

Induced grooming transitions and open field behaviour differ in high- and low-yawning sublimes of Sprague-Dawley rats

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Abstract. Water immersion-induced grooming sequences and open field behaviour were studied in two sublimes of Sprague-Dawley rats, *Rattus norvegicus*, selectively bred for high- (HY) and low-yawning (LY) frequency. HY rats were more active than LY rats in the open field: ambulation, rearings and wall-leanings were significantly higher in the former than in the latter group, indicating that LY rats are more emotionally reactive. Sequential analysis showed that HY rats exhibit more occurrences of a well-organized caudal grooming, while LY rats engage more frequently in well-organized facial grooming. Correspondence analysis revealed that both groups groom according to a hierarchical organization, with transitions between grooming elements depending on anatomical proximity. Clustering of grooming elements is related to a temporal recruitment and a reciprocal transition between them. Both groups, however, show distinct 'syntaxes' of grooming elements. Altogether these results indicate that along with a high or low frequency of yawning, there are other associated types of behaviour that separate both groups of rats. The structure of grooming between HY and LY rats indicates a strain-specific functional and neurophysiological difference. Yawning, grooming and emotional reactivity appear to be associated with arousal variations.

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In the last two decades the study of grooming has become the subject of extensive research, primarily because of its usefulness in modelling hierarchical motor control (Fentress 1988) and because grooming is structurally organized in a variety of movements that can be analysed for identifying rules that govern behavioural sequencing (Berridge 1990). This approach may provide insights into the way the central nervous system controls chains of rhythmical movements. In addition, grooming can be produced easily by either novel environments or water immersion (Jolles et al. 1979a; Colbern et al. 1981), which makes it possible to record many bouts of grooming for long periods.

A variety of evidence suggests that grooming in a number of vertebrate and invertebrate species is centrally organized (Fentress 1973; Zack 1978), and that rodents groom in a cephalo-caudal progression (Richmond & Sachs 1980; Thiessen et al. 1983; Sachs 1988) which resembles the order in

which grooming actions appear in developing animals (Richmond & Sachs 1980). The biological significance of grooming is still not clear, although studies indicate that it represents a de-arousal mechanism serving homeostasis (Delius 1967; Jolles et al. 1979b), and is generally considered to be a motor pattern with adaptive functions beyond the simple care of fur.

Most ethological studies regarding grooming have been concerned with the analysis of its temporal patterning, mainly by the use of two methods: serial dependence and hierarchical analysis models (Dawkins & Dawkins 1976; Lefebvre 1981), the latter appear to explain the patterning of grooming better than the former (Fentress & Stilwell 1973). Detailed studies in mammals (Fentress & Stilwell 1973), insects (Dawkins & Dawkins 1976; Lefebvre 1981), and birds (van Rhijn 1977; Lefebvre & Joly 1982) have led to the suggestion that grooming is hierarchically organized, that grooming movements cluster into anterior and posterior groups according to body regions (Russell & Giles 1974; Dawkins &

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Dawkins 1976; Thelen & Farish 1977; Lefebvre 1981), and that the transition between grooming acts appears to follow specific rules such as perseverance and reciprocity (Fentress and Stillwell 1973; Lefebvre 1981; Lefebvre & Joly 1982; Berridge 1990). These studies reveal that many features of grooming are common to several species, and that grooming appeared very early in the evolution of animals. However, some quantitative aspects of grooming may vary from one species to another, even within species. For example, Fentress (1968) found that duration of grooming differed between two species of voles after exposure to an overhead moving object, suggesting varying 'optimal arousal' levels amongst species. Moreover, face grooming frequency was distinct between two strains of mice (Fentress 1977). Berridge (1990) found a similarity in the patterning of grooming among several species of rodents. The small differences in duration of single elements were attributed to phenotypical (allometric control) or genotypical (phylogenetic relatedness) aspects. There is also evidence that aspects, such as grooming bout length, are distinct in species of American squirrels, and that these differences may be attributed to ecological factors (Ferron & Lefebvre 1982), which have rarely been considered in grooming analysis.

