

Ethology and Neurobiology of Grooming Behavior

B. M. SPRUIJT, J. A. R. A. M. VAN HOOFF, AND W. H. GISPEN

Department of Medical Pharmacology, Rudolf Magnus Institute, and Department of Ethology and Socio-Ecology, University of Utrecht, Utrecht, The Netherlands

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I. INTRODUCTION

The outer body surface of animals is complex and appears in a variety of forms from moist or slimy, dry, soft, and leathery to hard, horny, or bony. The skin is often equipped with devices, such as scales, spines, hairs, and feathers, primarily serving protective and insulating functions. In many species the state of this organ can be changed, for instance, for a thermoregulatory purpose by changing the degree of piloerection, moistening by transpiration, or dilatation of cutaneous blood vessels. Changes in body surface appearance may also serve as camouflage, adornment, and signal enhancement.

Apart from these autonomous regulatory reflexes there is in the various taxa a diversity of behaviors directed to the outer surface of the body. These may result in 1) a rearrangement of hairs, feathers, and other appendages; 2) removal of foreign objects, dirt, grease, and parasites; 3) applying certain substances, such as tallow; and 4) sensory stimulation of the skin. In most cases these immediate effects undoubtedly represent the adaptive advantages for which these behaviors, their motor pattern coordinations, and their underlying motivational mechanisms have originally been selected. Accordingly these behaviors are, often a priori, designated by names such as "grooming," "scratching," "preening," "rubbing against objects," and "dust, sand, mud, and sun bathing." All these behaviors have in common that they are directed to the outer body surface, which was the criterium for being taken into account in this review. They imply a primary biological function con-

cerned with care of the body surface (COBS). However, as outlined in this review, the display of behaviors directed to the outer body surface is often more related to the nature of the situation in which it occurs than to the condition of the skin. Therefore the hypothesis is pursued that these behaviors may also have conferred other effects than the presumed COBS function. Insofar as effects of behaviors directed to the outer body surface did contribute positively to the reproductive advantage of the respective animals, these also will have become involved in driving natural selection. Thus these effects will have added to further functional adaptation and differentiation of these behaviors and their underlying mechanisms.

A preoccupation with one's own body surface implies that other environmental issues are of less immediate concern. A possible secondary function of behaviors directed to the outer body surface lies in reducing attention, which forms the rationale behind this review. In addition, self-directed behavior, which is characteristic for specific situations, may signal to conspecifics the motivational preoccupation of the performer to its fellows. As a consequence, the behavior can acquire a role in the regulation of social relationships and come under the control of social factors. This is the case when the behavior is directed not only at one's own body (auto-grooming) but also at that of conspecifics (social grooming or allogrooming).

This review offers a survey of behaviors directed to the outer body surface shown in various animal taxa. In section II of this review, attention is drawn to the fact that, especially in birds and mammals, phenotypically

similar patterns such as preening and grooming have evolved to which an important share of the behavioral time budget is allocated. Recently, a number of studies, especially on primates, have emphasized the important social functions of such behaviors and have begun to unravel the ethological factors involved.

In addition to these behavioral studies, there is an increasing number of studies investigating the neuronal and endocrine mechanisms, in particular those of rodents. Knowledge of how the programming of behavior is implemented in the brain may substantially facilitate the understanding of the possible "secondary" functions of behavior. For instance, when the neurobiology of behavior directed to the outer body surface partly coincides with the neurobiology of stress mechanisms, a role of these behaviors in arousal reduction is more intelligible. Therefore both grooming behavior and its underlying neural mechanism are reviewed in close relation with each other. Especially the involvement of neuropeptides, hormones, and opioids, usually associated with arousal and coping with stressors, is in line with secondary functions other than taking care of the body surface alone, which seems to have evolved across species. When considering the functions and the causal mechanisms of COBS behaviors, it is important to realize that similar functions and the corresponding behavioral phenotypes may result from mechanisms having very different phylogenetical origins. As we well know, functional analogy does not imply homology of mechanisms. The reverse is equally true: a given mechanism may become adaptively tuned and differentiated to serve different functions. For a taxon such as the mammals it seems logical to expect that such universal and therefore phylogenetically old behaviors as COBS may have common underlying mechanisms, especially when similar neuropeptides and hormones are involved for which evidence is collected in section III of this review.

So far, there is still an appreciable gap between the insights gained by the (socio)ethological studies and the neuroendocrinological studies. There is a paucity of references attempting to connect the two. This is partly due to the fact that the latter studies are carried out in experimental settings in which the array of socioethologically relevant environmental conditions has substantially been reduced and are mainly conducted in rodents. Conversely, ethological studies often lack substantial neurophysiological evidence and are primarily investigated in primates. Clearly there is a need of investigations of the role of neuronal, endocrinological, and pharmacological factors in the programmatic embedding of grooming in environmentally and socially determined behavioral routines. This review attempts to incorporate comparative and physiological aspects of grooming behavior, since grooming is an appropriate model for understanding brain-behavior relationships when its function and neurobiology are taken into account. The abbreviation COBS is used for all behaviors directed to the outer body surface and does not specifically refer to the function of taking care of the outer body surface.

II. FUNCTIONAL ASPECTS OF GROOMING

A. Grooming in Arthropods

The morphology of grooming behavior in arthropods is often species specific and has been used to clarify the taxonomy and phylogeny of various groups, e.g., hymenopteran insects (160), embiopteran and zorapteran insects (508), cockroaches (48), and aeglids (325). Already in insects the function of grooming appears not to be limited to body maintenance. In honeybees visiting an artificial food source, a relationship was found between the frequency of antenna grooming and the sugar concentration of the food source, suggesting that it may act as a social signal (387, 497).

The occurrence of grooming fulfills the criteria defined for displacement activities usually known from birds and mammals (103). A special form of COBS is displayed by ants spreading antibiotic secretions of the metapleural glands over their body as a protection against the growth of bacteria and fungi (149). The occurrence of grooming marking a social context is seen in peacefully mixed, heterospecific colonies of ants of the same genus, whereas in a mixed society of different subfamilies agonistic behaviors are displayed (509). Allogrooming, as found especially in birds and mammals, occurs in arthropods as well. It plays a role in courtship behavior in the termite *Bifiditermes beesoni* (2); the duration of grooming varies greatly depending on the receptivity of the individuals. In honeybee colonies allogrooming is useful in ectoparasite and debris removal and is performed by a small number of specialists (291), who direct it preferentially to close kin (179). Thus in arthropods COBS behaviors seem to have evolved for more than mere taking care of the outer body surface.

B. Preening and Associated Behaviors in Birds

The avian plumage not only serves in thermoregulation and protection of the body surface but is a vital part of the organs of flight (321). Indeed, the feathers of birds have a far more complex structure than the fur of most mammals. Therefore it is not surprising that different types of COBS behavior play a crucial role in the behavioral repertoire of birds, such as bathing in water, sand, and even in ant heaps followed by preening (102, 504, 518, 528). In addition to cleaning and the removal of parasites (62), the rearrangement of a disordered plumage is given much attention. Birds may spend considerable lengths of time on COBS behavior. This is true especially for aquatic species, which appear to invest considerably in the greasing and water proofing of their insulating surface.

In addition to these autochthonous COBS activities, short bouts of sometimes perfunctory preening may be performed as displacement activities (416, 436, 448, 515, 518; see also sect. IIB1). In such cases the COBS function of preening may be superseded by functions in other

behavioral contexts. Thus, in many species, preening has become ritualized in the course of evolutionary adaptation to communicative functions as part of courtship behavior (244). This replacement of function is certainly facilitated by the fact that preening in its autochthonous contexts is associated with a state of relaxation. It is undoubtedly this association that renders preening its effectiveness as a message of peaceful and nonagonistic intent. The movements may have been modified into a stereotyped and stylized display of which the original function is recognized only after comparison with species in which the ritualization has advanced less far. This has been demonstrated most lucidly in the classic studies of courtship behaviors in ducks (320, 334). Bursts of preening and other comfort behavior occur, for instance, when animals return to a normal state of arousal after having been in a state of high behavioral arousal (104). Indeed, it was found that preening was accompanied by slow waves in the electroencephalogram (EEG) recorded from depth electrodes (104), which supports the hypothesis that grooming is associated with de-arousal (103, 247). Likewise, in rats, slow waves in the EEG of the cingulate cortex were recorded during grooming behavior (314).

Social preening or allopreening has an erratic distribution in birds (551). It is found in a minority of species that have a great deal of bodily contact and form enduring (pair) relationships, e.g., estrildid finches (458), babblers, white-eyes (551), parrots (410), parakeets (57, 58, 155, 312), and corvids (14, 224a, 319), where preening acts as an appeasement behavior and a bond-strengthening social reward.

1. Displacement

Grooming is often seen in situations in which two behavioral systems are activated simultaneously or in which the course of an activated behavioral routine is blocked. Grooming then gives the impression of being irrelevant. This was regarded as an indication that it could serve as an outlet of pent-up motivational energy. This energy would find an outlet into a different or "allochthonous" motivational channel to which it was displaced or into which it "sparked over." Therefore it has been called displacement behavior (103, 161, 292, 329, 347, 416, 436, 499, 500, 515). Such irrelevant or displacement grooming has been reported for a wide variety of taxa, such as insects (387), birds (105), and mammals (120).

