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**COMPARATIVE FINE STRUCTURE OF ACTION:
RULES OF FORM AND SEQUENCE IN THE GROOMING
PATTERNS OF SIX RODENT SPECIES**

by

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(With 10 Figures)
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Comparative analyses of behaviour provide at least two unique insights into the nature of behavioural control systems. The first insight concerns the degree to which patterns of behaviour are shared across phylogenetic groups. Knowledge of 'phylogenetic sharing' is valuable for validating the general applicability of descriptions of behavioural pattern (HINDE, 1970). This knowledge is also useful, when combined with neuroethological studies, for improving our understanding of brain-behaviour relations. To the extent that fundamental principles exist for the generation of behavior by mammalian nervous systems, the generality of these neurobehavioral principles can be established only by demonstrating that they apply to diverse species (LASHLEY, 1951).

The second insight concerns the nature of differences between species, which may occur in shared behavioural patterns that are otherwise similar. When there are distinctive features in the display by one species of a pattern that is shared with others, these features might arise from any of a variety of sources: a unique phylogenetic relationship to other species, allometric scaling effects derived from morphology, special ecological constraints, *etc.* Appropriate comparative analyses can allow us to identify the sources of pattern differences (LORENZ, 1941).

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A printing error occurs under the discussion heading, "*Neural substrates of syntax control*," on pages 52-53. These paragraphs should read as follows.

Page 52, para. 3:

Neural substrates of syntax control

Both brainstem and forebrain systems have been implicated in the control of the sequential patterns described here. The structure of syntactic chains and of global reciprocity and stereotypy appears to be characterized by a strong degree of central patterning in the rat: the structural integrity of these patterns remains essentially unimpaired after removal of sensory tactile cues from the face (Berridge & Fentress, 1987a).

Page 53, para 1:

Control of central patterning does not reside in any one brain structure, even for the most stereotyped syntactic pattern described here, but depends upon multiple operations carried out in a distributed fashion throughout the brain (see Berridge, 1987b).

The basic phase structure of the syntactic chain, for example, can be generated without forebrain input by decerebrate hindbrain mechanisms distributed in the pons and medulla oblongata (Berridge, 1989a). Basic reciprocity patterns also show a strong degree of hindbrain sufficiency (in preparation). But effective pattern execution requires more than the brainstem. The syntactic efficacy of chaining, as measured by chain completion rate, depends strongly upon forebrain systems. Damage to either the telencephalic corpus striatum (Berridge & Fentress, 1987b) or to the dopamine projection that ascends to the striatum from the substantia nigra and tegmentum (Berridge, 1989b) reduces syntactic efficacy to roughly 50% the normal rate of chain completion.

Also, Tables 3 and 4 are reversed.

The focus of this study was upon the rules that pattern the sequence and temporal structure of rodent grooming behaviour. Grooming, a natural behavioural pattern with a rich sequential structure, provides a fruitful target for comparative and neuroethological analyses of mechanisms of behavioural sequencing. This study identified a set of descriptive rules for sequential grooming patterns, which were shared with minor variations across 6 diverse rodent species. These shared sequential patterns were of four types: syntactic chaining, hierarchical clustering, transition reciprocity, and features of stereotypy revealed by information analysis. The study also identified two principles that accounted for most of the interspecific variation in these rules. The first principle of variation was allometric scaling by body size. Allometric scaling was found to account for specific timing features of actions and sequences. The second principle of variation was the degree of phylogenetic relatedness among particular species. This was found to account for many pattern features, such as the inclusion of particular actions in a pattern, the detailed sequential structure, and the predictability of various patterns.

Levels of pattern analysis.

