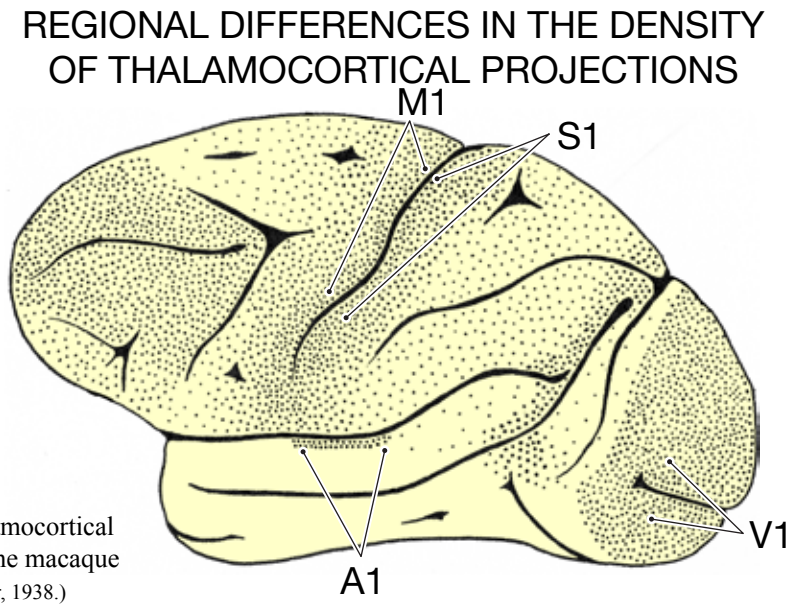
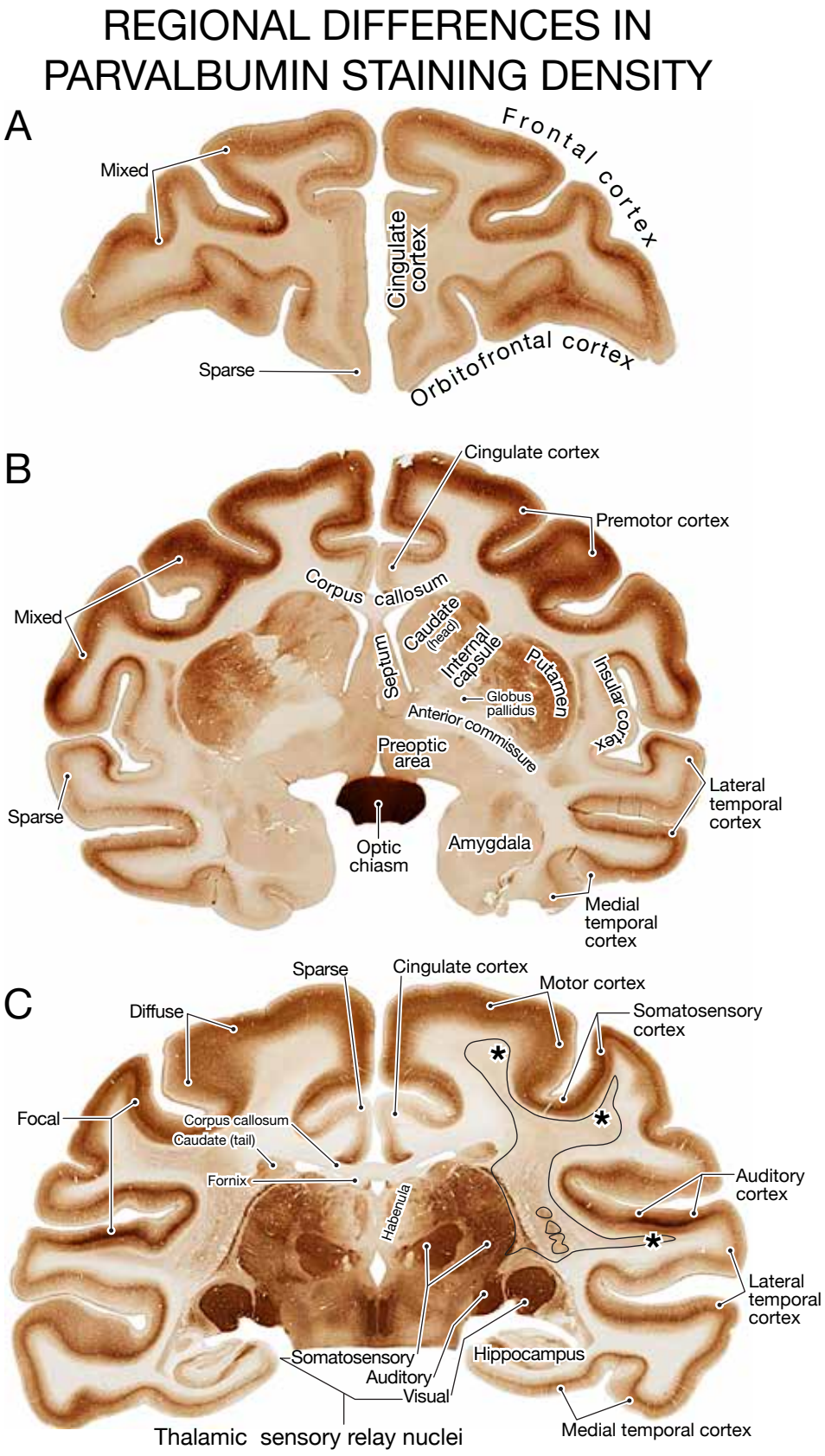


Fig. 7-28. Relative density of thalamocortical projections to different regions of the macaque cerebral cortex. (Modified, after Walker, 1938.)

and the visual, auditory and somatosensory relay nuclei of the thalamus (Fig. 7-29C). The fiber tracts of the cerebral hemispheres—the corpus callosum, internal capsule and the anterior commissure—are unstained (Fig. 7-29B), as is the white matter anteriorly. The staining pattern of the cortical gray matter varies considerably in different regions. Distinguished by a very dense band, presumably the granular layer where the thalamocortical fibers terminate, are the somatosensory and auditory projection areas (Fig. 7-29C). Diffusely stained infragranular and supragranular layers surround this "focal" band. "Diffuse" staining characterizes the entire agranular motor cortex (Fig. 7-29C) and premotor cortex (Fig. 7-29B). Adjacent to these densely labeled cortical areas is a band of white matter that shows light labeling (asterisks in Fig. 7-29C). These may be thalamocortical fibers. These sites constitute the extrinsic processing system of the cerebral cortex. Gray matter staining in the other cortical areas varies considerably, with some of them showing a "sparse," others a "mixed" pattern. The prefrontal, orbitofrontal, insular, cingulate, and medial temporal cortices are the least stained regions, representing the intrinsic processing system.

THE PREFRONTAL CORTEX AS AN INTERNAL INTEGRATIVE SYSTEM. With its scanty direct connections with the sensory projection areas but extensive connections with the association areas of the cortex, as well as the striatal and cerebellar loops, the prefrontal cortex may be considered an internal processor system. This feature differentiates it from the cortical projection areas as well as the lower-level association areas that are closely connected with the peripheral senses by way of the thalamocortical radiation fibers. This internal anatomic

Fig. 7-29. Regional differences in parvalbumin immunostaining in the forebrain of a monkey. The optic chiasm (**B**) and the thalamic relay nuclei show the most intense staining (**C**). In the cortical projection areas there is an intensely stained, thin band in the mid-portion of the central gray of the somatosensory and auditory projection areas, interpreted as the terminal sites of thalamocortical fibers (**C**). *Asterisks* point to the region of the white matter, adjacent to the projection areas, that show light staining. Mixed staining characterizes the different association areas, and sparse staining the subcortical (amygdala, hippocampus) and cortical (cingulate, orbitofrontal) components of the limbic forebrain. (Modified from Brainmaps.org)


REGIONAL DIFFERENCES IN
PARVALBUMIN STAINING DENSITY
A
Mixed
Frontal cortex
Cingulate cortex
Sparse
Orbitofrontal cortex
B
Cingulate cortex
Premotor cortex
Mixed
Corpus callosum
Caudate (head)
Septum
Internal capsule
Putamen
Insular cortex
Globus pallidus
Anterior commissure
Preoptic area
Sparse
Optic chiasm
Amygdala
Lateral temporal cortex
Medial temporal cortex
C
Sparse
Cingulate cortex
Motor cortex
Diffuse
Somatosensory cortex
Focal
Corpus callosum
Caudate (tail)
Fornix
Habenula
Auditory cortex
Lateral temporal cortex
Somatosensory
Auditory
Visual
Hippocampus
Medial temporal cortex
Thalamic sensory relay nuclei

organization would well fit a system concerned with deliberation and judgment, and the choosing and planning of actions rather than with their direct execution. The prefrontal cortex has been described as the "executive" center of the primate brain (Pribram, 1973; Fuster, 1997; Tanji and Hoshi, 2008). The term is used in analogy with the executive branch of a constitutional government or the executive officers of a large corporation. The term implies setting of goals and strategies, or a managerial function, rather than execution in the sense of implementation and performance.