The explanation of displacement behavior as the result of a sparking over of motivational energy into a different motivational channel has, however, fallen into disrepute with the criticism on energy models of motivation. Displacement grooming cannot, as was once thought, be merely a sparking over of pent-up energy, because it has been shown to be influenced by the causal factors normally controlling it (416, 436). A "disinhibition explanation" has found favor instead (436). In conflicts of incompatible motivational systems, the inhibi-

tory influence that motivational systems, once activated, exert on other systems is believed to become ineffectual. Low priority, "spontaneous" behavior systems, normally activated at times when high priority "reactive" behavior systems are not dominating, may be disinhibited and "breakthrough" under this condition (330, 331, 436). The COBS behavior is a low-priority behavior "lying in wait" until other systems leave it an opportunity to take place. The arousal of motivational conflict may evoke piloerection and sweating, thus producing the normal "autochthonous" releasing stimuli for grooming (359). However, the often perfunctory form and incomplete structure of displacement grooming suggests that it is no longer primarily functional as COBS. It clearly relates to a state of indecisiveness or motivational ambivalence of the animal. Such ambivalent movements may become useful in social communication to test the motivational inclination of partners. In this functional context they may become ritualized into displays and come under the control of new causal factors (500). Examples are the forms of ritualized preening in avian displays, e.g., in courtship ceremonies (9, 265, 320, 334).

A state of uncertainty can also be induced experimentally by several reward schedules. Displacement activities may also be performed in certain reinforcement schedules, for instance, as an "adjunctive behavior" to bar pressing for food (159). Lawler and Cohen (310) describe paw grooming as an adjunctive behavior and suggest that it may function to reduce the stress that is induced by an intermittent reinforcement schedule.

Apparently, grooming behavior in birds fulfills multiple functions: keeping the outer body surface in a good condition, as displacement behavior, as a signal for conspecifics as evidenced by the ritualization of these behaviors in courtship behavior, and as a strengthening bond. In the latter cases preening serves functions other than the COBS.

C. Grooming in Mammals

In mammals there are various forms of COBS behaviors (53), such as grooming, scratching, nibbling, rubbing, wallowing, and bathing. These behaviors serve to remove ectoparasites, dirt, or even aversive substances (326), and they may also aid in thermoregulation, chemocommunication, and by the antibacterial properties of saliva in wound healing (53). In analogy to what is suggested by the occurrence of grooming behavior in arthropods and birds, several functions other than COBS are discussed mainly in rats and primates. In various species of desert rodents, dust bathing improves the fur because the dust absorbs pelage lipids (18, 150, 224, 493). In rodents, water, saliva, or pigments and fatty acids are spread over the fur. Evaporation of the water serves as a means to regulate body temperature (226, 473) and water economy (405, 494). Desalivated animals cannot control their body temperature during high ambient temperatures (226). It is suggested that

both peripheral (skin) and central (the posterior hypothalamic region) temperature signals modulate grooming behavior (484).

Most studies were focused on the harderian gland, which is located in the ocular cavity in many vertebrate species, including rodents, but not in cats, dogs, or primates. The harderian gland has been found in a variety of marsupials, such as insectivores, edenta, lagomorphs, cetaceans, pinnipeds, and sirenians; it cannot therefore be associated with a particular ecology and life style (285, 425). The gland excretes material from the external nares of the nose (267, 425); this material consists of the pigment protoporphyrin (75, 285) and derivatives of alkanediol diacyl esters (374, 375). The insulating fatty acids and the radiation-absorbing pigments released by the harderian gland may protect the animal against cold.

Thermoregulation and chemocommunication are intimately related (490-492). The excreted material spread during self-grooming may also serve as an attractive chemosignal during social interaction (491, 548). This mechanism seems particularly adaptive for diurnal species living in an arid environment (desert) and is a sophisticated means for maintaining physiological homeostasis.

The spreading of saliva on the fur or skin may also be related to the antibacterial properties of saliva, which have been shown for human saliva in various ways (54, 77, 207, 287, 323, 486, 495, 496). Cutaneous injuries are often followed by licking, especially in carnivores and rodents. Apart from cleaning the wound of foreign material, rat saliva also may have antibacterial properties, which has been shown for two genital pathogens (233, 234). These antibacterial effects may prevent the transmission of genital pathogens from females to males during copulation (233, 234). Licking and spreading saliva may be involved in other grooming patterns, such as in periparturient licking by females of their mammary and anogenital areas (412). Licking of these areas has been demonstrated for rodents (420a), cats (432), and dogs (46), and changes in self-licking during pregnancy have been described for rats. The adaptive value of these behaviors is explained by the vulnerability of newborns, who do not yet have the protective intestinal flora against opportunistic pathogens, and thus spreading of bactericidal saliva on anogenital areas prevents the contamination of the pups.

1. *Grooming and dearousal*

In rats self-grooming is seen after a variety of different activities: social contact (341), sexual behavior (342), exploratory behavior (245), and it usually precedes sleeping (269). In rats, slow waves in the EEG of the cingulate cortex were recorded during grooming behavior (314). Furthermore, novelty and other stressors (82, 192, 471) can elicit grooming behavior in rats (45, 84, 87, 143, 149, 232, 257, 415). However, no correlation was found between grooming and indications of anxiety, such as urination, defecation, and freezing (170, 171). It

seems in rats that grooming coincides more with the period after arousal and rather reflects the process of dearousal due to the termination of or habituation to a stressful situation than enhanced fear. Then auto-grooming is clearly a response to changes elicited by anxiogenic stimuli. Presumably, anxiolytic drugs reduce novelty induced grooming by reducing the intensity of the perception of anxiogenic stimuli (144, 353).

2. *Allogrooming*

In many species animals direct COBS behavior to their companions. Such social grooming or allogrooming has also been observed more or less frequently in various mammals, for instance, in kangaroos (184); bovids (20, 230, 400, 431, 454); deer (229); antelopes (235); equids, such as ponies, horses (81, 95, 541, 542), and zebras (380, 430); canids (175, 514); felids, such as cats (176, 432) and lions (429); and rats (306). In these species it mostly consists of licking movements and careful nibbling with lips and teeth. Social grooming is seen, above all, in primates. The contexts in which it occurs indicate that in many of these species it has a function in the regulation of social relationships rather than the COBS function alone.

One of the most widely spread and undoubtedly most original forms of social grooming is maternal grooming of the offspring. Obviously this grooming has the classic function of the COBS of the offspring. There is evidence that in primates grooming cements the relation between mother and infant (311). In rats it has been shown that specific pup cues, such as water, salt, and odors in urine, codetermine the amount of maternal anogenital grooming (355). In some species, such as carnivores, maternal licking of the anal area of the pups or cubs reflexively stimulates urination and defecation and thus serves to maintain nest hygiene (176, 177). Besides the obvious immediate beneficial effects, the importance of maternal anogenital and body licking appears from the effects of different components of grooming behavior on later behavioral development of the rat pups (356). Body licking was more related to later juvenile activity, and anogenital licking was more related to copulatory performance of adult males (354).

Allogrooming is particularly conspicuous and common among primates and has drawn the attention of many investigators (e.g., see Ref. 555). An extensive review of the occurrence of grooming in this taxon has recently been given by Goosen (214). Most prosimians lick and scrape each other's fur; in the lemuridae the lower canines and incisors appear to be specially adapted as a "tooth comb" (64). In monkeys and apes the hand and fingers are used in a delicate and precise manner. This has even led to the suggestion that the evolutionary development of manual fine control may have been greatly stimulated by the grooming function. Social grooming may take up to ~20% of a primate's time, depending on species and circumstances (135). Obviously social grooming has important functions.

3. *Allogrooming and body hygiene*

In primates the classic function of grooming as COBS has been demonstrated for allogrooming as well. For instance, solitary living baboons and langurs were heavily infested with ticks in comparison with socially living conspecifics (51, 332, 538, 539). Actual removal of ticks through grooming under natural conditions has been observed in vervet monkeys (474). Wounds were also seen to be groomed attentively (43, 74). The assumption that grooming results in the removal of ectoparasites is evidenced by the fact that lice seem to be adapted to the grooming abilities of their hosts. Notable groomers such as baboons have small translucent lice (51). The black-and-white colobus, a clumsy groomer, is frequented by large black lice (296, 369, 475). Allogrooming certainly complements grooming insofar as areas are groomed that cannot be easily reached by the animal itself (251). Nevertheless, this does not necessarily mean that COBS of unaccessible spots is the object of such grooming. It has been pointed out that subordinate animals may approach the animal to be groomed from a side that is least risky (327). In hanuman langurs, 69% of ventrodorsal allogrooming occurred in a context of agonistic tension, whereas only 23% of ventroventral grooming did (332, 333).

Because in primates grooming often involves the swallowing of the particles found, there have been suggestions that grooming also serves to provide extra nutrients (e.g., salt) to the groomer. This would explain the interest that groomers have in rendering this service, although the material found in the fur makes it unlikely that it represents an adaptive effect of more than marginal significance (157).

However important the hygienic function of grooming may be under certain circumstances, it certainly is not the only function. Monkeys, virtually free of parasites, still solicit for and submit themselves to being groomed. Grooming is not necessarily elicited by or directed to irritating and obnoxious substances such as parasites. Apparently allogrooming encompasses more than the mere COBS function; in the same vein some adaptive regulatory effects of self-grooming may also be obtained by allogrooming. The latter may, therefore, supplement or partly replace self-grooming. Self-grooming as well as allogrooming seem to serve both COBS and social functions.

4. *Social functions of allogrooming*

As early as in 1908, Watson (540) recognized a social function for grooming. It was suggested that grooming served to establish, renew, maintain, or strengthen social bonds (25, 43, 74, 156, 214). Thus grooming might be involved in promoting the cohesiveness and persistence of groups (130, 317), whereas others reasoned that grooming merely reflects an already existing bond (372). There is a wealth of reports on the relationship between grooming and social bonds in various species, particularly of primates such as macaques (293, 479), baboons

(48, 51, 55, 228, 301, 540), mangabeys (24, 76), guenons (227, 357), guerezas (391), and langurs (23, 264, 272, 332, 457, 480). Allogrooming has even been observed between members of different species (208, 386) that normally show agonistic behavior toward each other. The bond-strengthening effect of grooming can easily be understood to result from the association with the rewarding hygienic consequences an animal being groomed experiences. It is also associated with a "service friendly" attitude of the social companion, which is reminiscent of the earliest experiences of social grooming, the comforting and relaxing effects of maternal grooming. This certainly must be a strong reinforcing consequence of letting oneself being groomed and of other behaviors that reinforce a companion to groom (213).