Grooming and other types of behaviour, particularly yawning, are elicited by intracerebroventricularly injected neuropeptides (Ferrari et al. 1963), suggesting that both behaviour patterns share some of the neural mechanisms involved in their generation. Yawning, like grooming, is a current behaviour in many species and has gained the attention of many investigators. Contrary to grooming, yawning seems to be an arousal mechanism that serves to preserve wakefulness (Ferrari et al. 1963). It has been suggested, however, that yawning and preening, which is the avian equivalent of grooming, are comfort patterns that are related to each other, either motivationally or functionally (Delius 1988). In humans, yawning has been considered as a stereotyped action pattern associated with sleeping and waking (Provine 1986). Little is known, however, of what function yawning may serve or what environmental circumstances modulate its rate (Provine et al. 1987). There is no further information about the relationship between grooming and yawning, probably because in contrast with grooming, yawning can not be elicited by environ-

mental manipulations, but only by the administration of drugs. This makes it difficult to carry out experiments to assess which environmental conditions modulate yawning rates and its relation to other types of behaviour such as grooming.

In this paper we present a comparative analysis of grooming in two sublines of Sprague-Dawley rats selectively bred for high- (HY) and low-yawning (LY) frequency (Urbá-Holmgren et al. 1990). The main advantage of using these two strains of rats is that it allows us to assess the effect that yawning has on the structure of behaviour patterns that are sensitive to environmental manipulations. Our study focuses mainly on quantitative aspects of grooming structure, and because in preliminary observations we detected that HY rats were more active than LY rats, we also included open field tests, which are commonly used for measuring behaviour believed to be involved in emotional reactivity (Walsh & Cummins 1976). Besides ease of performance, some of the open field measured behaviour patterns are sensitive to genetic and experimental manipulations which reinforce their ecological validity.

METHODS

Subjects

We used 15 HY and 15 LY male rats, all aged between 2.5 and 3.5 months old. Age differences between sublines were restricted to 2 days. All subjects were bred in the laboratory, maintained under a 12:12 h light:dark cycle with lights off at 1900 hours. We weaned the pups when they were 30 days old and housed them (four rats per cage) in collective transparent plastic cages (46 × 32 × 20 cm) lined with wood shavings. Tap water and Purina laboratory chow were freely available.

Apparatus

We used a black wooden cage (60 × 60 × 50 cm) with a glass front for the open field, and a plastic box (70 × 40 × 30 cm) filled with tap water (21–25°C) for the swimming tank. The room housing the field cage and swimming tank was illuminated with an overhead incandescent lamp (149 lx).

Procedure

To estimate ambulatory behaviour, we divided the floor of the open field cage into nine squares

grooming. For instance, patterns of locomotion based on rhythmic movements have been studied in a number of lower vertebrate groups, revealing an alternation of muscular activity between head and tail portions that might be determined centrally (Soffe 1985). The findings relating to the polarization of grooming behaviour between HY and LY rats opens new possibilities for studying the underlying neural mechanisms that control grooming organization. Whether this polarization is related to a functional significance is not yet clear, but it is likely that differences in grooming between HY and LY rats are associated with other behavioural traits. Concerning this, results in our laboratory indicate that spontaneous and pharmacologically-induced yawning in HY rats is positively correlated with penile erections (Holmgren et al. 1985). Thus, the 'excessive' caudal grooming of the HY subline may be related to sexual function, a conclusion reached by Moore & Rogers (1984), showing that self-grooming in young male rats contributes to the maturation of genitalia. Similarly, the fact that LY rats have a higher number of body shakes suggests that this behaviour has an adaptive function. By performing it repeatedly, animals rid their fur of a great quantity of water. Accordingly, we predict that LY rats would dry their body fur in less time, which is consistent with the finding that they engage in less caudal grooming. Therefore, LY rats would direct most of their grooming behaviour towards facial instead of caudal areas. This suggestion is consistent with the results of correspondence analysis of LY rats that indicate that body shakes and pauses are closely related, with the latter serving as transitional elements between facial and caudal grooming.