TOP-DOWN MESSAGE FLOW FROM THE PREFRONTAL CORTEX TO THE MOTOR CORTEX. Information transmission is fundamentally different in the anterior hemisphere than in the posterior hemisphere (Fig. 7-30). In the posterior perceptual areas of the occipital, parietal and temporal lobes, message flow is a bottom-up process: from the peripheral sense organs, by way of the relay nuclei of the thalamus, to the cortical primary sensory projection areas, to the unimodal association areas, and finally to multimodal integrative areas. In contrast, the anterior hemisphere command flow is a top-down process: from the prefrontal cortex to the premotor cortex, to the primary motor cortex, to the spinal cord, and finally out to the muscular system. Translating this into functional terms, the prefrontal cortex is where the intent to achieve a goal originates; the intention is transformed into an action plan in the premotor cortex; the plan is translated into action command in the primary motor cortex; and the command that reaches the spinal cord is dispatched to the periphery to produce skeletomuscular movements.

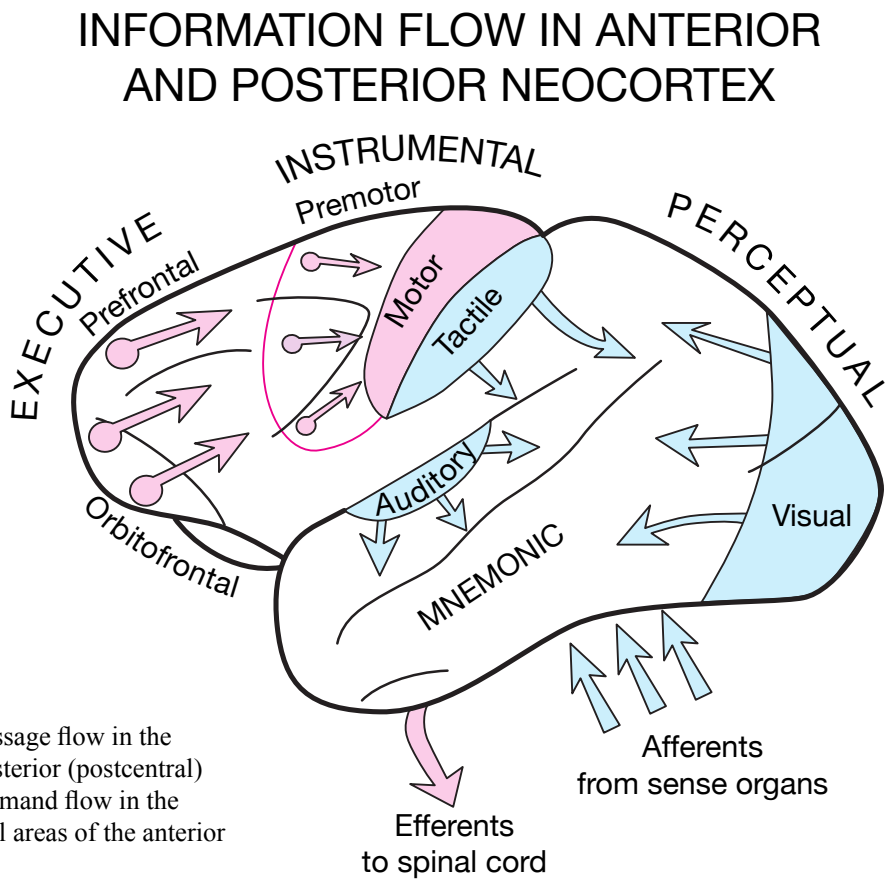


Fig. 7-30. Bottom-up message flow in the perceptual areas of the posterior (postcentral) cortex, and top-down command flow in the executive and instrumental areas of the anterior (precentral) cortex.

Cognition: The Role of the Simian Prefrontal Cortex in Rule Learning. In a pioneering study, Jacobsen (1936) found that prefrontal ablation impairs the performance of monkeys in a simple delayed reaction task. This apparent working memory deficit following prefrontal lesions has been confirmed subsequently by several investigators in more complex behavioral tasks, such as delayed spatial or object alternation (Mishkin and Pribram, 1955; Pribram and Mishkin, 1956; Mishkin, 1957; Butters et al., 1971; Mishkin and Manning, 1978) and delayed stimulus matching (Passingham, 1975). Similar deficits on delayed response performance were reported following mediodorsal thalamic lesions (Isseroff et al., 1982; Aggleton and Mishkin, 1983; Zola-Morgan and Squire, 1985), the thalamic site (as noted earlier) that is a major source of afferent input to the prefrontal cortex. Memory storage is, of course, not a unique function of the prefrontal cortex; as we saw earlier, the major site of mnemonic processing is the temporal cortex. More recent studies suggest that the role of the prefrontal cortex is, rather, the integration of multiple pieces of salient information—mnemonic as well as perceptual and affective—which enable monkeys to solve difficult problems.

LIMITED WORKING-MEMORY CAPACITY OF MONKEYS WITH PREFRONTAL LESIONS. Petrides (1995) first trained monkeys to select one of three objects differing in color and shape to obtain a reward. On the first trial, the selection of any one of the three objects was rewarded. Once the animal has chosen a particular object, its task became to choose, after a 10-second delay, an object it has not previously selected. Testing continued until all objects were chosen only once; that is, until the animal learned to monitor in its short-term awareness what it has already chosen previously and abstain from selecting the same object twice in a given trial. Prefrontal lesions produced deficits in this rule-learning task, although not in simpler memory tasks, such as distinguishing familiar objects from novel ones. In a subsequent experiment, the monkeys with prefrontal lesions were compared to monkeys with anterior inferotemporal lesions (Petrides, 2000b). A modification of the same learning task was used but the number of choice objects was increased up to five items and the delay period lengthened up to 120 seconds. The results indicated that lengthening the delay interval between trials produced severe deficits in the monkeys with anterior inferotemporal lesions but not with prefrontal lesions. In contrast, dorsolateral prefrontal lesions produced deficits if the number of choice objects was increased but not if the delay was lengthened. This finding suggested that the prefrontal cortex plays an important role in extending working-memory capacity (how many items can be held in awareness) and the inferotemporal cortex in lengthening working-memory (how long items can be retained in short-term memory).

RESPONSE PERSEVERATION AND IMPULSIVITY IN MONKEYS WITH PREFRONTAL LESIONS. Memory storage facilitates adaptive behavior by allowing the recognition of an immense variety of objects and beings in the environment and their salience or utility. But situations change over time and habits that were beneficial in the past may become useless or even harmful. The ability to inhibit bad habits—overcome the perseverative tendency—is a prerequisite of behavioral flexibility. A simple method to study that ability is reversal learning. In a two-choice discrimination task, the cue that was signaling reward is changed to signal frustration, and the animal has to learn to reverse its reaction. Reversal learning has been demonstrated in all higher vertebrates and, when exposed to a succession of reversal tasks, monkeys perform better than most other mammals do (Warren et al., 1966; Beran et al., 2008). Monkeys with frontal

lesions display a perseverative tendency in reversal learning tasks; selecting the previously rewarded cue even if the changed regimen requires them to select the opposite cue (Mishkin, 1964; Iversen and Mishkin, 1970). This perseverative tendency was also seen in prefrontal monkeys that kept responding to a cue when that no longer signaled reward or when they were satiated (Butter et al., 1963; Butter, 1969). Monkeys with prefrontal lesions also display impulsivity, as indicated in tests with "go" and "no-go" cues. In these tests, the animal has to wait either for the "go" signal before responding or learn to discriminate a "go" and a "no-go" signal. Early studies suggested that the learning deficits of monkeys with prefrontal lesions could be attributed to their inability to refrain from responding in "no-go" trials (Settlage et al., 1956; Rosvold and Mishkin, 1961; Battig et al., 1962). The failure of monkeys to inhibit responding to a "no-go" signal was recently reported following chemical inactivation of the prefrontal cortex (Ma et al., 2003).