On the accounts given the adaptive consequences for the animal being groomed seem to be obvious. It is less clear what the benefits are for the groomer. Because, at first sight, the direct costs in terms of time and energy expenditure of behavior seem to outweigh any immediate benefits, it gives the impression of being an altruistic act in the sociobiological sense (e.g., see Ref. 96). Such bioaltruistic behaviors can evolve, nevertheless, in two contexts. If the groomer and the receiver are related, the behavior could derive its adaptive value from indirect benefits, namely, its contribution to the inclusive fitness of the groomer and it could be promoted by kin selection (231). Indeed, grooming often takes place between relatives [(216); macaques (98, 111, 148, 199, 283, 303, 348, 372, 413, 423, 427, 446, 554); baboons (427); and chimpanzees (209, 210, 393, 404)]. The most intense grooming bonds are often found between mother and offspring (303, 348, 372); this context is undoubtedly the root of the development of social grooming, since there are species in which grooming occurs only in this relationship [e.g., *Saimiri* (15)]. Species may differ in the extent to which kin are preferred as grooming partners. For instance, bonnet macaque females groom both kin and nonkin regularly, whereas the females of the related pigtail macaque direct their grooming almost solely to females of their own kin group (20, 98, 445). A similar difference in bonds is reflected in the greater tolerance by bonnet females of interactions of other females with their offspring (282). Another situation in which a reduced distance between two individuals is combined with increased grooming is the approach of a mother with a neonate by other females (43, 56, 283, 317, 419, 420).

Relationships with kin clearly tend to be less tension filled than those with nonkin. In Japanese macaques, approaches to groom directed toward nonkin are often accompanied by displays such as lip smacking. This display can be regarded as a ritualized intention movement of grooming, signaling a positive social attitude toward a recipient. The display is used when there is uncertainty about the relationship, requiring appeasing or reassuring emphasis on the affiliate, or at least nonhostile, orientation of the sender (512). In other words, grooming between kin tends to be a relaxed bond-reinforcing process, whereas grooming between

nonkin may more often be a tension-reducing bond-establishing process.

Grooming between nonrelated animals has been interpreted as "reciprocal altruism" (e.g., see Ref. 303), i.e., when it is performed as a mutual service (505). Indeed, grooming often tends to be reciprocal (23, 235, 238, 532). However, the reciprocity is mostly far from absolute (427); for instance, in many species of primates, higher ranking animals tend to receive more grooming than lower ranking ones. These asymmetries suggest that the groomer derives other direct social benefits, namely in terms of social relationships that yield, perhaps delayed, returns. This is also suggested by the sex difference in grooming frequency and partner choice in a female-bounded species such as the rhesus macaque (217); while males direct grooming preferentially to potential sexual partners, females use grooming to consolidate social relationships with regard to their status with other females. Indeed, castrated males behaved much more like females.

5. *Allogrooming and social relationships*

Long-term benefits of social grooming can be understood only if the distribution of grooming is viewed in relation to other aspects of social relationships, such as proximity, tolerance, support, and cooperation, on the one hand, and competition, aggression, and rank relationships, on the other hand.

In many primate species, adult females show more allogrooming than males and younger group members [e.g., among Old World primates: macaques (130, 283, 317, 394, 402), baboons (437, 452, 535-537), mangabeys (76), geladas (132-134, 136, 137), talapoins (553), most colobines (369, 475, 478); among New World primates: howlers (93, 248, 273-275, 361), *Saimiri* (15)]. However, there are notable exceptions to this rule. In chimpanzees the males groom each other almost four times as much as the females (363-365, 447). Among colobines the red colobus (369, 391, 476-478) and among baboons the hamadryas (1) are similarly exceptional and not only regarding grooming behavior. In the red colobus the females remain in their natal group as a rule, whereas the males tend to emigrate during adolescence. The females may, therefore, be more related among each other than with the immigrant males and the immigrant males among each other. In many of these species, the so-called female-bounded species, the females are organized in close kin groups. They depend on each other for support in competitive interactions with members of other kin groups. However, with the chimpanzee, the red colobus, and the hamadryas baboon, the females are the exogamous sex; the males remain in their natal group or clan. This is mirrored in similar differences in tolerance, support, and cooperation (364). Thus chimpanzee males of the same community are believed to be more closely related among each other than females; in contrast to females, they share food, in particular meat, obtained after cooperative hunting (485). Not only do they cooperate systematically in hunting (50) but also in

the warlike defense of a community territory (68, 210, 364, 366). In other male-bonded species, analogous relationships are shown or supposed to exist. Presumably, kinship is one of the factors facilitating allogrooming.

Dominance relationships appear to be important determinants of the direction of grooming between unrelated females. Dominant animals are groomed more than subordinates. These direct their grooming preferentially to group members of higher rank [macaques (e.g., see Refs. 86, 283, 423, 445, 446), baboons (79, 437), vervets (158, 438)]. The same may hold for the grooming relations between males in species where these occur; it has been demonstrated for chimpanzees (447). An exception is an old male chimpanzee groomed by the alpha-male, who never returned the grooming; this old male, however, was very influential in the formation of coalitions (364, 365). The dominants selected are often those of adjacent ranks (86, 513). In female-bonded groups where relatives occupy adjacent rank position in matriarchal rank groups, this preference might therefore even be a kin preference. However, the preference is also found after there has been a correction for kinship (239).

In most cercopithecine species where the females are philopatric, females direct most of their grooming toward other females. This is understandable, since these are lifelong relationships, both with close kin and with nonkin. Hamadryas and gelada baboons, living in so-called "one male harem units," show primarily within-unit grooming, whereas members of different units do not groom each other, although different units meet each other daily at sleeping sites (55, 94, 301). However, even in some of these species where females are philopatric, males have been found to groom each other as well. Adult troop males of Japanese macaques on the isle Yakushima frequently maintained proximity and subsequently allogroomed in both the mating and nonmating season, much unlike many other Japanese macaque troops. Few agonistic interactions occurred, and the dominance relationship rarely appeared in such intermale associations (180, 181). Long residence caused by lack of migration possibilities and subsequent strong familiarity may set the stage for such affiliate male relationships. However, also in groups of rhesus and Japanese macaques where males emigrate in adolescence, juvenile males were observed to groom other males, namely their brothers and peers (85, 348, 480). The bonds thus formed may be of value later, even though these animals will leave their natal group, because they tend to immigrate into groups where they find support from male relatives (516).

These data concerning the distribution of grooming strongly suggest that it often serves as an investment in valuable relationships, decreasing the risk of harassment and reinforcing tolerant and supportive behaviors, such as giving help in coalitions and providing access to resources (437, 439). The fact that vervets gave more support to those group members from which they received more grooming has been taken as evidence for this (440). Similar reciprocities have been found for chimpanzees (106, 110, 239). These suggest that the ani-

mals engage in an exchange of grooming and other favors by keeping a mental record of the exchange balance and adjusting their "investments" in accordance with this (106, 110). What we have come to know about the cognitive capacities of higher primates and chimpanzees, in particular in recent years, makes it quite plausible that such advanced intuitive "calculations" are possible (109). Although we may accept the existence of such advanced cognitive "bargaining" processes, we should carefully exclude more parsimonious explanations, namely that the correlations are to be attributed to side effects of other relations (21, 67, 239).

Also the relation between grooming and sexual behavior is suggestive of "transactional" processes. In some primate species both grooming and support in conflicts are given more easily by males to females when the latter are sexually receptive (e.g., see Refs. 7, 217, 283, 301, 302, 417). Young adult male baboons invest in this way in "special" relations with females that may eventually bear fruit in preferential sexual access to the female (452). The grooming of females by males seems to be hormone dependent. Rhesus males groom unrelated females mainly in the mating season, especially during the female fertile period (129, 283, 510, 552). During so-called "consort periods," partners are frequently engaged in mutual grooming (74, 87, 130, 345, 346, 417, 421). Sexually active males restrict and concentrate their grooming activities to their preferred sexual partners; this is in contrast to females, who do not restrict their grooming activities to their sexual partners. Goy et al. (217) supposes that this sex difference arises as a result of pubertal androgens.

6. *Allogrooming and regulation of social tension*

Agonistic involvement is associated with an instantaneous activation of the adrenomedullar system (catecholamines) and, next, an activation of the adrenocortical system (corticosteroids), mobilizing energy reserves. These changes are adaptive in that they turn metabolic and other physiological processes into a state allowing the animal to invest energy in sudden and intense action (426). After this is ended the animal usually returns to a more relaxed state. However, a sustained activation of the adrenal system has been demonstrated in both rodents (e.g., see Ref. 433) and primates (531) in situations of unpredictable threats, requiring the animal to maintain a state of ready to act or react. Especially the loser of a conflict is confronted with this requirement, uncertain as he may be about further harassment. The respective emotional and physiological changes are subsumed under the term stress (315). If the response is maintained too long, anabolic restoration is thwarted and negative consequences on growth, development, immunity against diseases, and reproductive functions ensue (240, 507, 529, 530). Also sex differences in coping with social tension have been demonstrated (107).