The hierarchical organization of grooming of HY and LY rats also agrees with predictions derived from the decision-making hypothesis of Dawkins & Dawkins (1973). HY and LY rats show different 'decision points' (Dawkins & Dawkins 1973) mainly at the transition between facial and caudal grooming. Alternatives of drying distinct parts of the body may be partially determined at the level of these decision points; mouth-abdomen for HY and pauses for LY rats. Although the structure of grooming behaviour of HY and LY rats appears to have a strong influence from the central nervous system, it is also clear that external factors are involved in their initiation and termination (van Rhijn 1977). In

our experiments, we wet the rats, eliciting the initiation of a natural sequencing of grooming, which rats execute to dry their fur quickly and efficiently because body temperature may drop. Efficient drying requires a continuous flow of information between the peripheral and central nervous system. But once such goal-directed behaviour has been displayed, feedback mechanisms should either switch to other areas of activity or stop ongoing activity (van Rhijn 1977). We would expect that with warm water, rats also exhibit a natural sequence of grooming, but complete their drying in less time. It remains, however, to be discovered which parts of the central nervous system command these decisions. Recently, Berridge & Wishaw (1992) showed that neuronal structures like the striatum are involved in the control of the serial order of grooming. Therefore, HY and LY rats may have endogenous modifications in the basal ganglia imposed by selection, and that may explain some of the differences in grooming sequences that we have found. Although grooming appears to depend to a large extent on the influence of the central nervous system (Fentress 1973; Zack 1978), evidence suggests that it is also under the control of postural facilitation (Dawkins & Dawkins 1976), feedback mechanisms (van Rhijn 1977), allometric control (Berridge 1990), and as our results suggest, strain-specific functional and neurophysiological aspects.

A crucial question is whether yawning, grooming and emotional behaviour are related. Our results show that along with a high or low frequency of yawning, there are other traits that altogether separate HY and LY rats. A possibility is that all these differences are only side-products of the inbred selection and that the behavioural heterogeneity we found between both groups of animals is a mechanism evolved against homozygosity which might be disadvantageous for a population (van Oortmerssen 1970). In this context, small genetic changes may cause behavioural differences of great importance in the speciation of animals (Baerends 1976). A second alternative is that these differences represent the separation of behavioural systems, a concept that makes it possible to explain that a number of behaviour patterns are related either functionally or motivationally (Baerends 1976). The behavioural system we detected resembles that reported by Delius (1988). When gulls were disturbed by an external

(20 × 20 cm each). We put a wooden right angle (20 × 50 cm each side) in the left front corner of the open field, and introduced each rat into that compartment to ensure a departure from an initial placement square. After 60 s, we removed the angle leaving the rat in freedom and recorded its exploratory behaviour in the novel environment for a 15-min period. At the end of this task, we immediately removed the rat from the open field and placed it in the swimming tank for 60 s. We then returned the rat into the open field cage and videotaped its grooming behaviour for 30 min. We thoroughly cleaned the open field cage after each observation.

Behavioural catalogue

We randomly tested each individual between 0900 and 1300 hours, and recorded the following indices according to an ethogram modified from Díaz (1988).

Departure latency: time (s) elapsed from the removal of the wooden right angle to departure from the initial placement square.

First corner latency: time (s) elapsed in reaching one of the two immediate corners.

Entries to the central square: total number of visits to the central square and latency (s) of the first and second visits.

Opposite corner latency: time (s) taken to reach the opposite corner.

Rearing bouts: frequency of vertical standing on rear legs, and latency (s) of the first and second rearing bouts.

Vertical wall-leaning acts: frequency (number of episodes) and latency (s) of the first episode.

Travelled distance: number of squares crossed (distance in metres).

Grooming frequency: latency (s) to the first and second bouts, total duration (s), and mean grooming bout duration (s).

Defecation frequency: (number of faecal boluses).