THE ROLE OF PREFRONTAL NEURONS IN TASKS INVOLVING SEQUENTIAL CUES. Supplementing the ablation method, experimenters have recorded the activity of prefrontal neurons while monkeys were engaged in complex learning tasks (Fuster and Alexander, 1971; Fuster, 1973; Kubota and Niki, 1973; Rosenkilde et al., 1981; Watanabe, 1981, 1986a, 1986b, 1990, 1992; Quintana and Fuster, 1999; Watanabe et al., 2001, 2002, 2005). For instance, in an early study by Watanabe (1981), a monkey sitting in front of a video monitor was briefly shown an instruction cue (a red or a green light), informing it about the rule that it will have to use in that particular trial. This was followed by a brief delay, which requires the animal to retain the instruction cue in its memory. After that delay, two different visual figures appeared on the left and right side of the video screen. To obtain a reward, the monkey had to respond differently to these visual stimuli, depending on the initial instruction cue. There was then a second brief delay, while the animal had to wait for a new cue, the "go" signal, to make its choice. An analysis of the firing pattern of different prefrontal neurons during the performance of this complex task indicated that the activation of some neurons was time-locked with the instructional cue, that of others with the delay interval, still other neurons fired during the presentation of the visual stimuli or in relation to the action taken by the animal. That is, some neurons appeared to be involved in the short-term retention in awareness of the instructional cues; other neurons in the long term-recollection of the correct visual pattern cued by the instructions; and still other neurons were involved in the choice made in the visual discrimination task.

In a variation of this test, monkeys were trained to self-initiate a trial by pressing a lever (Watanabe, 1990). This triggered an instructional cue (a particular visual pattern) that informed the animal whether or not it will receive a reward in that particular trial. After a delay, discrimination cues appeared on the screen and if the animal made the correct choice, it received a reward only during rewarded trials. The animals quickly learned to refrain from responding during non-rewarded trials. Regarding the firing pattern of prefrontal neurons, Watanabe found that some of them became active in relation to the physical properties of the cue (color or pattern), others to their significance (whether the trial was a rewarded or a non-rewarded one), still others in relation either to the onset or termination of a trial. When both auditory and visual cues were used, some neurons responded only to the visual cue, some only to the auditory cue, while other neurons responded to both modalities in terms of their contextual significance (Watanabe, 1992). Quintana and Fuster (1999) reported similar

findings. In that study, the trial began with the presentation of a color (red, green, blue or yellow) that served as a cue about the probability of a reward. This was followed by a long delay. Then a discrimination cue was presented that informed the monkey what type of movement it had to make in that particular trial to receive a reward. Three broad classes of prefrontal neurons were identified. One set of neurons responded transiently to the color of the cue irrespective of its significance; a second set sustained its activity during the delay period; a third set appeared to reflect the animal's prediction of the likelihood of receiving a reward. In a more recent experiment, Watanabe et al. (2005) investigated the role of prefrontal neurons in the mediation of several memory processes, such as remembering the cues that assured a reward, whether it will be a rewarded or a non-rewarded session, and the kind of reward, preferred or non-preferred, that will be delivered. Some prefrontal neurons were identified that fired transiently during the preparatory period prior to the test session, some in relation to the presented cues, some during the waiting period, others in relation to the quality of the expected reward in a given test, and still others in relation to the animal's failure or success in getting the anticipated reward.

Another experiment sought to assess the role of premotor and prefrontal neurons in learning a rule based on object categorization (Wallis and Miller, 2003b). The monkey's task was to judge whether two successively presented novel pictures were the "same" or "different" and respond, accordingly, by holding or releasing a lever, in a given set of trials. The results indicated that more premotor neurons were involved in holding or releasing the lever (the motor part of the task), and more prefrontal neurons were involved in the discrimination of the presented pictures (same or different). In another experiment, monkeys were trained to categorize computer-generated images as "cats" or "dogs" (Freedman et al., 2002). The visual patterns were systematically varied in the course of the experiment and some evidence was obtained that lateral prefrontal neuron activity was related to the initial categorization of a stimulus and to learning that the same stimulus could belong to one or the other category.

Volition: The Role of the Prefrontal Cortex in the Planning and Orchestration of Actions. The translation of deliberate plans into volitional actions requires the proper sequencing of movements; inhibition of the tendency to respond impulsively, prematurely or in a stereotypic manner; keeping track of what has already been accomplished and what needs to be done; and the assessment of success and failure in achieving the end sought.

THE ROLE OF PREFRONTAL NEURONS IN THE SEQUENCING OF ACTIONS. Barone and Joseph (1989) trained monkeys to sequence a series of arm movements in the proper order by following a demonstration. In the first phase of the experiment, three targets appeared at the top, the right, and the left of a screen in a random order and the monkey received a reward by pressing them all in any order. In the second phase, the animal had to observe the sequence in which the targets appeared on the screen and then touch the targets in the same order. That is, the animal had to appreciate a sequential rule and act accordingly in different trials. Some prefrontal neurons were identified that were selectively active when the arm movements were correctly sequenced. In a related series of studies by Ninokura et al. (2003, 2004), monkeys were trained to observe the sequential order of a set of differently colored and shaped images on the screen as cues in what order they had to carry out a series of reaching movements (Fig.

7-31A). In the first phase of the training, the monkey had to place its hand on a pad to make a dot appear in the center of the screen. If the monkey held its gaze on the dot for 0.5 second, a yellow circle, a blue rectangle, and a red cross appeared successively on the screen in a random order, and touching them all in any order delivered a reward. In the second phase, the order of the appearance of the three colored figures on the screen (ABC, ACB, BAC…..) became a sequencing cue, and after a delay of 1.5 seconds, when the monkey received the "go" signal, it had to touch the three patterns in the same order. Lateral prefrontal neurons were identified which selectively responded to the particular figure irrespective of its position (Fig. 7-31B), the sequential position of the figure irrespective of its identity (Fig. 7-31, cells 1, 2), or to both features (cell 3). Another study, which required monkeys to move a cursor stepwise from a starting position to a goal position, with an interposed delay, likewise implicated some prefrontal neurons in coding the sequencing of movements (Saito et al., 2005).