The period after arousal and tension is manifested afterwards behaviorally by, among others, patterns of the COBS complex, such as scratching, body shaking,

and autogrooming (10, 12, 43, 120, 277, 418, 506). An increase of two of these behaviors and the physiological manifestations of stress could be evoked by electrophysiological and pharmacological brain stimulation (305, 306, 511). Nevertheless, there are indications that scratching and body shaking are connected more directly with an acute stressor than self-grooming. Not only are there different patterns in their response toward neuroendocrine activation (462, 519), but also their temporal organization and embedding in behavioral structures are different (10, 466, 506). Scratching and body shaking are considered as more immediate and reactive behaviors in response to disarrangement of the pelage and irritation of the skin. These may be the result of behavioral activity and the thermoregulatory responses associated with it. Self-grooming, on the other hand, should be considered more as a restorative action by which the animal redresses a foul-up of the pelage once the state of activation to which this was due has subsided (10).

7. *Allogrooming and reconciliation*

In macaques allogrooming has been shown effective in reducing the above-mentioned behavioral symptoms of sustained arousal and stress (10, 12, 443) as well as heart rate (49). For instance, the high level of scratching during the first few minutes after a conflict is reduced considerably after an affiliative contact, such as grooming, has taken place between the former contestants (49). This reduction is understandable, since the occurrence of postconflict affiliative contacts indeed appeared to be associated with a substantial reduction of the increased likelihood of further attacks to which the victim is exposed after a conflict [chimpanzee (109), long-tail macaque (12)] not only from the former opponent but also from the latter's kin and from other group members. This indicates that the postconflict affiliative contacts indeed function as reconciliation behaviors (11).

Recently there have been a number of studies demonstrating that individuals involved in agonistic interactions perform affiliative behaviors shortly after this interaction [chimpanzees (108, 114), macaques (12, 92, 112, 115, 276), patas (556), and vervet monkeys (80)]. These highlight the role of grooming as an expression of nonagonistic intent (488) and an instrument of social manipulation. The occurrence of reconciliation appears to depend on the value a long-term good relationship has for those involved irrespective of the short-term interests clashing in a momentary conflict. The likelihood of reconciliation is higher between kin (12, 92, 112, 115, 556) and is determined also, independently, by the overall quality of the relationship (12, 115). Obviously, both victor and victim may come to lose from a disturbed relationship inasmuch as their relationship was associated with mutually beneficial tolerance, cooperation, and exchange of services (12, 368).

On theoretical grounds grooming might be expected to play a role in consolation behavior, namely when rela-

tives or allies of a victim restore his emotional balance by soothing him. Although there is some evidence that such processes occur in chimpanzees (113, 114), consolation processes could not so far be demonstrated in macaques (11). Studies of integrated captive colonies and of feral groups with more than mere correlational methods were needed to reveal these relationships. Earlier investigations were focused on assessing a relation between aggression and grooming in pairs of group-housed animals (4, 74, 327, 372, 423, 526). However, these correlational laboratory studies neither yielded convincing evidence for such a relation nor for a relation between grooming and social rank, whereas a clear rank dependence of display of aggression was found (283, 317, 402, 424, 526). For one thing, these earlier studies did not take into account whether grooming and aggression were directed toward the same individual or not. When grooming, not directed to the same individual as aggression, is taken into account, there is evidence that self-grooming and/or allogrooming may reduce tension and aggression in primates. During the mating season members of a consort pair groom each other frequently and behave aggressively toward others, yielding a positive correlation between aggression and allogrooming; however, grooming and aggression are directed toward different individuals (283, 317, 560). When the amount of aggression increases in general in a group due to the introduction of an intruder (456), this period of aggression is followed by a period of enhanced grooming, not directed to the intruder but to group members (22, 24, 527, 532).

The relationship between grooming and aggression was also studied in solitary animals. The occurrence of self-grooming reduced self-oriented aggression (215). Self-oriented aggression and probably alloaggression was lower when social grooming was allowed (74, 212, 215, 317).

D. Concluding Remarks

Both self-grooming and allogrooming serve a great variety of functions. The main original function undoubtedly is concerned with COBS. This function has developed in arthropods, birds, and mammals. Important as this function may be, it is a low-priority behavior in the temporal allocation system of behaviors; it is not time locked to urgent external behavioral requirements, and it fills the time gaps left by high-priority functions. In the laboratory, rat grooming behavior may occupy 25–40% of the awake time, depending on housing conditions, with most of the behavior seen just before and after the diurnal sleep period (52, 308). Behaviors directed to the outer body surface have also been recognized as displacement behaviors and as behaviors with specific signal value in arthropods, birds, and mammals. Probably this is an example of functional analogy and indicative how appropriate these COBS behaviors are for being driven by natural selection in the same direction. Because grooming mainly occurs after various activities and stressors, it seems related to a state of relax-

ation, at least in mammals. Grooming may thus acquire signal value in notifying conspecifics about a relaxed mood. Hence it may have evolved into a device of social manipulation, and grooming itself may have acquired a function in dearousal. Social grooming probably originated in the mother-infant relationship. The soothing and comforting effects, which were brought about by the hygienic manipulation, made grooming suitable for developing a pacificatory and a social bonding function also among adults. It plays an important role in the regulation of relationships in social groups. The performance and exchange of the behavior has come to be governed by rules that are in accordance with the predictions forwarded by sociobiological theory on kinship relations and reciprocity of "altruistic" investment.

In addition to the peripheral properties of the skin controlling grooming behavior, external social requirements exert a more important influence. Ethoexperimental analyses suggest that grooming is strongly controlled by internal programmatic routines, especially when its COBS function is preeminent. Most studies on the neural and hormonal regulation of this behavior have been done in rats using peptide-induced grooming as a model for grooming behavior, which seems controlled by similar internal programmatic routines and which is often seen after various stressors. Because there is a lack of grooming studies on "spontaneously" occurring grooming behavior, the validity of such models can be discussed.

III. NEURAL SUBSTRATE OF GROOMING

A. Peripheral Versus Central Control

One of the main questions concerning the control of grooming behavior is to what extent are sequences of motor acts controlled by peripheral sensory input as opposed to more centrally controlled motor programs. The grooming of rodents bearing brain lesions is not only less effective in terms of COBS but may be initiated at an inappropriate time as well (163, 164, 290). In these animals grooming movements occurred during locomotion or swimming (165). Furthermore, these animals lacked the possibility to perform compensatory movements in case of deviating body posture to make the grooming efficient (206). Adult house mice, although having their forelimbs neonatally amputated, continued to display patterns of facial grooming with their stumps "identical" to those of normal mice (162). If one limb of a grooming, intact mouse was gently pulled away, the other free grooming limb also moved away from the face and continued grooming in front of the face (206). Furthermore, normal grooming behavior can be studied in genetically furless Wistar rats (192). Thus grooming is displayed in the presence of an abnormal feedback and without serving its regular maintenance function. Moreover, sectioning of the trigeminal nerve did not abolish grooming exhibited by mice in their home cage (34, 35), again pointing to an important central input in the control of grooming resulting in a fixed pattern of grooming

acts. In another experiment rats were mechanically prevented from body and foot licking by wearing a collar (465). A dramatic increase in rapid forelimb movements (vibration), usually initiating the grooming bout, was seen. However, foot scratching, which could still be displayed, was hardly seen, apparently because foot licking normally following scratching could not be performed. It was concluded that the mechanical interference with the normal grooming repertoire resulted in a continuous attempt to initiate grooming as evidenced by the increased forelimb vibrations (465).

The relative importance of central versus peripheral control of grooming behavior is dependent on the motivational context (34, 166, 422). For instance, some grooming elements, such as rhythmic tongue protrusions, forelimb strokes, and high-frequency flails, are displayed in various combinations and in various motivational contexts (37), such as taste-elicited ingestion/aversion and postprandial grooming. Berridge and Fentress (34) found that trigeminal deafferentation decreased tongue protrusions in ingestive but not in postprandial grooming contexts, whereas alterations of forelimb movements were restricted to postprandial grooming contexts. Grooming behavior elicited by specific stimulation of the skin or tongue also appears to be directed to, i.e., controlled by, these stimuli. Variations in stimulus-directed grooming are absent in more stereotyped forms of grooming, which are not associated with a particular stimulation of the skin or the tongue but rather with a certain state of the animal, such as uncertainty, dearousal, or after being exposed to a stressor (103). For instance, a rat placed in a novel environment displays a stereotyped form of grooming (269). Detailed analyses of grooming behavior (167) demonstrate that the motivational context (e.g., taste or novelty induced) and the sequential phase of grooming are determining the rules for control of grooming behavior. The stereotyped forms of grooming, although containing similar grooming elements, seem more independent of peripheral control. This distinction between stereotyped forms of grooming and stimulus-controlled forms of grooming has been observed both in rodents and in birds. Some bird species respond with sand bathing whenever the sun breaks through and with rain bathing whenever it begins to drizzle (101, 528). These particular short-lasting bouts of grooming (448) also occur as a reaction in offensive activities of parasites, disturbances due to feather loss, wind gusts, or activities of the bird itself (62). On the other hand, it has been documented that the structure and the initiation of grooming is independent of any particular stimulus (313). In undisturbed environments grooming is displayed periodically (312), maybe due to a central rhythm or secondary to a light-dark cycle (449). Similar to what was found in rodents, the spontaneously occurring grooming in birds is not affected by partial denervation of the skin (104).