Induced grooming: we divided grooming after water immersion into 10 specific action/postures according to the body segments that established contact: mouth–hands, hands–face, hands–ears, mouth–sides, mouth–abdomen, mouth–genitals, mouth–tail, mouth–feet, feet–head and feet–sides. We recorded separately lateral body movements as well as body shakes. Grooming interruptions were recorded as follows: 1–4 s as a brief pause,

5 s or more as a long pause. In further sections, occurrence of action/postures of grooming will be referred to as acts or movements.

Statistical Analysis

We used Student's *t*-tests to compare scores in open field performance and the occurrence of water immersion-induced grooming acts between HY and LY rats. The Bonferroni test (Rice 1989) was used to eliminate type I errors arising out of the comparison of categories that are not necessarily independent. With this adjustment, the results in Table I are not severely affected (the significance level for rejecting the null hypothesis of 'no difference' was set to $0.05/18=0.0027$), but those in Table II cannot be taken as significant (significance level set to $0.05/17=0.0029$). Because our study is exploratory rather than confirmatory, we preferred to present exact *P*-values to show potentially interesting relationships.

Correspondence analysis

To detect the organizational principles according to which grooming of HY and LY rats is structured, we used correspondence analysis (van der Heijden et al. 1990). This method is appropriate for exploratory studies of sequences of activities. The sequences obtained are collected and presented in contingency tables with discrete variables (see Hill 1974). In addition, correspondence analysis of a transition matrix is a procedure that results in a picture in which relationships between points (acts) is based on chi-squared distances, and all elements of behavioural structures are represented in one whole view (van der Heijden et al. 1990). Correspondence analysis decomposes the chi-squared value of a matrix. This value measures whether the observed values differ from independent values. If the differences, the residuals, are not a result of random variation from independence (tested with the chi-squared test), correspondence analysis decomposes them into a number of dimensions. The proportion of decomposition of chi-squared for each dimension is called inertia (van der Heijden et al. 1990).

We reduced correspondence analysis to 14 HY and 14 LY rats because one videotape recording was damaged. We generated transition matrices from the videotape recordings and summed these matrices for each subline of rats. We recognize

Table I. Statistical summary of the open field test between high-(HY) and low-yawning (LY) rats

Behavioural parameter	HY rats $\bar{X} \pm SD$		LY rats $\bar{X} \pm SD$		t^*	P
Latencies (s)						
Departure	5.07 ± 4.59	4.40 ± 4.07	4.40 ± 4.07	4.07	0.42	0.677
First corner	8.07 ± 4.86	8.13 ± 4.61	8.13 ± 4.61	4.61	-0.04	0.969
First visit (central square)	283.53 ± 339.21	224.67 ± 350.74	224.67 ± 350.74	350.74	0.47	0.643
Second visit (central square)	475.60 ± 388.54	323.53 ± 365.58	323.53 ± 365.58	365.58	1.10	0.279
Opposite corner	20.33 ± 18.43	22.33 ± 19.18	22.33 ± 19.18	19.18	-0.29	0.773
First vertical wall-leaning	13.53 ± 8.37	20.53 ± 15.38	20.53 ± 15.38	15.38	-1.55	0.132
First rearing	38.27 ± 26.08	205.47 ± 281.82	205.47 ± 281.82	281.82	-2.29	0.029
Second rearing	88.33 ± 62.62	290.87 ± 326.73	290.87 ± 326.73	326.73	-2.36	0.025
First grooming bout	114.33 ± 63.21	112.80 ± 87.97	112.80 ± 87.97	87.97	0.05	0.956
Second grooming bout	157.40 ± 83.06	176.73 ± 123.75	176.73 ± 123.75	123.75	-0.50	0.619
Occurrences						
Travelled distance (m)	25.51 ± 7.67	16.65 ± 6.08	16.65 ± 6.08	6.08	3.50	0.002
Vertical wall-leaning acts	34.20 ± 11.19	18.40 ± 10.32	18.40 ± 10.32	10.32	4.02	0.000
Rearings	20.60 ± 8.30	9.73 ± 9.12	9.73 ± 9.12	9.12	3.41	0.002
Visits to the central square	3.87 ± 4.36	5.07 ± 4.37	5.07 ± 4.37	4.37	-0.75	0.457
Grooming bouts	18.60 ± 2.87	18.27 ± 10.50	18.27 ± 10.50	10.50	0.12	0.906
Faecal boluses	1.20 ± 1.08	2.67 ± 3.11	2.67 ± 3.11	3.11	-1.72	0.095
Duration(s)						
Grooming total duration	155.07 ± 32.38	136.67 ± 66.80	136.67 ± 66.80	66.80	0.96	0.345
Grooming mean bout duration	8.54 ± 2.39	9.27 ± 5.52	9.27 ± 5.52	5.52	-0.47	0.640