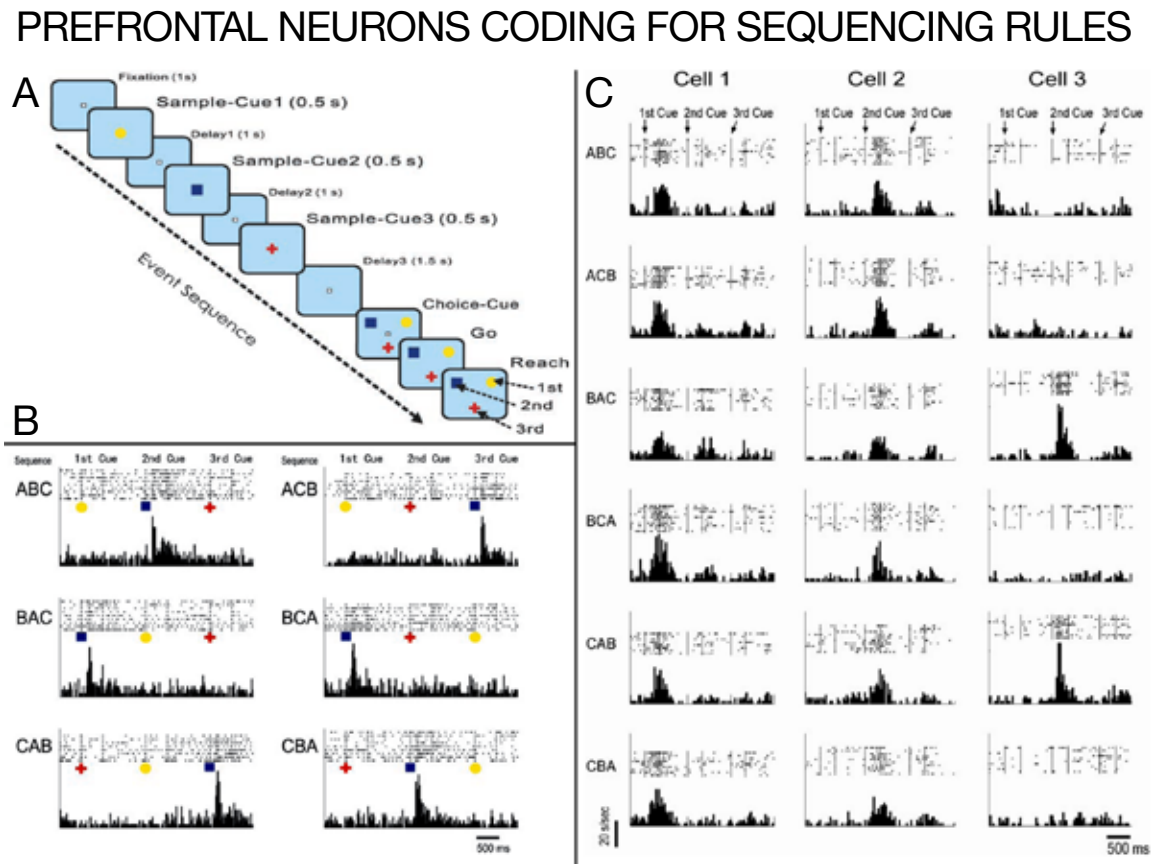


Fig. 7-31. A. A complex serial learning task in which monkeys had to memorize the order of three successively presented sample figures and, to get a reward, touch the figures in the same order when those appeared simultaneously on the screen. **B**. A single prefrontal cell that discharged briskly during the presentation of a particular figure (blue square), irrespective of its serial position (ABC, ACB, BAC …). **C**. Cell 1 (first column) displayed heightened discharge to the first sample cue, irrespective of its identity (ABC, BCA, CBA...). Cell 2 displayed heightened discharge to the second sample cue, irrespective of its identity (ABC, CBA, BCA …). Cell 3 displayed heightened discharge only to the second cue if that was also the same figure (BAC, CAB). (After Ninokura et al., 2003).

THE ROLE OF PREFRONTAL NEURONS IN ADAPTIVE RESPONSE INHIBITION. Single-cell recording experiments have implicated prefrontal neurons in complex tasks involving multiple steps with both "go" and "no-go" signals (Komatsu, 1982; Kubota and Komatsu, 1985; Watanabe, 1986a, 1986b; Sakagami and Niki, 1994). In the experiment by Sakagami and Niki, monkeys were trained to initiate an experimental session by pressing a lever and holding their gaze on a fixation point on the computer screen. This combined action triggered the brief appearance of a colored dot on the screen, serving as an instructional cue. A purple dot signified that the salient cue in the subsequent discrimination test will be the color of geometric figures; a blue dot that the salient cue will be their shape; green dot that the salient cue will be their location on the screen. The dot disappeared and after a delay period, the monkeys had to solve the following complex discrimination task to receive a reward. A colored, geometric figure appeared for a brief period in one of four locations on the screen, and a color change of the fixation point informed the animal whether it was a "go" trial, requiring a prompt response, or a "no-go" trial, requiring withholding the response for a period and giving a delayed response. If the initial instructional cue indicated that color is the salient feature in that particular trial, the monkey was rewarded if it ignored the shape or position of the figures and gave a prompt response to a figure of one particular color but delayed its response to figures with other colors. If the instruction cue indicated that either shape or the position was the salient cue in that trial, the animal had to make the corresponding choice and decide whether it had to react promptly or after some delay. Probe tests showed that the animals mastered this complex task almost perfectly. In the subsequent sessions with cellular recording, the experimenters found that while a few dorsolateral prefrontal neurons responded preferentially to the color or the shape of the stimulus irrespective of their assigned significance, a high proportion of them responded to their significance.

ROLE OF PREFRONTAL NEURONS IN THE ORCHESTRATION OF COMPLEX ACTS. In a study by Mushiake et al. (2006), monkeys were trained to operate two handles to make a cursor follow a particular path on a checkerboard displayed on a computer screen to obtain a reward (Fig. 7-32). The cursor could be moved, one square at a time, in four different directions (up, down, right, left) by using four different motor actions (rotating one handle clockwise or counterclockwise with either the right or the left hand) to reach a designated square as the target. There was a delay between each move and some of the squares were blocked. As the monkey took hold of the handles, a "start" cue appeared and that was followed by the display of the "goal." When the start cue changed its color, the monkey had to make its first move in a particular direction. Subsequently, the monkey had to make a second and a third move, with delays between each, to reach the goal. This experimental design allowed the dissociation of planning the correct direction of the cursor's path and the motor action needed to move the cursor. It took the monkeys about 1 year to master this difficult task but by the time the physiological recordings were initiated in two monkeys, their success rate was about 90 percent. The question posed was: Does the activity of single dorsolateral prefrontal neurons reflect the motor movements performed or the plan to move the cursor in a particular direction to reach the target? The result indicated that the activity of a high proportion of the more than 1,000 neurons recorded from was correlated with the planned cursor path during the first, second and third move, rather than the particular hand movements used. The researchers noted that the activity of prefrontal neurons contrasted with that of motor cortex neurons whose activity is typically correlated

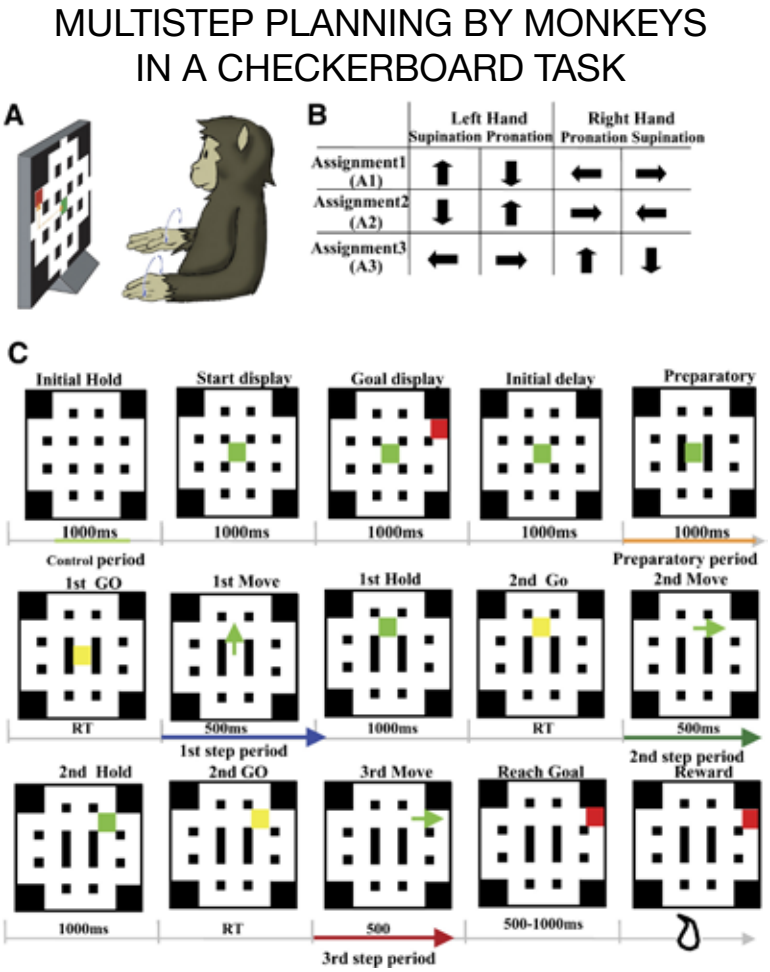


Fig. 7-32. A complex task that requires a monkey to use both hands to operate two handles, turning them clockwise or counterclockwise, in order to move a cursor on the computer screen from a center position, one step a time, to a goal. In different assignments, a particular cue signals the goal position; other cues inform the animal when to wait and when to make the next move. (From Mushiake et al., 2006.)

with arm movements, concluding that their finding supports the idea that the primary function of prefrontal neurons is the planning of actions rather than their execution.