B. Grooming Controlled by Adrenocorticotrophic Hormone/Melanocyte-Stimulating Hormone

Because arousing conditions such as novelty and stressors are among the activators of both grooming

and the hypothalamo-pituitary-adrenal systems (84, 143, 144, 192, 268-270), the relationship between pituitary hormones and grooming has been extensively investigated. It was concluded that the induction of grooming did not depend on the integrity of the hypothalamo-pituitary-adrenal system (192, 269, 546). Hypophysectomized animals still displayed enhanced grooming behavior when exposed to a novel environment (191, 270). Adrenocorticotrophic hormone (ACTH)-induced grooming was successfully elicited in hypophysectomized, adrenalectomized, or gonadectomized animals (198, 546). Moreover, structure-activity studies showed grooming induced by fragments, which do not stimulate the adrenals (428). Adrenocorticotrophic hormone seems of importance to grooming behavior, albeit only intracranial but not systemic injection of ACTH resulted in the stretching and yawning syndrome (168, 169, 185) in rodents preceded by extensive self-grooming behavior (198, 258). Dunn et al. (143) injected antibodies against ACTH into the cerebroventricular system of rats and found that this treatment suppressed novelty induced grooming. However, this observation has not been replicated so far. Experiments conducted with the central administration of ACTH or melanocyte-stimulating hormone (MSH)-like peptides strongly suggest the involvement of these peptides in mediating the grooming response.

1. Grooming bout of adrenocorticotrophic hormone-induced grooming

In an attempt to assess the biological relevance of ACTH-induced grooming, detailed frequency and duration analyses of the behavioral elements collectively constituting grooming behavior were made (192). It appeared that ACTH enhances the display of grooming behavior without changing the frequency distribution of elements. An ethological analysis of sequences of behavioral elements revealed that the basic structure of ACTH-induced and novelty induced grooming was rather similar (466). In a given grooming bout there is a cephalocaudal progression of grooming acts both in birds (237) and in rodents (466); in case of rats the bout is interrupted by behavioral elements such as scratching and shaking of the whole body. In the case of ACTH-induced excessive grooming these interruptions did not lead to behaviors other than grooming and hence resulted in prolonged grooming bouts. Interestingly, the cephalocaudal order within a bout closely resembles the ontogeny of the grooming repertoire (403). In both cases scratching behavior did not have a fixed position in this sequence of grooming behaviors. Although many drugs have the ability to induce some kind of grooming, so far only ACTH/MSH-like peptides and dynorphin induce grooming behavior with characteristics similar to centrally controlled grooming behavior (3, 463). Therefore in studying the underlying neural substrate of grooming behavior, quite often ACTH-induced grooming has been used as a model.

2. Specificity of adrenocorticotrophic hormone-induced grooming (versus other neuropeptides)

Although ACTH was the first peptide reported to induce excessive grooming (168), it soon became apparent that other peptides were active as well. Both α - and β -MSH were as active as the sequence ACTH, and no qualitative differences in the behavioral responses were detected (198, 463). β -Lipotropic hormone itself, the precursor peptide, does not elicit grooming in rats unless an extremely high dose (2.5 mg icv) is used (261), possibly resulting in a sufficient supply of active fragments. Other grooming-inducing peptides are vasopressin (337), oxytocin (377), prolactin (124), substance P (152, 280), somatostatin (521), bombesin (204), thyrotropin-releasing hormone (295, 522), and corticotropin-releasing factor (CRF) (140, 142, 358, 441).

Studies on the nature of vasopressin-induced grooming and scratching showed that it can be readily distinguished from such behaviors induced by other peptides (337). [Lys⁸]vasopressin, [Arg⁸]vasopressin, and [Arg⁸]vasotocin, but not des-glycinimide-vasopressin (116, 119), administered intracerebroventricularly to mice provoke a dose-dependent grooming response. With higher doses, occasionally, barrel rotations are observed (47, 70, 100, 336, 399). Potencies in the induction of excessive grooming paralleled the potencies in the induction of reduced immobility and increased escape activity in the tube test (338). Blockade of the effects with a specific vasopressin V₂-antagonist suggests the involvement of V₂-receptors (338). The effects of vasopressin on grooming in rats are smaller than the corresponding effects in mice (71, 336).

Grooming responses on oxytocin treatment were seen in studies on the display of maternal and sexual behavior (376, 378, 379). Oxytocin- and prolactin-induced grooming (71, 100, 127, 336) involve mechanisms other than those underlying ACTH-induced grooming (125). First, subcutaneous administration of both peptides is effective in contrast to ACTH (122, 123, 128, 198). Second, the grooming bout of oxytocin and prolactin is characterized by a high incidence of genital grooming (126, 128). Third, oxytocin- and prolactin-induced grooming are not fully abolished by naloxone in contrast to ACTH-induced grooming (124, 196, 377). Fourth, a second injection of either of the peptides a few hours after the first is still effective on grooming (377), whereas a second injection of ACTH 4 h after the first is ineffective in eliciting grooming. This so-called "short tolerance" has been extensively described by Jolles et al. (271). In addition, oxytocin had additive effects on ACTH-induced grooming but not on prolactin-induced grooming (377). Structure-activity studies also indicate a different mechanism of action for oxytocin versus [Arg⁸]vasopressin and [Arg⁸]vasotocin (324). The structural properties of oxytocin fragments are similar to those required for uterus activity (71, 338). Dopaminergic systems play a role in oxytocin-/prolactin-induced grooming, as oxytocin-induced grooming is very sensitive to 6-hydroxydopamine or haloperidol treatment in the nucleus accumbens; furthermore, dopamine neuro-

transmission in the nucleus accumbens, substantia nigra, and neostriatum was enhanced by prolactin treatment (182, 183, 316, 382).

Tachykinins, such as eleoisin, kassinin, neurokinin A, physalaemin, and substance P, injected intracerebroventricularly or directly into the ventral tegmentum area induce mainly facial grooming (278-281, 284, 322, 520). High doses of substance P lead to barrel rotation (520). Facial grooming induced by tachykinins can be suppressed by neurotensin-like agents such as xenopsin (281). Intrathecal injection of substance P and neurokinins induces caudally directed scratching and biting. It has been suggested that intrathecal administration of substance P and excitatory amino acids mimics the perception of a noxious stimulus (174, 252-254, 388), as these peptides are putative transmitters in the central projection of nociceptive information (69, 246, 266, 284, 362, 383, 395, 550). Apart from the three neurokinins, excitatory amino acids active at *N*-methyl-D-aspartate or quisqualate receptors also produce caudally directed tail biting, scratching, or licking when given intrathecally. Monoamines, opioids, and neurotensins have been proposed as inhibitory transmitters in the spinal cord (550).

Bombesin, a peptide derived from amphibian skin (6) but also present in the central nervous system and the gut (352, 483, 534), mainly induces scratching (299, 328, 360, 406, 459, 462, 519). Bombesin has been proposed to be involved in temperature regulation (61, 524) and as a satiety signal in the short-term control of feeding behavior (186, 187) and drinking (97). After peripheral administration, satiety, including grooming and sleeping, has been observed (188, 297, 450, 534). However, in a systematic study (298) it was shown that variance in ingestion was not related to bombesin-induced scratching. Central cholinergic systems (340) as well as dopaminergic systems (339) are involved in bombesin-induced scratching. In the search for the involvement of opiate systems in bombesin-induced scratching, λ -type receptor activation was shown (200-205, 297). Compounds with affinity for μ -receptors moderately induced scratching, although Van Wimersma Greidanus et al. (519) showed a preferential suppression of bombesin- and β -endorphin-induced scratching with naloxone. As for β -endorphin, it was also shown for bombesin that local administration into the periaqueductal grey (PAG) resulted in excessive scratching behavior and analgesia (304, 385). Cholecystokinin (CCK), another brain-gut peptide, induces satiety and grooming as well (8, 189, 451, 557, 558). The display of grooming is similar to the grooming induced by ACTH (300) with respect to topography and time course. Ceruletide (451) only induced grooming, in contrast to CCK-S, which shows most or all of the physiological and behavioral actions of CCK (19, 121, 154, 525), again emphasizing a dissociation between mechanisms of satiety and grooming (451). Because CCK stimulates the release of ACTH (260, 392, 401), it has been proposed that CCK elicits grooming via ACTH. However, there is a clear dissociation between the grooming response and circulating peripheral ACTH (546). Thus the central rather than the periph-

eral ACTH release should be taken into account. Intracerebroventricular administration of somatostatin induces low frequencies of scratching, which can be suppressed by naloxone (521). Higher doses lead to barrel rotation, which is also seen after high doses of vasopressin and substance P.

The administration of neuropeptides, such as ACTH, endorphins, enkephalins, vasopressin, or substance P, into the hippocampus or cortex of the rat induces massive changes in EEG activity and the DC slow potential referred to as spreading depression (250). Behaviors seen after peptide treatment, such as immobility (65, 219, 489, 442), changes in activity/reactivity to foot shock (66), circling behavior, grooming (381, 442), barrel rotation, and wet dog shake (444), may accompany spreading depression (250). These effects of neuropeptides are considered to be the result of nonphysiological interactions of neuropeptides with the brain. However, the criticism does not concern ACTH-induced grooming, since it is not accompanied by signs of spreading depression. Moreover, the behaviors accompanying spreading depression appear to be more aberrant forms of behavior in contrast to ACTH-induced grooming, which is similar to novelty induced grooming.

In summary, various peptides induce grooming behavior and sometimes aberrant forms of changes in EEG activity accompanied by components of grooming behavior. Adrenocorticotrophic hormone, however, elicits long-lasting grooming bouts that are structurally closely related to normally occurring grooming. The remarkable similarity between the structure-activity relationship studies with respect to grooming behavior and melanophore dispersion suggest that similar peptides and similar mechanisms have been conserved across species in different species. These findings favor a role for MSH-like peptides in the display of grooming behavior.