*Student's t -test for independent samples ($df=28$). Data for 15 HY and 15 LY rats.

Table II. Mean frequencies of acts for water immersion-induced grooming in high-(HY) and low-yawning (LY) rats

Act	HY rats $\bar{X} \pm SD$		LY rats $\bar{X} \pm SD$		t^*	P
Mouth-hands	36.71 ± 10.45	47.50 ± 16.27	47.50 ± 16.27	16.27	-2.09	0.047
Hands-face	46.21 ± 15.30	62.00 ± 20.48	62.00 ± 20.48	20.48	-2.31	0.029
Hands-ears	16.07 ± 9.10	19.79 ± 7.66	19.79 ± 7.66	7.66	-1.17	0.253
Mouth-right side	19.93 ± 7.30	22.21 ± 7.53	22.21 ± 7.53	7.53	-0.82	0.421
Mouth-left side	21.21 ± 6.86	18.00 ± 4.98	18.00 ± 4.98	4.98	1.42	0.167
Mouth-abdomen	6.57 ± 2.82	6.07 ± 3.77	6.07 ± 3.77	3.77	0.40	0.694
Mouth-genitals	8.93 ± 7.53	3.71 ± 3.41	3.71 ± 3.41	3.41	2.36	0.026
Mouth-tail	3.00 ± 2.77	0.64 ± 0.74	0.64 ± 0.74	0.74	3.07	0.005
Mouth-right foot	21.00 ± 8.96	14.71 ± 7.75	14.71 ± 7.75	7.75	1.98	0.058
Mouth-left foot	17.00 ± 9.33	9.86 ± 4.28	9.86 ± 4.28	4.28	2.60	0.015
Right foot-head	2.36 ± 4.48	3.64 ± 7.22	3.64 ± 7.22	7.22	-0.57	0.576
Left foot-head	1.14 ± 1.75	1.50 ± 2.31	1.50 ± 2.31	2.31	-0.46	0.648
Right foot-side	0.71 ± 1.64	0.57 ± 1.16	0.57 ± 1.16	1.16	0.27	0.791
Left foot-side	0.86 ± 1.30	0.14 ± 0.36	0.14 ± 0.36	0.36	1.99	0.057
Body shakes	4.57 ± 2.87	8.00 ± 3.74	8.00 ± 3.74	3.74	-2.71	0.011
Brief pauses	56.00 ± 24.21	54.50 ± 19.86	54.50 ± 19.86	19.86	0.18	0.859
Long pauses	12.07 ± 4.49	14.64 ± 5.03	14.64 ± 5.03	5.03	-1.43	0.165

*Student's t -test for independent samples ($df=26$). Data for 14 HY and 14 LY rats.

rats engaged in more caudal grooming (mouth-tail, genitals and feet) than the former. Trunk grooming acts (mouth-sides and mouth-abdomen) did not differ between HY and LY rats.