In another study, monkeys were given the task to heed a visual cue that instructed them whether they should pursue a previously set goal (a target in a special location) or shift to a new goal (Genovesio et al., 2006). The activity of some prefrontal neurons reflected the previous goal (P cells), while the activity of other neurons reflected the future goal (F cells), rarely did neurons reflect both. A subsequent study showed that when monkeys shifted from a previous goal to the new goal, there was a stronger correlation in the activity of pairs of F-F or F-P cells than when they stayed with the previous goal (Tsujimoto et al., 2008). The authors speculated that when pairs of neurons issue convergent messages, their correlated activity enhances the selection of a contextually correct choice. In a different experimental design, Shima et al., (2007) trained monkeys to heed a visual instruction cue to perform a multi-step act—pull, push or turn a handle—in a particular sequence (Fig. 7-33). In the "alternate sequence," two motions had to be performed alternately (turn-push-turn-push; turn-pull-turn-pull; push-turn-push-turn; pull-turn-pull-turn). In the "paired sequence," the same motion had to be performed in pairs (turn-turn-push-push; turn-turn-pull-pull; push-push-turn-turn; pull-pull-turn-turn). In

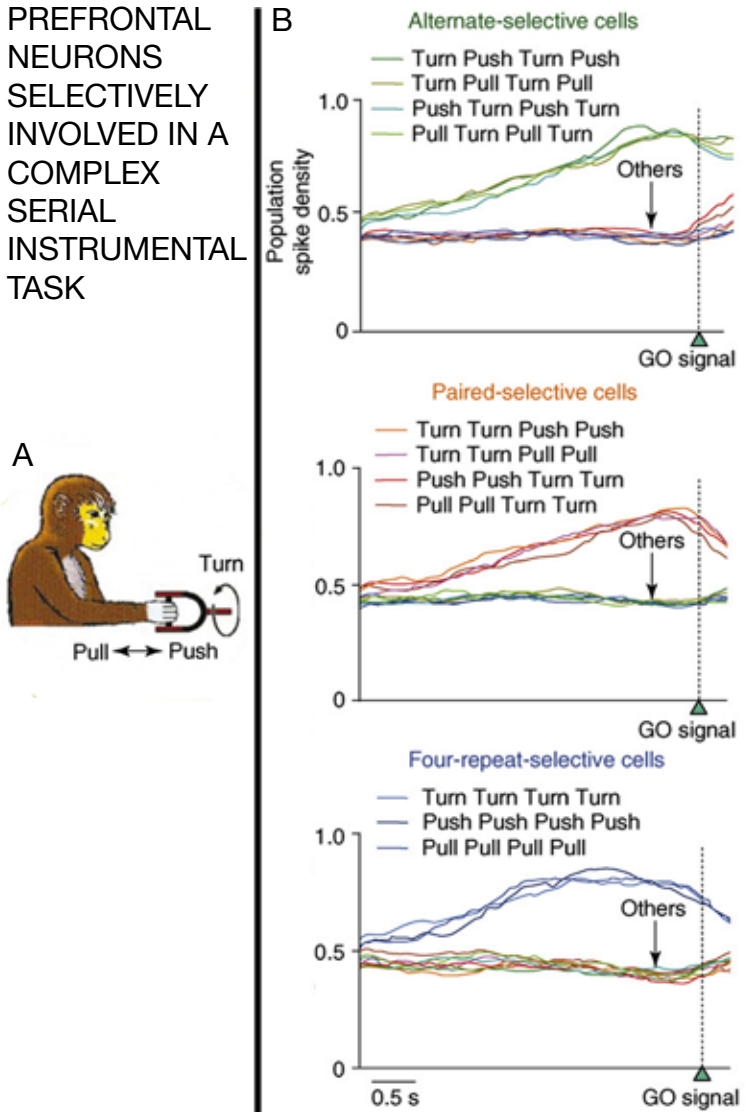


Fig. 7-33. A. In this complex instrumental task, monkeys were trained to perform four movements – turn a handle and/or push it and turn it and/or pull it in a particular temporal sequence to get a reward. The required order in different tests were "alternating" (turn-push, turn-pull, push-turn, pull-turn); "pairing" (turn-turn, push-push…); and "repeating" (turn turn turn turn…). **B**. Prefrontal neurons were identified that became selectively active *before* the go signal was given to either alternate, pair or repeat moves, and the animal correctly followed the required sequence. (After Shima et al., 2007.)

the "four repeat sequence," the same action had to be performed four times (turn-turn-turn-turn; push-push-push-push; pull-pull-pull-pull). Recordings from prefrontal neurons indicated that a fair number of neurons became active during the preparatory period (before the "go" signal was given) when the animals correctly carried out the "alternate," the "paired," or "four-repeat" sequence.

In summary, there is accumulating evidence that the simian prefrontal cortex is a superordinate executive system that enables monkeys to follow complex rules and engage in the intentional control of complex multistep activities. That cognitive and volitional ability is made possible by the integrative process of using current experience retained in short-term memory, past experience retrieved from long-term storage, the inhibition of useless habits and impulsive tendencies, paying attention to different cues, and assessing the rewarding outcomes of actions.

7.5. Functional Localization in the Simian Cerebral Cortex and the Organization of Operational CNS Networks

7.5.1. Functional Divisions of the Simian Cerebral Cortex. Beginning with Plato, philosophers have recognized that, notwithstanding its unity, the human mind is a composite dynamic system. When facing a difficult situation, our feelings, emotions, sentiments and passions prompt us to behave one way; ingrained memories of past experiences, and what we have been taught and assimilated as our habits, beliefs and convictions, incline us to behave another way; and our reasoning and critical thinking instigate us to behave still another way. Attempts to relate these affective, mnemonic and cognitive mental dispositions and faculties to different brain regions also has a long history. The idea, popularized by Galen, that the spirit-filled brain ventricles were the seat of the soul were elaborated in the Middle Ages by the fanciful idea that the anterior ventricles were the seat of sensations ("common sense"); the middle ventricle of reasoning and the intellect; and the posterior ventricle of memory. (The heart, instead of the brain, was for a long time believed to be the source of emotions.) Gall's 19th century phrenology, which was based on the inspection and measurements of "bumps" on the skull—on the erroneous assumption that those reflected hypertrophied cortical regions with different functions—came up with a far more elaborate localization hypothesis. Gall localized over two dozen "organs of mental faculties" in different regions of the cerebral cortex. The "mental faculties" were an admixture of emotional, temperamental, and character traits (affection, courage, pride, vanity, stinginess, obstinacy, etc.), intellectual aptitudes (sagacity, linguistic facility, memory for words, numbers, places and people, etc.), and artistic abilities (talent for music, poetry, mimicry, satire, etc.). Fodor (1983) revived the idea of mental organs (without speculating about neural correlates), referring to them as "modules." Fodor defined these modules as "encapsulated" (impenetrable), "domain-specific" (visual, auditory, etc.) and "hard-wired" (genetically specified) mental entities that coordinate in an automatic and mandatory fashion different categories of behaviors. He also argued that separate from these lower-level modules are a set of higher-level supra-modular cognitive functions—such as imagination, thought and judgment. Fodor's theory has been modified more recently by a broader concept of the composite mind, consisting of a multitude of special-purpose modules and a single general-purpose mechanism. These two mechanisms have been variably described, again without reference to brain correlates, as System 1 and System 2, automatic and deliberate, intuitive and analytic, and, from the perspective of consciousness, as tacit and explicit (Frankish, 2004; Barrett and Kurzban, 2006; Carruthers, 2006; Evans, 2008). What we are presenting in the present work is an evolutionary theory of the hierarchically organized brain-mind consisting of an older primitive paleocephalic system and a recent advanced neencephalic system. In this scheme, the higher mental functions—substantive perception, recollection based on imagery, categorization based on sketchy concepts, and online deliberation and reasoning—are neencephalic functions that emerged in basal mammals and evolved considerably in monkeys.

The Functional Organization of the Simian Neencephalon. The current view about the structural and functional organization of the highly developed simian neencephalon is as follows. The hub of the neencephalon is the neocortex, a superordinate neural system that has its own peripheral sensory input by the relay nuclei of the thalamus; is internally connected

with the cerebellum, the striatum and the limbic system; and has its motor output to the spinal cord.

BASIC ORGANIZATION OF THE SIMIAN NEOCORTEX. The currently available evidence, as reviewed in this and the preceding chapter, suggests that the simian neocortex has the following organization. Its two basic components are the projection areas and the association areas. There are three afferent projection areas: the occipital visual cortex mediating sight, the postcentral somatosensory cortex mediating touch, and the superior-temporal auditory cortex mediating hearing (Fig. 7-34A). The precentral projection area of the motor cortex mediates volitional movement. The association cortex has several components. (*i*) The parietal region behind the central fissure together with the caudal portion of the temporal lobe constitutes the posterior association cortex; it is the hub of perceptual processing. (*ii*) The region in front of the central fissure, the prefrontal and premotor areas, are hubs of deliberation, action planning, visual attention and object manipulation. (*iii*) The region below the lateral fissure is the anterior temporal association cortex; it is the hub of memory storage and recollection imagery. (*iv*) The medially situated limbic components of the simian forebrain—the cingulate cortex, insular cortex (not shown), and the septum, amygdala, and hippocampus—mediate affective functions (Fig. 7-34B).