C. Structure-Activity Studies With Adrenocorticotrophic Hormone

In search of the active sequence involved in ACTH-induced grooming, gradual shortening of both NH₂ and COOH termini of the peptide was performed, and the capacity to induce grooming was tested in equimolar doses. In one of the first studies on structure activity (198), the following sequences were active: α -MSH, β -MSH, ACTH-(1-16), [Lys¹⁷,Lys¹⁸]ACTH-(5-18), ACTH-(5-16)-NH₂, ACTH-(1-13)-NH₂, and ACTH-(5-14). Decreasing potency was seen in the following list of MSH derivatives: racemized MSH, α -MSH-(1-12), α -MSH-(1-11), α -MSH-(5-13), des-acetyl- α -MSH, Met(O)₄- α -MSH, and α -MSH-(1-10) (463). Apart from peptides with partial activity there is also a list of peptides without any excessive grooming-inducing activity; ACTH-(1-10), ACTH-(11-24), ACTH-(4-10), ACTH-(4-9), ACTH-(4-8), ACTH-(4-6), ACTH-(5-7), ACTH-(7-10), ACTH-(7-16), and [Leu⁹] α -MSH had hardly any grooming activity (198, 546, 563). On the

basis of the results of these structure-activity studies it was concluded that the message site resides in the fragment 5-13, and presumably in fragment 5-7, as ACTH-(4-7) and α -MSH-(5-13) are active. As ACTH-(5-7) itself is without activity, proper elongation of the message site, playing a role in the intrinsic activity and the receptor affinity, is required for full expression of the behavioral activity as described for other biological effects of ACTH-(1-24) and α -MSH (435).

Another structural modification-inducing activity is the *N*-acetylation of ACTH-(1-13)-NH₂ producing α -MSH (198, 371). O'Donohue and co-workers (198, 546, 563) suggest that acetylation may be an important post-translational mechanism to regulate biological activity of ACTH/MSH-like peptides. Furthermore, expression of the latent activity within the sequence 4-10 can be obtained by D-amino acid substitution at the Phe⁷ residue. Interestingly, combined intracerebroventricular treatment of ACTH-(4-10) and [D-Phe⁷]ACTH-(4-10) did result in a grooming response as if the rats were treated with a equimolar dose of [D-Phe⁷]ACTH-(4-10) alone (543, 545). As other D-substitutions were inactive, differences in metabolic state are unlikely to account for the expression of the behavioral activity. It seems more likely that the stereoconfiguration makes the message-encoding sequence more accessible for receptor interaction. Such reasoning is supported by the observation that ACTH-(1-24) is active, whereas an equimolar concentration of ACTH-(1-10) and ACTH-(11-24) is not (198). It is difficult to conclude that the enhanced potency of the COOH-terminal elongated message sequence is due to a second message site, since ACTH-(7-16) is not effective, whereas ACTH-(5-14) is. The role of methionine is complex, since the sequence 5-7 itself is devoid of activity in grooming and avoidance behavior (367). Methionine⁴ is a prerequisite for α -helix formation, as it was shown that ACTH-(5-10) is not proven to form random helix coils in the transition on going from water to trifluorethanol (221). According to Schwyzer (434) the presence of fragment 4-8 is required for this process. In addition, peptides containing oxidized methionine show a loss of grooming activity (99). When peptides were protected against oxidation by replacing methionine by norleucine, such a modification led to prolonged biological activity (243). Reduced enzymatic degradation and prolonged biological activity was also reported for [Nle⁴-D-Phe⁷] α -MSH (225, 249). This "sticky and long-lasting" MSH derivative was the most potent grooming-inducing peptide (463).

The importance of methionine in the biological activity of ACTH/MSH is further supported by the fact that ACTH-(1-4), and not Met(O)₄-ACTH-(1-4), has a potentiating effect on other active peptides (99, 147). The relatively low grooming frequencies seen after administration of MSH-(5-13) and ACTH-(5-16) could be enhanced by concomitant injection of ACTH-(1-4) (99). Even peptides such as ACTH-(1-16) and α -MSH, which already contained the sequence ACTH-(1-4), showed more grooming behavior when the fragment 1-4 was injected (99).

Peptidergic systems regulating adaptation are

widely spread among various animal phyla (294). In amphibians color adaptation to the environment is regulated by α -MSH. The primary structure of these peptides has remained rather similar over different phyla, indicating a remarkable preservation of endocrine communication during the course of evolution (151, 411). This notion has led to comparative studies between different species regarding the biological effects of neuropeptides. A comparative structure-activity study on melanophore dispersion in *Xenopus laevis* and excessive grooming in rats yielded a striking similarity in structure activity (463). Similar to what was demonstrated for ACTH-induced grooming in rodents, a reduced melanotropic activity was seen in the *Xenopus* assay, *Rana pipiens* and *Anolis carolinensis* and tyrosinase activity in melanoma cells (147, 434) as a consequence of COOH-terminal shortening, des-acetyl derivation, or changes in the fragment 4-9 sequence. Also potentiation by the fragment 1-4 has been observed in melanophore assays. The similarity in structure activity of MSH effects in amphibian adaptation and rodent grooming suggests a MSH-like nature of the brain peptide receptor involved in grooming.

D. Opioid Systems in Peptide-Induced Excessive Grooming

One of the most important functions of opioid systems is the defense against noxious effects of various stressors, i.e., inhibition of pain perception and activation of the pituitary-adrenocortical axis via CRF (255). The involvement of opioid systems in the display of grooming behavior may attribute to the understanding of the functional role of grooming other than the COBS function. The assumption that opiate receptor activation is involved in ACTH-induced grooming is based on several facts: 1) a low dose of morphine or β -endorphin induces a behavioral activity, including grooming behavior (13, 195, 197, 462); 2) ACTH-, MSH-, β -endorphin-, and dynorphin-induced grooming can be blocked by the opiate antagonist naloxone (3, 141, 196, 197, 561); 3) a similarity in structure activity of ACTH-like peptides on grooming and affinity for opiate receptors in vitro has been demonstrated (487); and 4) in the PAG, local application of ACTH and β -endorphin resulted in the excessive display of grooming and scratching, respectively (462). Scratching is also the preferentially suppressed grooming behavior after naloxone treatment (523). There are two reasons for associating β -endorphin-induced scratching with opiate receptor activation. First, scratching is preferentially suppressed by naloxone in ACTH-, bombesin-, and β -endorphin-induced grooming (519, 523). Second, des-Tyr- β -endorphin, which has lost its opiate activity, has also lost its scratching-inducing ability (462). At high doses of β -endorphin no signs of grooming or excitation are seen, since the rats invariably are in a catatonic state (462, 547). Excessive scratching is particularly associated with endorphins, since even at high doses Leu- and Met-enkephalin are inactive (198). In mice and rats a low

dose of dynorphin was reported to enhance eating and grooming behavior, whereas a high dose in rats resulted in barrel rotation, which may lead to death (3, 279, 561).

The PAG was the site in which Jacquet (262) demonstrated hyperreactivity and immobility for ACTH and morphine, respectively. Although the PAG is a site of action for both ACTH and endorphins, lesion studies in the PAG demonstrated differences in the site of action within the PAG for ACTH and β -endorphin. In lesioned animals, intracerebroventricular ACTH-induced grooming was reduced, whereas β -endorphin-induced immobility was facilitated (462).

In addition, it seems that opiate receptor activation is not the first event leading to ACTH-like grooming behavior. First, affinity for an opiate receptor is not a prerequisite for inducing grooming: α -MSH, devoid of affinity for opiate receptors (487), is a potent grooming-inducing peptide (198). Second, the nonopioid fragment des-Tyr-dynorphin (3, 78) induces grooming similar to ACTH- and dynorphin-induced grooming (3, 533). However, both α -MSH- and des-Tyr-dynorphin-induced grooming can still be blocked by naloxone (3, 370, 533).

Depending on the dose used, opioids may function synergistically (low dose) or antagonistically (high dose) with ACTH (5, 38-42, 72, 118, 178, 195, 222, 263, 370, 390, 559). The involvement of opiate receptors in grooming and the involvement of the PAG with differential sites of action for ACTH and β -endorphin are in agreement with previously postulated functional agonistic/antagonistic properties between ACTH and opioids. It may be that release of ACTH and β -endorphin at low levels during environmental changes attribute to the process of adaptation by a synergistic action. If environmental events cannot be coped with, such as during chronic stress, the effects of endorphins prevail and functionally antagonize the effects of ACTH. This may lead to a state of immobility and/or analgesia, which prevents the animal from inadequate reactions.

E. Opioids and Aberrant Grooming

An aberrant form of grooming has been seen in animals kept in captivity (468). The high frequency of grooming, scratching, or biting leads to damage of the fur. This is reminiscent of other stereotypic behaviors, which have been described for pigs and cattle housed under stressful conditions (549). The hypothesis was forwarded that the release of endorphins while performing the "nonfunctional" and possibly painful behaviors serves to protect the animal against damage due to the continuous stress (468). Moreover, by their reinforcing properties, they are thought to maintain the performance of stereotypic behavior, which led to the release of the endorphins. Because grooming is performed after stress and opioids are involved in the display of grooming, it seems not unlikely that in the case of regular stressful circumstances, grooming develops into a more aberrant form of behavior. If the endorphins play a role in the maintenance of this behavior, then a blockade of the reinforcing properties of the endorphins with nalox-

one should at least temporarily diminish the excessive grooming. Indeed, in a preliminary study (468), naloxone-treated house cats suffering from such aberrant grooming showed an improvement of the condition of their fur. The occurrence of grooming after stress and the involvement of opioid systems and its known function of inhibiting noxious consequences of stress indicate that grooming and opioids are part of a system counteracting the effects of stressors.