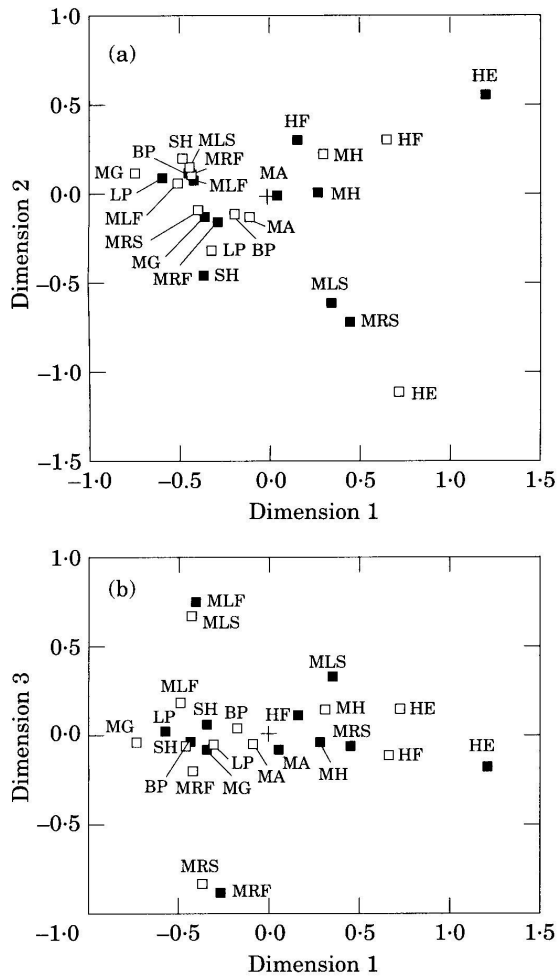


Figure 1. Correspondence analysis of data in Table III for HY rats. Decomposition of residuals from quasi-independence for (a) dimensions 1 and 2 and (b) dimensions 1 and 3. □: Preceding acts; ■: following acts.

0.238(0.11), 0.216(0.09), for HY and 0.476(0.38), 0.408(0.28), 0.286(0.14), 0.233(0.09), 0.204(0.07) for LY rats. The first two dimensions explained 57% (0.38+0.19) and 66% (0.38+0.28) of the total inertia for HY and LY rats, respectively.

Figure 1a shows a plot of the first two dimensions of correspondence analysis for HY rats. The first dimension, on the right side, contains the facial acts: hands-face and mouth-hands whose relative proximity indicates that they occupy a similar position in a grooming sequence either as preceding or following movements. Mouth-abdomen as a following act has a central position, suggesting that this movement serves as a

transitional element between facial and caudal grooming. In contrast, preceding caudal acts (mouth-sides, mouth-abdomen, mouth-feet, mouth-genitals) and following caudal acts (mouth-feet, mouth-genitals) are closely clustered on the left hand side, with some overlapping. Pauses and body shakes occupy the space within these caudal grooming movements. Dimension 1 is therefore interpreted as a cephalo-caudal component. In the second dimension hands-ears grooming dominates as a following act, and is distant from the majority of the other movements. Thus, once an animal has performed any other act, there is a small chance that it will lead to a hands-ears act. In the lower part, a mouth-sides act is likely to be preceded by hands-ears grooming. The third dimension, which explains 17% of the total inertia (Fig. 1b), reveals that many of the movements cluster into a single cephalo-caudal component with the caudal acts more grouped than the facial. This dimension also shows two directed sequences: mouth-left side followed by mouth-left foot, on the upper part, and mouth-right side followed by mouth-right foot on the lower part.

To summarize, nearly three-quarters of the total inertia is accounted for by a cephalo-caudal component reflecting that caudal grooming, with pauses and body shakes included, has a more organized structure than face washing. In addition, transitions in grooming structure are based on anatomical proximity.

Figure 2a is a plot of the first two dimensions of correspondence analysis for LY rats. The first dimension reveals a strong tendency, for most acts, to cluster into a single group around the mean profile. On the right side, are facial acts: hands-face, hands-ears and mouth-hands are closely grouped, with mouth-sides as following movements in between. This clustering indicates that these acts share similar places in grooming sequences. Pauses and body shakes have a central position, between facial and caudal grooming, and serving as transition elements. On the left side are the majority of the caudal acts, though they do not show a strong grouping. The second dimension is explained in terms of two directed sequences: mouth-left side followed by mouth-left foot, on the positive side and mouth-right side followed by mouth-right foot, on the negative side. Examination of dimension 3 of correspondence analysis, which explains 14% of the total