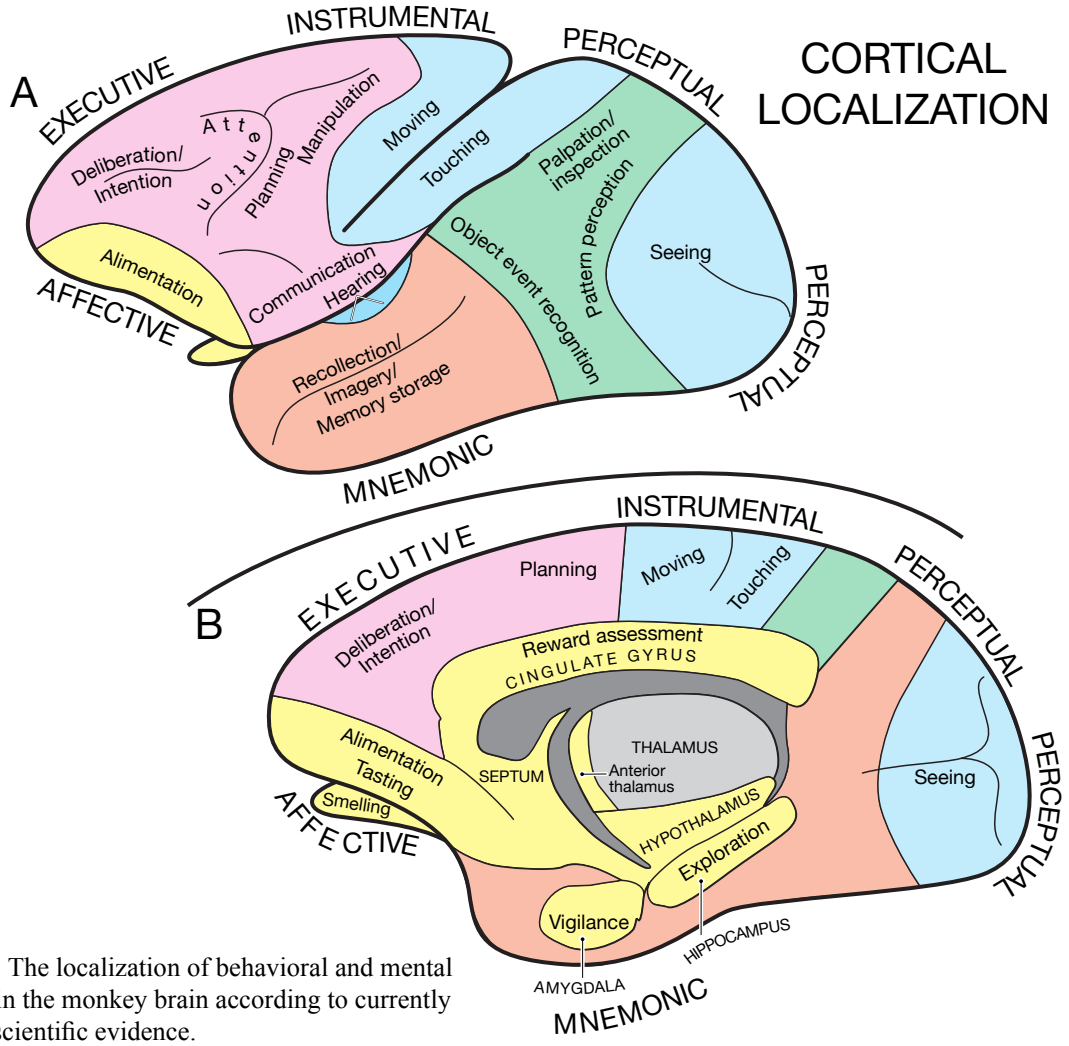


Fig. 7-34. The localization of behavioral and mental functions in the monkey brain according to currently available scientific evidence.

FUNCTIONS OF THE POSTERIOR ASSOCIATION CORTEX: PERCEPTUAL PROCESSING. The perceptual system of the posterior association cortex has several functional divisions. (a) The region abutting the occipital lobe mediates *pattern perception*, the ability to discern the pictorial features—outline, texture, 3-D configuration—of stationary or moving entities in the visual field. (b) The parietal region sandwiched between the somesthetic and visual projection areas, is concerned with *object inspection* and *palpation*. This is accomplished by using the eyes for scrutinizing the visible features of objects in combination with using the dexterous fingers to palpate them (hand-eye coordination). This neural mechanism enables monkeys to obtain a fine-grained substantive representation of the physical properties of the diverse objects that they come in contact with. (c) The ventral division of the posterior association cortex, the caudal portion of the temporal lobe, mediates *object and event recognition*. Stationary or moving visual images, mere pictures, are transformed at this site into the perceptual experience of dealing with specific objects and events in the environment that are of importance to the animal.

FUNCTIONS OF THE ANTERIOR TEMPORAL ASSOCIATION CORTEX: MNEMONIC PROCESSING. This region has several functional divisions. (a) The topmost part of the temporal cortex abutting the auditory cortex (which lies buried along the lateral fissure) is the auditory association cortex. It is assumed to be concerned with vocal *communication*. (b) Underneath are the superior and inferior temporal gyri, two regions in the temporal convexity that have been implicated in long-term *memory storage* and the *recollection* of past experiences in the form of visual *imagery*. (c) Ventrolaterally, and continuing along the base of the cortex and then turning ventromedially, is the region referred to as the medial temporal cortex. This is a transitional neocortical and allocortical region that is closely connected with the inferior temporal gyrus laterally and the amygdala, and the parahippocampal areas and the hippocampus medially (Figs. 7-16 to 7-18). It is presumed that this region is involved in the complex process of turning what is retained in short-term memory into long-term storage.

FUNCTIONS OF THE ANTERIOR ASSOCIATION CORTEX. In contrast to the posterior perceptual association cortex—which is closely connected with the visual and haptic projection areas, and can thus be thought of as a bottom-up, or reactive, system processing peripheral input—the anterior association cortex has only indirect external connections. Rather, its connections are principally internal: with the posterior and temporal neocortical association areas that supply processed perceptual and mnemonic data, and components of the limbic system that supply information about the animal's bodily needs, likes and dislikes, and safety concerns. As such, the anterior instrumental association cortex may be considered a top-down, or proactive, neencephalic mechanism. This region has two divisions, the prefrontal and premotor cortices. (a) The dorsolateral prefrontal cortex plays a pivotal role in *deliberation* before acting. This includes focusing on the end state pursued, inhibiting impulsive and habitual response tendencies, and bringing past experience and anticipated outcomes to bear on the decision before acting one way or another. (b) The premotor cortex plays an important role in translating intentions and plans into motor programs. One of its components, the frontal eye field, coordinates *visual attention*. Finally, the execution of the volitional commands is conveyed to the primary motor cortex, which has a direct outflow, by way of the large corticospinal tract, to the final motor neurons of the brainstem and spinal cord.

FUNCTIONS OF THE LIMBIC SYSTEM. This is a heterogeneous system, composed of neocortical, allocortical and ganglionic structures; its function is thought to be the interfacing of affective and cognitive processes. (a) The apparent function of the orbitofrontal cortex is the control of *alimentation* in relation to the changing needs and wants of the organism, and *reward assessment*, maximizing gratification and gain, and minimizing frustration and loss. (b) The anterior component of the cingulate cortex has been linked to pleasure and its posterior component to pain. (c) It is well established that the amygdala is concerned with *vigilance*, the fear and anger reactions elicited by threat and danger. (d) The function of the hippocampus is controversial. We hypothesized that it is the motivational mechanism for *exploration*, instigating the curious animal to acquire a spatial map of its environment and become familiar with the things it contains.