F. Adrenocorticotrophic Hormone-Induced Grooming and Neurotransmitter Systems

1. Dopamine

Excessive grooming can be elicited both after intracerebroventricular and after local administration of ACTH or α -MSH into the substantia nigra (91, 501). Dopaminergic agents, such as haloperidol and apomorphine, affect ACTH-induced and novelty induced excessive grooming in rats (203, 218, 461, 502, 544). Local administration of haloperidol or apomorphine into the neostriatum enhanced diminished intranigral ACTH-induced grooming, whereas the effect on intracerebroventricular ACTH-induced grooming was precisely reversed (90, 461). Lesions carried out in the neostriatum showed a significant disruption of the completion of sequences of spontaneously occurring grooming behavior and not on the number of grooming sequences (36). Stereotypic grooming behavior was seen after apomorphine treatment in striatal lesioned rats (236). Intracranially applied α -MSH modified both grooming behavior and the dopaminergic content of the striatum (501). These findings strongly suggest the involvement of the neostriatum and the substantia nigra in the modulation of ACTH-induced excessive grooming behavior. Given the existing pathways between the neostriatum and the substantia nigra it is evident that striatonigral pathways and dopaminergic receptors form part of the network in which the neural substrate underlying ACTH-induced grooming is embedded. Likewise, specific dopaminergic agents in the nucleus accumbens affected both intracerebroventricularly and intranigraly elicited ACTH-induced grooming. Adrenergic agents remain ineffective in this area according to Spruijt et al. (461), although Dunn (138) reported activity of phentolamine and yohimbine. When the nucleus accumbens is lesioned by 6-hydroxydopamine, ACTH-induced grooming is suppressed (460), underlining the role of this nucleus for this behavior. This lesion study could not be replicated by others (139). The endorphin fragment des-Tyr- β -endorphin, having similar behavioral effects to those produced by neuroleptic drugs (117, 517) given into the nucleus accumbens, blocked ACTH-induced excessive grooming (194), whereas other endorphins remained inactive. Biochemical studies on dopaminergic receptors have documented the presence of two subclasses of dopaminergic receptors (472), D₁- and D₂-receptors. The specific D₁-receptor agonist SKF 38393 failed to influence

body temperature while it evoked an unusual pattern of intense grooming and stimulated motility (73, 351). However, in two studies it was reported that SKF 38393 elicited no signs of stereotyped behavior or grooming episodes (373, 498). It was suggested that D₁-receptors induce EEG desynchronization and behavioral arousal (373). Studies carried out with the D₁-antagonist SCH 23390 supported the involvement of D₁-receptor activation in grooming (190, 469).

Local application of D₁-agonist SKF 38393 into the neostriatum induced grooming behavior (172). As discussed, the effect of local administration of dopaminergic agents into the neostriatum on ACTH-induced grooming depends on the site of administration of ACTH (intracerebroventricular or intranigral). This difference in grooming scores, due to a difference in the site of administration of ACTH, suggested an additional site of action for ACTH other than the substantia nigra. In addition, a second injection of ACTH via a similar route as the first has appeared to be ineffective in inducing grooming (short tolerance). However, a second injection of ACTH intracerebroventricularly after a first injection intranigraly is still effective in inducing grooming. Both notions have led to the search for another active site, resulting in the finding that an injection of ACTH into the PAG elicited excessive grooming (462). The complex role of central dopamine in ACTH-induced grooming can be reconciled with the role of the PAG in excessive grooming. The PAG is innervated by both the substantia nigra pars reticulata, i.e., the output station of the striatonigral neurons, and by the substantia innominata, one of the main output stations of the tegmental accumbens dopaminergic neurons (91). The involvement of striatonigral pathways in the regulation of grooming behavior seems nonspecific for ACTH-induced grooming. The hierarchical control of movements from neostriatum, substantia nigra, colliculus superior, and further downstream has also been evidenced in studies on moving patterns of cats (88). The involvement of dopamine in grooming behavior has not only been evidenced for rodents, but also in birds it was shown that dopaminergic agonists facilitate displacement behavior and are mainly effective in the avian nucleus basalis (318).

2. γ -Aminobutyric acid

The involvement of γ -aminobutyric acid (GABA)-ergic structures in ACTH-induced excessive grooming was established by the local administration of the GABAergic agonist muscimol and antagonist picrotoxin into the substantia nigra and into the colliculus superior (464). Several authors have pointed to a relationship between dopaminergic activity in the striatum and GABAergic activity in the colliculus superior (89, 397). The described dopaminergic modulation of intranigraly ACTH-induced grooming is probably exerted via the GABAergic striatonigral pathway (464). It is assumed that the effects of haloperidol and apomorphine on intracerebroventricularly ACTH-induced grooming and

on intranigally ACTH-induced grooming correspond with the relationship between the GABAergic activity in the substantia nigra and the colliculus superior (288, 470). Lesion studies showed that the colliculus superior was not indispensable for the grooming behavior. In addition, the attenuating effects of benzodiazepines suggest the involvement of GABAergic systems (353). Pentylentetrazole and FG7142 both, anxiogenic and acting via the GABA-benzodiazepine complex, enhanced grooming (170).

3. Acetylcholine

Little is known about the role of cholinergic systems in grooming. Muscarinic cholinergic antagonists, atropine and scopolamine, are effective in inhibiting ACTH-induced excessive grooming. Hemicholinium, which depletes central nervous system acetylcholine, when given intracerebroventricularly also prevents ACTH-induced grooming (138, 146). However, atropine induced a stereotyped form of grooming, which could be suppressed by clonidine (350).

4. 5-Hydroxytryptamine

Although not thoroughly investigated, it has been demonstrated that a 5-hydroxytryptamine_{1a} (5-HT_{1a}) agonist 8-hydroxy-2-(di-*n*-propylamino)tetralin and BAY R 1531 reduce ACTH-induced and novelty induced grooming (211, 503) probably via the 5-HT_{1a} receptors. It is assumed that this modulation is exerted through the projection from the raphe nuclei to the substantia nigra (503). In addition, pontile lesions elicited grooming reflexes (481). The involvement of the nucleus raphe also appears from lesion studies performed in adrenalectomized cats (482). Furthermore, it was shown that increased grooming seen after immobilization was related to enhanced 5-HT postsynaptic activity (286). Drugs such as monoamine oxidase inhibitors, tryptophan, morphine, methysergide, and diazepam abolish grooming behavior and are associated with enhanced serotonergic functioning, in particular in the colliculus superior (384, 396, 455). However, a depletion of 5-HT only leads to a reappearance of grooming reflexes when combined with adrenalectomy, since glucocorticoids influence 5-HT receptors in the colliculus superior (396).

G. Specific Brain Structures Involved in Grooming

1. Lesions

The appearance of spontaneous grooming behavior in the decerebrate cat clearly indicates that part of the neural substrate underlying grooming responses is organized at the lower levels of the neuraxis (29). The decerebration procedure completely isolates lower levels of the neuraxis from the cerebral hemispheres, dorsal dien-

cephalon, basal ganglia, and septal area. The mesencephalon was largely intact in all animals, as was the posterior and ventrobasal hypothalamus and the septal preoptic area. Despite the similarities in grooming behavior, notable differences were detected (223). The responses often appeared fragmentary and poorly directed in rats as well (28, 32). In addition, differences were apparent in the serial organization of grooming components. The progressive cephalocaudal pattern was not generally observed in the decerebrated animal, which tended to show a more disjointed appearance of all grooming components. The infrequent occurrence of scratching and shaking was not temporally integrated with other grooming components. These results are in agreement with the retention of effective grooming responses following decerebration in cats (44). Adrenocorticotrophic hormone-induced excessive grooming was studied in rats bearing lesions in a variety of brain regions. Electrolytic lesions placed in the septal complex, the anterior hypothalamic/preoptic area, the mammillary bodies, the amygdala, the posterior hypothalamus, and the dorsal and ventral hypothalamus did not interfere with ACTH-induced grooming (83). Lesioning large parts of the hippocampal complex by aspiration led to an inhibition of excessive grooming (153, 257), albeit that higher doses of ACTH were effective. In addition, it was observed that the hippocampal destruction led to a suppression of novelty induced grooming but did not diminish water immersion-induced grooming (17). Haloperidol was more effective in reducing ACTH-induced grooming in hippocampectomized rats than in sham-operated controls (257). Isaacson (256) and Isaacson and Colbern (257) suggested that the behavioral changes seen after this lesion were secondary changes due to changes in the dopaminergic system of the neostriatum and the nucleus accumbens (see also Ref. 17). The most effective lesions in suppressing ACTH-induced grooming were those destroying parts of the substantia nigra (193) and dorsal parts of the PAG (462), pointing to their crucial role in the neural substrate underlying grooming behavior in the rat.

2. Electrical stimulation

Apart from lesioning structures to assess crucial brain areas involved in grooming behavior, other techniques focused on inducing grooming behavior have been applied. Electrical brain stimulation in freely moving animals was already applied many years ago (241) and has revealed multiple brain sites for grooming in birds, cats, and rats. Displacement grooming in birds could be elicited in the lateral wall of the anterior section of the forebrain ventricle, including the nucleus accumbens, the medial neostriatum, the lateral neostriatum, the posterior hippocampal complex and perhaps the ventral hypothalamus, and two loci near the nucleus basalis (104). Stimulation of local zones in the diencephalon of the cat led to the expression of organized behaviors among others grooming. These findings were replicated in a wide variety of species (349, 407). In a large

study in cats performed by Berntson et al. (28), multiple electrode sites in cerebellum and brain stem were found to induce robust and stimulation-bound grooming behaviors. The most effective electrodes were distributed in three general areas: 1) the paleocerebellum (16, 31, 33), anterior cerebellar vermis, and fastigial nucleus (30); 2) the parabrachial region surrounding the superior cerebellar peduncle (26); and 3) the ventrolateral medulla (27). In addition, a few points were located in the dorsal reticular formation and locus coeruleus (344). The cerebellar superior peduncle is not essential for grooming, since fastigial stimulation continues to induce grooming following bilateral destruction of the peduncle (344). Although the cerebellum receives afferent input from all levels of the neuraxis and exerts control over all major neural systems including limbic systems (59, 309, 453, 540), it is not a prerequisite for grooming, as animals with lesions in the paleocerebellar structures or without a cerebellum will still groom (32). The nature of the elicited grooming responses seems not to reflect simple motor automatisms directed against an aversive sensation of the skin. The electrode sites that yield grooming responses can also support self-stimulation (16, 541).