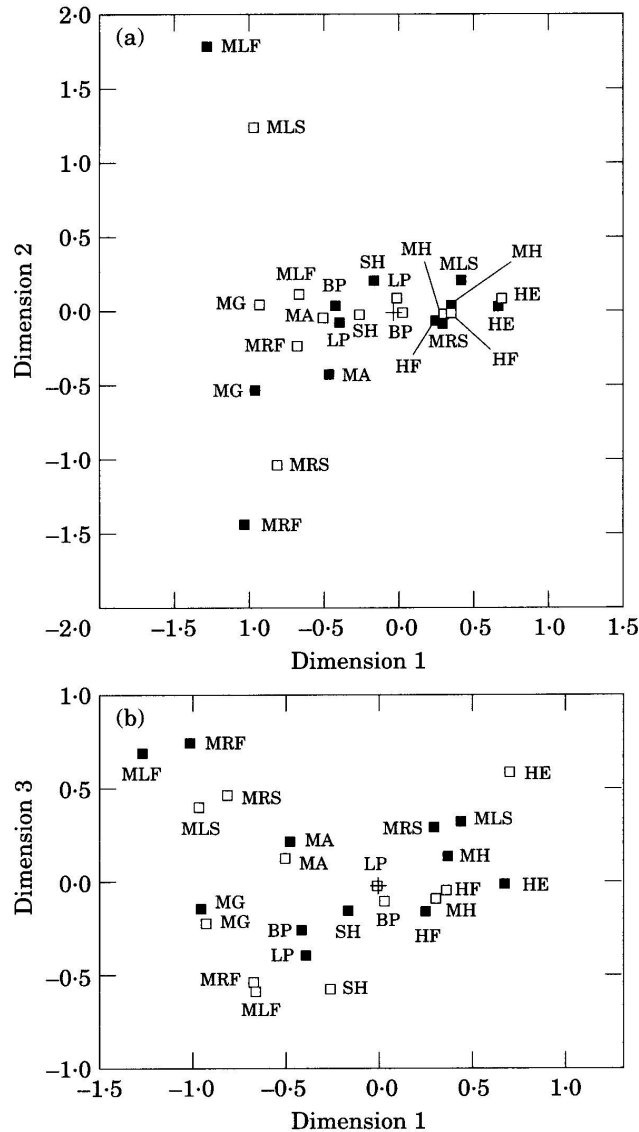


Figure 2. Correspondence analysis of data in Table IV for LY rats. Decomposition of residuals from quasi-independence for (a) dimensions 1 and 2 and (b) dimensions 1 and 3. □: Preceding acts; ■: following acts.

inertia, suggests that many of the movements have become separated from the centre (Fig. 2b). The main structure remains, however, with facial acts tending to be close to each other, whereas caudal acts are more spaced. These results indicate that LY animals groom according to a cephalo-caudal progression in which transitions are based on anatomical proximity. LY rats have a more organized facial than caudal grooming, and the transition between them is with body shakes and pauses.

DISCUSSION

High- and low-yawning Sprague-Dawley rats differ in many open field and induced-grooming behaviour patterns. This finding is consistent with inbred selection studies revealing that genetic influences are ubiquitous for animal behaviour (Plomin 1990). The results of the open field test show that HY rats are more active than LY rats, indicating that they are less emotionally reactive than the latter. This suggestion is supported by the

fact that both groups of rats varied with respect to ambulation, and to a lesser extent, defecation, the two most reliable parameters in open field tests (for a review see Walsh & Cummins 1976), and in accordance to current open field behaviour interpretations (Denenberg 1969). We conclude that the inbred selection carried out on HY and LY rats appears to parallel a low and high level, respectively, of emotional reactivity, and from this we can predict the existence of an inverse correlation between yawning frequency and emotional reactivity. With the present results we cannot confirm the above-mentioned hypothesis, in part because we did not record yawns and in part because the open field test lasted only 15 min, which is a short period for yawning behaviour to appear. A corroboration of this is the suggestion that yawning might signal the termination of a stressful situation instead of being present throughout it (Dourish & Cooper 1990). Although we did not find any significant difference in open field grooming behaviour, it is possible that the continuous sampling method we used (Altmann 1974), was not appropriate to detect differences in grooming between the two groups of rats, or that the difference between the groups was in time engaged in behaviour other than grooming. These results agree with the suggestion that in open field tests, grooming does not seem to be related to indexes of emotional reactivity (Archer 1973).