7.5.2. Organization of the Operational Networks of the Simian CNS. The preceding description could be construed to imply that the functional divisions of the neocortex are modules that work in isolation from one another and from the rest of the central nervous system (CNS). But modern research indicates that is not the case. These divisions are better considered to be hubs of operational networks that become dynamically interconnected with one another in different combinations, depending on what the animal pursues or reacts to at any given moment in time. Monkeys are not interested in processing sensory information, making perceptual discriminations, memorizing experiences, solving serial tasks, or using tools; although they may be goaded to do that in the laboratory setting. Depending on their bodily state and desires, and external conditions and circumstances, they are motivated to satisfy organic needs and affective desires: find food and eat when hungry, and if possible, procure appetizing nutrients; find water when thirsty and preferably get that from a reliable source; watch out for danger to themselves, their young and the group; seek companionship, groom each other and engage in various sexual activities; when mothers deliver young, suckle them and take care of them; and finally, compete with one another to gain advantage and dominant social status, by fighting and politicking. To be successful in these undertakings, monkeys rely on their mental faculties mediated by different interacting networks of their nervous system. Setting out in the morning to procure nutrients activates networks that provide images of trees laden with ripe fruit, and a spatial map how to get there. Seeing prowling cheetahs looking for prey along the way activates imagery networks that select a route along the canopy to avoid these predators. Having had their fill and wishing to relax, activates other networks that enables them to gather at a water hole and socialize there.

THE THEORY OF DISTRIBUTED FUNCTIONAL NETWORKS. It has been hypothesized some time ago that there are two functional pathways emanating from the visual cortex, the dorsal stream targeting the parietal cortex and the ventral stream targeting the temporal cortex (Ungerleider and Mishkin, 1982; Desimone and Ungerleider, 1989). The dorsal stream was proposed to mediate spatial vision ("where"), the ventral stream object discrimination ("what"). The basis for this hypothesis was the contrasting behavioral effects in monkeys of parietal lobe and temporal lobe lesions (reviewed by Pohl, 1973). Several studies showed that parietal lesions produce no impairments in visual discrimination learning but severe deficits in judging which of two objects is located closer to a visual landmark. These were interpreted as spatial deficits. In contrast, inferior temporal cortex lesions produced severe impairment in visual

pattern discrimination. These were interpreted as object recognition deficits. In light of what we have learned since, these "streams" are better conceptualized as examples of "distributed networks" (Felleman and Van Essen, 1991), temporally linked brain structures involved in the coordination of particular behavioral functions. Thus, the dorsal stream may be considered a network involved in the coordination of close visual inspection, tactile palpation, and kinesthetic feedback for the assessment of the detailed structure of handled objects. The effort to identify these networks is the subject of ongoing research, much of it using functional brain scanning techniques. Examples are proposed networks in the human or monkey brain for novelty encoding (Tulving et al., 1994), visual reaching and hand-eye coordination (Johnson et al., 1996; Mascato et al., 2003), object manipulation (Binkofski et al., 1999), spatial navigation (Ekstrom et al., 2003), and getting rewards (Sesack and Grace, 2020).

7.5.3. A Tentative List of Operational Networks. We postulate that the behavior of monkeys is coordinated by a set of distributed networks, some of them pre-established morphogenetically, others acquired and greatly modified by daily experience and life's vicissitudes. Our current knowledge of the anatomical organization of the simian brain permits the tentative identification of a few of these networks, which we briefly review below. (The details on which this summary is based and bibliographic references are presented in the preceding and the present chapter.)

Perceptual Networks. The distributed networks mediating different facets of perception have their hubs in the posterior association areas. Among the components of all of these circuits are the visual and haptic projection areas, the relay nuclei of the thalamus and the pulvinar, and parts of the temporal and frontal lobes.

THE VISUAL IMAGE FORMING NETWORK. The ability to recognize the multitude of things that exist in the environment requires the formation of mental images, distinguishing as many of them as possible by their distinctive shape, texture, size, and other visual features. The hub of the network mediating this unimodal function is the hierarchically organized occipital association areas of V2 and V3. This field is closely linked, by way of the striate cortex, with the thalamic lateral geniculate nucleus and the pulvinar.

THE OBJECT AND EVENT RECOGNITION NETWORK. This multimodal network is centered in the association areas of the occipital lobe and posterior temporal cortex. Among its important components are V4 at the interface of the temporal and occipital lobes, MT in the posterior portion of the inferior temporal gyrus, and MST in the superior temporal gyrus. The function of this network is twofold. First, the identification of some of the perceived images as real objects with specific structural and functional properties. Second, the detection of changes that the identified objects undergo in space and time, such as their speed, direction of movement, and changes in their size and shape as they get nearer or farther.

THE OBJECT INSPECTION NETWORK. This multimodal network has its hub in the parietal association cortex, sandwiched between the unimodal somesthetic and visual projection and association areas. In addition to its extensive connections with these areas, this network is closely linked with the frontal eye field and the supplementary eye field of the anterior

cortex that control eye movements and visual attention by way of the superior colliculus and the oculomotor nuclei. The function of this network is to use tactile, kinesthetic and visual information to construct a multimodal representation of the various objects that can be palpated and manipulated.

THE FACE RECOGNITION NETWORK. This posterior temporal cortical network uses subtle visual details to distinguish different facial features from one individual to another. This ability plays an important role in the establishment and maintenance of hierarchically organized monkey societies.

Mnemonic Networks. This system, concerned with memory storage and retrieval, and imagery-based recollection, has two components, the neocortical anterior temporal convexity and the transitional medial temporal cortex. The former consists of the superior and inferior temporal gyri, TA, TG and TE, the latter of the perirhinal, entorhinal and parahippocampal cortices. These areas have close links with other neocortical association areas and other parts of the limbic system. The former are the source of information what is transpiring in the external world, the latter of their existential significance. The exact role of the different components of this network in the transformation of short-term retention into long-term memory, and in the evocation of past experiences in the form of quasi-perceptual imagery, is not yet fully understood.

Motivational Networks. The forebrain limbic system consists of cortical and ganglionic components: the neocortical cingulate, insular and orbitofrontal cortices; the allocortical hippocampus; and the ganglionic amygdala, septum, and nucleus accumbens. These structures play an important role in linking affective-motivational processes with perceptual, mnemonic and cognitive processes.

THE VIGILANCE NETWORK. Security is a vital concern to all animals and the amygdala is an ancient structure implicated in triggering fear or anger, defensive or offensive reactions, when exposed to danger. The simian amygdala has a complex organization with extensive connections both lower-level paleocephalic affective mechanisms and higher-level neocortical mechanisms. It may be considered the hub of an advanced vigilance network that brings to bear past experience and cognitive considerations to the assessment of who and what constitutes threats to the individual.

THE ALIMENTARY NETWORK. For omnivorous monkeys, food selection is a challenging task. Two limbic regions have been implicated in the regulation of food selection: the anterior insular cortex and the adjacent orbitofrontal cortex. The anterior insula receives indirect olfactory and gustatory input and has close connections with components of the orbitofrontal cortex. The function of this circuit is to regulate food intake on the basis of information supplied by brain mechanisms that process olfactory, gustatory and visual information. The orbitofrontal cortex receives both processed external olfactory, gustatory and visual input about the features and properties of nutrients, and processed visceral internal input from the body regarding the animal's nutritional needs. This circuit has been implicated in the assessment of the palatability and hedonic quality of nutrients.

THE HEDONIC NETWORK. The pursuit of pleasure is a hallmark of simian behavior and a structure that has been implicated in motivating animals to work for rewarding outcomes is the nucleus accumbens, a component of the ventral striatum. The nucleus accumbens has extensive connections with the dopaminergic system of the ventral tegmental area, the amygdala and the orbitofrontal cortex. This network appears to play a role not only in inducing the animal to gorge itself with delicacies but also with making life more pleasurable, such as associating and bonding with others.

THE NOCICEPTIVE NETWORK. A limbic region that appears to play a major role in the perception of pain, a mechanism that protects animals from tissue damage, is the posterior insula. This region has close connections with the somesthetic projection and association areas and responds to nociceptive stimuli.

THE REWARD ASSESSMENT NETWORK. A limbic structure involved in reward assessment is the cingulate cortex. The anterior cingulate cortex has close links with the adjacent prefrontal and premotor areas as well as the striatum. The available evidence suggests that this network monitors rewarding or frustrating outcomes as an animal pursues a goal. The posterior cingulate cortex is more closely connected with the frontal eye field and the parietal cortex. This network may play a role in motivating the animal to keep its gaze on targets of interest.

THE EXPLORATORY NETWORK. A distinctive trait of monkeys is their inquisitiveness. The motivation to explore one's surroundings and pay attention to unfamiliar things, and overcome the fear of the unknown, is the affect of curiosity. We believe that the hippocampus plays a major role in this function. The uniquely organized hippocampus is closely connected with ganglionic components of the limbic system, the septum and the hypothalamus, and with cortical structures, in particular the entorhinal cortex and the medial temporal cortex, implicated in short- and long-term memory processes. The benefit of curiosity is a cognitive expansion of one's acquaintance with the surrounding world.