Grooming responses could be elicited from paleocerebellar areas in cats, rats, and opossums (16, 63). The elicitation of grooming from the parabrachial region reflects the excitation of the parabrachial nuclei or the activation of cerebellar afferents. In this regard the locus coeruleus has been implicated in the induction of groominglike behaviors (28, 42, 344). The direction and the topography of the stimulus-induced grooming behavior appeared to be under control of the stimulus features of the environment (28, 29, 31). The complexity and coordination of grooming behaviors evoked by brain stimulation suggest that the serial organization of these responses does not solely arise from the neurons at the stimulation site. The efferents from the stimulated tissue appear to either directly or indirectly facilitate response substrates located elsewhere. Berntson et al. (28) suggested that stimulation-bound grooming responses do not result from direct activation of motor mechanisms but rather arise from the sensitization of behavioral systems to the sensory inputs that normally serve to control grooming behaviors. However, the organization of elementary behaviors, such as biting, chewing, swallowing, and licking, may be located at brain stem levels (131, 173). This is further supported by the finding that decerebration at a thalamic level does not disrupt grooming responses (63).

Electrical stimulation of the periventricular/medial hypothalamic region in the opossum led to very short bouts of grooming behavior (407, 409). Thermoregulatory grooming could be induced by local warming of the anterior hypothalamus in the opossum (408). A detailed study on mapping the hypothalamus has been performed by Lammers and co-workers (305-307). Individual sites sensitive to stimulation are all located in efferent ACTH projections from the arcuate nucleus (289, 343, 389), which emphasizes the involvement of ACTH in grooming behavior. An elegant approach was

conducted by Van Erp et al. (511), who combined electrical brain stimulation and local application of ACTH into the hypothalamic paraventricular nucleus with a detailed analysis of the differently induced grooming responses. Those results suggest that the ACTH-containing part of the hypothalamus around the paraventricular nucleus is crucially involved in the organization of grooming behavior. This is in agreement with the results of Dunn and Hurd (145), who found by a mechanical blockade of potential active sites that injection of ACTH intracerebroventricularly is mediated through the anteroventral part of the third ventricle. The arcuate nucleus also projects to the PAG, which is in agreement with the results of Spruijt et al. (462).

Interestingly, grooming induced by electrical stimulation could not be blocked by naloxone. Also the morphology of the grooming seemed different from ACTH-induced grooming (305, 511). Naloxone exerted its suppressing effect on ACTH-induced grooming during the second part of the 50-min observation session (259). It may be that the electrical stimulation-induced grooming is too short to involve opiate systems and therefore not sensitive to naloxone suppression. Likewise, stretching and yawning, which are seen in the late phase of ACTH-induced excessive grooming, are not seen after electrical stimulation.

IV. CONCLUDING REMARKS

Self-grooming and allogrooming occur in a great variety of species. The primary function originated from the care of the outer body surface. Grooming behavior has been studied from an ethological point of view in group-living animals to elucidate its secondary functions as forwarded in the INTRODUCTION. Theoretically, grooming is of interest as an example of how behaviors can fulfill different functional roles in the course of evolution. Examples are the ritualized grooming behavior in the courtship behavior of insects and birds. It is interesting that in arthropods, birds, and mammals grooming has apparently developed in an analogous way from a mere taking care of the outer body surface to displacement behaviors and social signals. The COBS behavior is organized in distinct sequential patterns, which sometimes are so species specific that the characteristics can be used as taxonomic criteria. As such, these have been used both in arthropods (sect. IIA) and in reptiles (220). In rodents two main forms of grooming have been distinguished, stimulus-directed grooming behavior (more under control of sensory input) and stereotyped grooming patterns (more under central control). This difference in control of the behavior suggests a difference in function.

The relationship between grooming and tension reduction or dearousal has been studied especially in mammals such as rodents and primates. In various species of birds, and particularly in mammals, social grooming has developed undoubtedly as an emancipation of parental hygienic care. Both the hygienic effects and the dearousing effects may have been developed

from the care-giving attitude and the nonagonistic intent that grooming signifies, making it suitable as a means of social manipulation and regulation of relationships. Particularly in primates allogrooming is employed as an appeasing, a reassuring, and an affiliating behavior. It is invested as a service in the exchange of favors, such as tolerance and support.

To understand the conditions under which COBS occurs, its integration in the hierarchical system of behaviors is essential. Grooming occurs in three general, although partly overlapping, contexts. First, it occurs as a direct reaction to peripheral stimulation, such as moisture, particles, dirt, and parasites, causing a disturbance of the condition of the skin and a disarrangement of the pelage. Second, grooming behavior or fragments of it are observed in situations of behavioral conflict, as so-called displacement activities. Third, grooming can be observed following a situation of activation, arousal, or stress. Grooming as performed in the last context can also be elicited by hormones, neuropeptides, and opioids (vasopressin, oxytocin, prolactin, CRF, ACTH), which are normally released after exposure to a stressor.

There may be two reasons why grooming tends to be performed after the organism has been in a state of activation and therefore in close association with the process of dearousal. 1) Although COBS is an essential function for many species, its performance is not critically coupled to a certain stimulus context, time, or place, at least when compared with more stimulus-bound behaviors, such as fighting, fleeing from a predator, or copulatory behavior. The latter behaviors easily take over the behavioral hegemony in a conflict of functional priorities (307). On the completion of such higher priority behaviors their inhibitory influence on other behavior systems wanes, and grooming may be disinhibited and subsequently elicited (330, 331). 2) A preceding phase of intense activity may have added to the strength of the causal factors normally responsible for the occurrence of taking care of the body surface. This may have happened because such intense activities disturb the condition of the skin and the pelage or enhance the body temperature. Activation of the organism and mobilizing it to cope with environmental challenges is at times essential for survival. This activation is under hormonal control of the hypothalamo-pituitary-adrenal system. Intracerebroventricular injection of ACTH may experimentally create such a state of enhanced alertness and activation (118). When no environmental challenges are perceived, justifying the maintenance of a high level of arousal, grooming may be disinhibited. The same neuropeptides involved in coping with environmental challenges also seem to trigger this disinhibition of grooming and thereby to initiate the process of dearousal. The involvement of opioid systems in grooming behavior is in agreement with the "dearousal hypothesis." Grooming may not only be the behavioral consequence of a general process of dearousal. The involvement of opioids suggests that grooming will also facilitate this process and in turn inhibit the activation processes associated with other behavioral systems.

Interestingly, the inhibiting effects of autogrooming on activation can be recognized in social grooming, both in the active role of performing and the passive role of receiving grooming. This qualifies grooming behavior for emancipation into new functional domains. Its soothing effects may act as rewards predisposing it to become a pacifying, reassuring, and affiliating means of regulating social relationships. It has come to function in social bargaining and reconciliation processes, which have been studied particularly in higher primates. The dearousal hypothesis of grooming (103) explains its social emancipation.

Grooming behavior and its neurobiological and neurochemical aspects have been studied extensively in rodents with the objective of assessing brain-behavior relationships. Furthermore, it has been applied as a screening test for detecting behavioral activity as a consequence of, for instance, drug treatment (60, 198, 338, 463, 521) or naturally occurring changes, such as aging (467). Structure-activity relationships demonstrated that the involvement of ACTH/MSH-like peptides has been conserved across very different species (amphibians and mammals). This implies that similar neurohormonal mechanisms have been used for various adaptational processes.

Grooming has been analyzed at different levels of integration. These analyses have yielded insights in the architecture of grooming sequences, the context in which these occur, and the rules according to which these are controlled (167). The interpretation of behavioral changes following changes in the environment or experimental manipulations in the brain depends on the concept of how the continuous programming of behavior takes place. Behavior may be conceived as a process by which the organism controls its input; the brain is a hierarchy of negative feedback systems controlling this input (88). Thus the organism receives input representing information on its current state, input signals, compares it with the desired state, reference signals, and produces error signals representing the difference between the current and desired state and as a result produces output signals directing motor commands. Two main streams of information can be distinguished, information perceived by the senses coming from the outside world (exteroceptive information) and information from within the organism (proprioceptive information). The appropriate balance between the processing of these two flows of information is essential for survival. Naturally, such balance depends on the necessity to deal with environmental or internal demands. The "dearousal hypothesis" formulated in these terms would be that grooming reflects a shift from the processing of exteroceptive information to proprioceptive information. The involvement of the striatonigrocollicular pathway, which has been identified as a hierarchical feedback system for grooming, is in agreement with this approach. The neostriatum is involved in the serial ordering of behavior. The substantia nigra, pars reticulata, processes proprioceptive information into behavior and the colliculus integrates exteroceptive information (88).

All these structures have been shown to be involved in ACTH-induced grooming.

In summary, the consistency in occurrence of grooming either as a consequence of the condition of the skin or as a consequence of environmental factors across species indicates that a "secondary" function has become important especially in primates. Grooming behavior appears to be suitable for a combination of behavioral and neurobiological approaches and for developing models of how the brain programs and controls behavior and of how the function of a certain behavior develops across species. For a full understanding of brain-behavior relationships a comparative multidisciplinary approach integrating behavioral and neurobiological evidence is indispensable, and although far from complete, the data available for grooming behavior are stimulating for such an approach and for further research on the proximate and ultimate causation of behavior directed to the outer body surface.

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