The analysis of water immersion-induced grooming revealed that LY rats include more movements than HY rats in their grooming sequences. This overall difference indicates that LY rats perform longer sequences of grooming, and that they also spend more time in each sequence of grooming. Of course, it might be that both HY and LY rats spend the same time in each sequence of grooming, but with LY rats performing the task more quickly than HY rats. Our initial suggestion, however, is supported by the analysis of grooming transitions, which indicated that LY rats execute more transitions between grooming acts. Our results partially parallel those of other studies suggesting quantitative differences in grooming behaviour between different strains of mice or rats (van Oortmerssen 1970; Fentress 1977; File et al. 1988). Despite the quantitative differences in grooming between HY and LY rats, both groups of rats groom according to a cephalo-caudal progression, as has been found by other

authors (Richmond & Sachs 1980; Thiessen et al. 1983). It should be noted that this progression also implies that animals use more acts for grooming their facial than caudal part (see Table II). Therefore, there is a cephalo-caudal progression not only of order but also of number of grooming movements.

Correspondence analysis revealed that grooming acts, in both HY and LY rats, are hierarchically organized. This complex structure, instead of a serial dependence of grooming acts, has been found by other authors (Fentress & Stilwell 1973; Dawkins & Dawkins 1976; van Rhijn 1977; Lefebvre 1981; Lefebvre & Joly 1982) and appears to be a common feature in many species. The functional implications of this structure have not been clarified, although it might be that in terms of costs and benefits it is more advantageous for an animal to groom by recruiting several movements and directing them to specific areas than to groom by executing a chain of single movements, which would require a repetitive 'coming and going' mechanism, investing more time and losing efficiency of grooming. HY and LY rats also groom according to precise rules: the transitions between grooming acts depend on anatomical proximity, whereas their clustering, which is the main characteristic of a hierarchical organization, requires not only the recruitment of a number of acts but also certain degree of transitional reciprocity between them. This implies that clustering of grooming acts does not necessarily have to be related to anatomical regions as has been suggested (Lefebvre 1981). For instance, our results indicate that clustering of facial acts include mouth-sides, which is a movement directed to the trunk, anatomically far and distinct from the facial area.

The present study also detected a quantitative and organizational 'polarization' of grooming movements between HY and LY rats. LY rats perform more clustered facial acts, whereas HY rats engaged in more clustered caudal acts. This distinct 'syntax' of grooming indicates a functional and neurophysiological difference between both groups of rats. If this suggestion is correct it would indicate that the central nervous system commands grooming movements in a distinct way for HY and LY rats, maybe by emphasizing the action of certain neural structures and inhibiting others. Also it might be that two neural sub-systems exist for controlling facial and caudal

stimulus, they exhibited a sequence of behaviour patterns that included preening, yawning and sleeping, suggesting that when there is a change in the ongoing arousal level, animals display a set of behaviour patterns leading to restore the previous state of arousal. In mammals, yawning has been associated with transitions between waking and sleeping (Provine 1986), and after exposure to stressful situations (Dourish & Cooper 1990), whereas grooming is believed to be involved in decreasing an enhanced arousal (Jolles et al. 1979b). Therefore, both types of behaviour seem to be associated with changes of ongoing arousal. It might be that the selection carried out on HY and LY rats also separated those types of behaviour that are associated with specific thresholds of arousal. Because of the obvious advantages of having a high yawning strain, the majority of the studies in our laboratory have focused on them, and preliminary results have revealed that HY rats in a novel environment, other than an open field cage, show increased grooming followed by yawning and sleeping (unpublished data), confirming the observation of Delius (1988). Further results are necessary to confirm these hypotheses, but we believe that with this initial approach, new insights are gained about yawning, grooming and their relationship.

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