Instrumental Networks. Monkeys are distinguished not only by their curiosity but also by their agility and manual dexterity—instrumental activities that aid them in exploiting valuable resources. These activities require extractive procedures and complex behavioral skills. Monkeys are greatly aided in these efforts by neural networks that have their hubs in the premotor and supplementary motor areas of the anterior cortex.

THE VISUAL ATTENTION NETWORK. There are involuntary and volitional aspects to keeping the gaze on a target and tracking it as it moves about. The slow and quick ocular movements (saccades) that align the eyes with the direction of the turning head, as the animal's attention is drawn to a conspicuous target, are bottom-up reactions carried out mostly involuntarily. But focusing the eyes on some chosen target while the animal is engaged in some specific endeavor requires voluntary control. The network mediating top-down, volitional gaze control has its hub in the frontal eye field (FEF) and the frontal pursuit area (F7). This system is closely connected with subcortical structures controlling eye movements, in particular, the superior colliculus and the midbrain oculomotor nuclei.

THE MANIPULATORY NETWORK. We have considered earlier the object inspection network that, using hand-eye coordination, enables monkeys to form a realistic representation of the structural properties of the objects they examine. That is a bottom-up perceptual process, where object-manipulation is the means rather than the end. The function of the closely related manipulatory network is to become proficient in handling objects and making use of them under close visual guidance. In this top-down function, instrumental effectiveness is the goal; inspection and palpation are the means to that end. The hub of this network consists of premotor areas F5 and F4, which are closely linked with the motor cortex as well as the parietal and occipital association areas, the striatum, and the cerebellum.

Executive Networks. Volitional behavior implies proactive behavior, actions initiated by internal forces rather than as reactions to external stimuli. These endogenous forces may originate internally from bodily conditions, which is the case in hunger, thirst, pain, or discomfort. Or they may be of neural or mental origin, as is presumably the case with wishes, hopes and fears (affective motives), and ideas, intentions and plans (cognitive motives). We assume that much of the behavior of lower vertebrates is reactive in nature, and to a lesser extent affectively motivated. Proactive behavior initiated by cognitive motives is a trait emerging in mammals, and one that evidently plays an important role in the daily life of monkeys. The purposive foraging expeditions of monkeys, their use of tools, and their political maneuverings indicate that planning is within their ken, and experimental studies clearly show that they can initiate activities and solve complex problems by deliberation. The currently available evidence indicates that the networks mediating intentional behavior in monkeys have their hubs in the prefrontal cortex.

THE INTENTION GENERATING NETWORK. The executive system of the simian cortex is hierarchically organized, with intentions apparently generated in the prefrontal cortex, action plans and strategies formulated in the premotor areas, and the latter translated into action commands in the motor cortex. The hub of the neural system that generates intentions is probably located within areas 45 and 46 of the dorsolateral prefrontal cortex. This region is not targeted by the thalamic sensory relay nuclei and lacks close connections with the visual, haptic and motor projection and association areas. Its direct connections are with the visceral orbitofrontal cortex, the mnemonic temporal cortex, and the premotor cortex that acts upon the motor cortex.

THE ACTION SEQUENCING NETWORK. The translation of intentions into action plans and strategies requires the orderly sequencing and recruitment of available templates for routines and singular movements that constitute a skillful performance. There is emerging evidence that a prefrontal-premotor network closely linked with the cingulate cortex, the striatum and the cerebellum mediates this function. This, or a related network, may also be monitoring ongoing performance in terms of the cost and the benefit of a planned undertaking, and the success or failure of achieving an end.

THE IMPULSE CONTROL NETWORK. When facing a novel situation, effective behavior requires the suppression of the disposition to respond impulsively or with a maladaptive routine. While monkeys tend to behave impulsively, they can inhibit these tendencies. For instance, those with a lower rank in the social hierarchy yield to and behave deferentially toward those with a higher status, or learn to delay gratification if by inhibiting their greediness they can secure a larger or more preferred reward. Monkeys also learn to abandon ingrained habits in an experimental setting where the significance of cues or test rules is changed. Area 9 of the frontal pole, which is abutting the orbitofrontal cortex and the dorsolateral convexity, might be the hub of the network concerned with the volitional inhibition of emotional and habitual dispositions.

7.5.4. Our Simian Legacy of Higher Mental Functions. We have listed in the preceding chapter the somatic, sensorimotor, behavioral and neural advances of monkeys that constitute part of our simian heritage. They included, relative to basal mammals and prosimians, the following: reduction of the snout; increased hand specialization; sitting upright without hand support; reduction in the number of fetuses carried by the mother; lengthened gestation period; prolonged infancy and intensified maternal care; enlargement of the social group; and increased encephalization. Here we add several simian advances in the realm of higher mental functions that are also part of our simian legacy. We have attributed all of them to the expansion and elaboration of the simian neocortex, and the complex neencephalic networks that mediate their advanced mental dispositions and aptitudes.

(*i*) *Simian Affective Advances*. In addition to the basic affects of likes and dislikes, hunger and satiety, relish and distaste, coziness and suffering, anger and fear, desire and abhorrence, which are exhibited by all mammals, monkeys also display intense maternal and filial affection, pining and grief, social amicability as well as animosity, curiosity and boredom, manic exuberance, and depressed apathy. There are also indications for more complex emotions and temperamental traits in monkeys, such as trust and mistrust, generosity and malevolence, courage and timidity.

(*ii*) *Simian Perceptual Advances*. The perceptual world of monkeys closely resembles ours. Relying on monocular and binocular cues of depth and distance, and palpating and manipulating anything within reach, they must be aware of things as solid substances with multifarious features and properties, what we have earlier called substantive perception (Section 6.5). But beyond this ability, monkeys also form categories into which entities with similar properties can be assigned. We postulated that monkeys develop imagery-based sketchy concepts as prototypic mental representations, such as cats, dogs, monkeys and people, and utensils, tools and devices that can be used for specific purposes.

(*iii*) *Simian Mnemonic Advances.* There is ample evidence for the highly developed ability of monkeys to retain their awareness of ongoing events for a brief period in short-term memory (working memory), as well as hold a vast amount of information, including some that they have witnessed only once, in their long-term memory. Apparently they can do that by recollecting past experiences as quasi-perceptual copies of them, i.e., in the form of mental

imagery. That advanced mental process may underlie the exceptional factual learning and procedural learning ability of monkeys.

(*iv*) *Simian Cognitive and Volitional Advances.* Monkeys are distinguished among mammals in their ability to adapt themselves to different habitats, be they dense forests, open grasslands or even cities occupied by people. They tend to feed on the best resources available, including high-value nutrients that have to be extracted from their coverings. Some species of monkeys regularly use not only their dexterous hands but also natural tools for nutrient extraction. As experiments indicate, monkeys can learn to appreciate different cues to carry out multistep actions in an orderly sequence and, reflecting their emerging cognitive abilities, they display some insight into the relationships that prevails among different things in space or time.

However, the mental limitations of monkeys relative to humans must not be ignored. In the affective realm, they lack generosity, in the sense of offering goods to others, and they do not display in their social interactions such higher feelings as shame or guilt. In the mnemonic realm, they can recollect single events, but there is no evidence for hindsight, the ability to reconstruct what transpired in the past in a chronological order as an autobiographical or episodic narrative. To do that requires the insertion of relational concepts into isolated memory images, such as before and after, last week and yesterday; however, nonverbal monkeys cannot entertain abstract ideas of relationships that cannot be pictorially represented. Also, their insight in comprehending means-ends relationships in tool use, and foresight of carrying tools to a working site, is limited. They display no ability to learn by observing the performance of others or collaborating with one another when more that two hands are needed to achieve some end. Finally, their ability to reason and deliberate is confined to the servicing of vital needs and wants, not the endeavor to understand the causes or reasons why things undergo changes. As nonverbal animals they do not engage in introspection, display no ability to reflect upon what they experience, and lack self-awareness, as attested to by their failure in recognizing themselves in a mirror. We conclude, therefore, that the awareness of monkeys is an implicit one—feeling pleased or frustrated, afraid or enraged, seeing and hearing what transpires in their environment, recognizing objects and beings and remembering past encounters, and so forth—but they lack explicit consciousness, the ability to introspect and reflect upon what they experience.