A number of aspects of grooming structure have been shown to be shared by rodent species. These shared aspects include properties of grooming duration (*e.g.*, EISENBERG, 1963; SLATER, 1974; FERRON & LEFEBVRE, 1982), the existence of particular transitions among different types of grooming actions (FENTRESS & STILWELL, 1973; RICHMOND & SACHS, 1980; FERRON & LEFEBVRE, 1982), tendencies to direct grooming to body parts along a progressive cephalocaudal dimension (EWER, 1967; RICHMOND & SACHS, 1980), the existence of Markov or higher-order sequential dependencies among grooming actions (*e.g.*, BOLLES, 1960; FENTRESS & STILWELL, 1973), and the clustering of successive actions into larger groups (FENTRESS & STILWELL, 1973; FERRON & LEFEBVRE, 1982; see FENTRESS (1988) or SACHS (1988) for reviews).

The unit of analysis in previous studies has ranged from the 'molecular' action (*i.e.*, each stroke or lick scored separately) to more 'molar' categories (*e.g.*, all repetitions of a single action type, such as face wash strokes, scored as a single unit). Because rules may exist at different levels simultaneously, and because the relation between rules at different levels is of interest, an effort was made in this study to use multiple measures that were sensitive to different, although overlapping, levels of

organization. This was done in two ways. First, two separate scoring systems were adopted from earlier studies, which employed different molecular units. These scoring systems permitted analysis of different unit combinations at higher levels of organization: sequential pairs, triplets, specific defined sequences and, at the most abstract level, overall statistical stereotypy of grooming sequences. Second, because all unit-based systems necessarily coarsen the fine structure of the action they represent (by ignoring intra-unit variability among units of the same type) this study also used a continuous graphic notation system for representing forepaw trajectories and head and tongue motion. This graphic notation provided a continuous representation of grooming action that was not based on arbitrary units, and that allowed patterns to be seen at more than one level simultaneously.

Phylogenetic representation.

The primary question for this study was the degree to which the descriptive patterning rules for grooming behaviour, revealed by these techniques, were shared by rodent species that belonged to widely separated superfamilial groups. Six laboratory-bred or wild-caught species were chosen to provide representatives from each of the three classical rodent suborders: Hystricomorpha, Myomorpha, and Sciuromorpha (Fig. 1, top). In order to allow within-suborder comparisons of family groups as well as comparisons across different suborders, four of the myomorph species were selected to represent two different families, Cricetidae and Muridae, within the suborder Myomorpha. Myomorph cricetids were the gerbil (*Meriones unguiculatus*) and golden hamster (*Mesocricetus auratus*). Myomorph murids were the com-

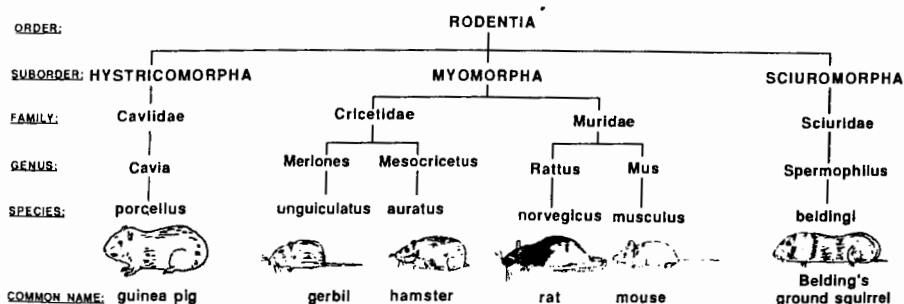


Fig. 1. Phylogenetic classification of the six rodent species used in this study.

mon laboratory mouse (*Mus musculus*) and rat (*Rattus norvegicus*). The hystricomorph (Caviomorpha) suborder representative was the guinea pig (*Cavia porcellus*). The representative of the sciurid suborder was the North American Belding's ground squirrel (*Spermophilus beldingi*).

Experimental methods

Animals and testing.

Nine male and female rats (Long Evans and Sprague Dawley strains), 15 male and female mice (Swiss Webster strain), 8 male and female hamsters, 7 male and female gerbils, 6 male and female guinea pigs, and 2 female ground squirrels were videotaped individually while grooming in response to fur wetting. The ground squirrels had originally been wild-caught in the California Sierra Nevada, and had lived in the laboratory 5 years. All other individuals were laboratory bred.

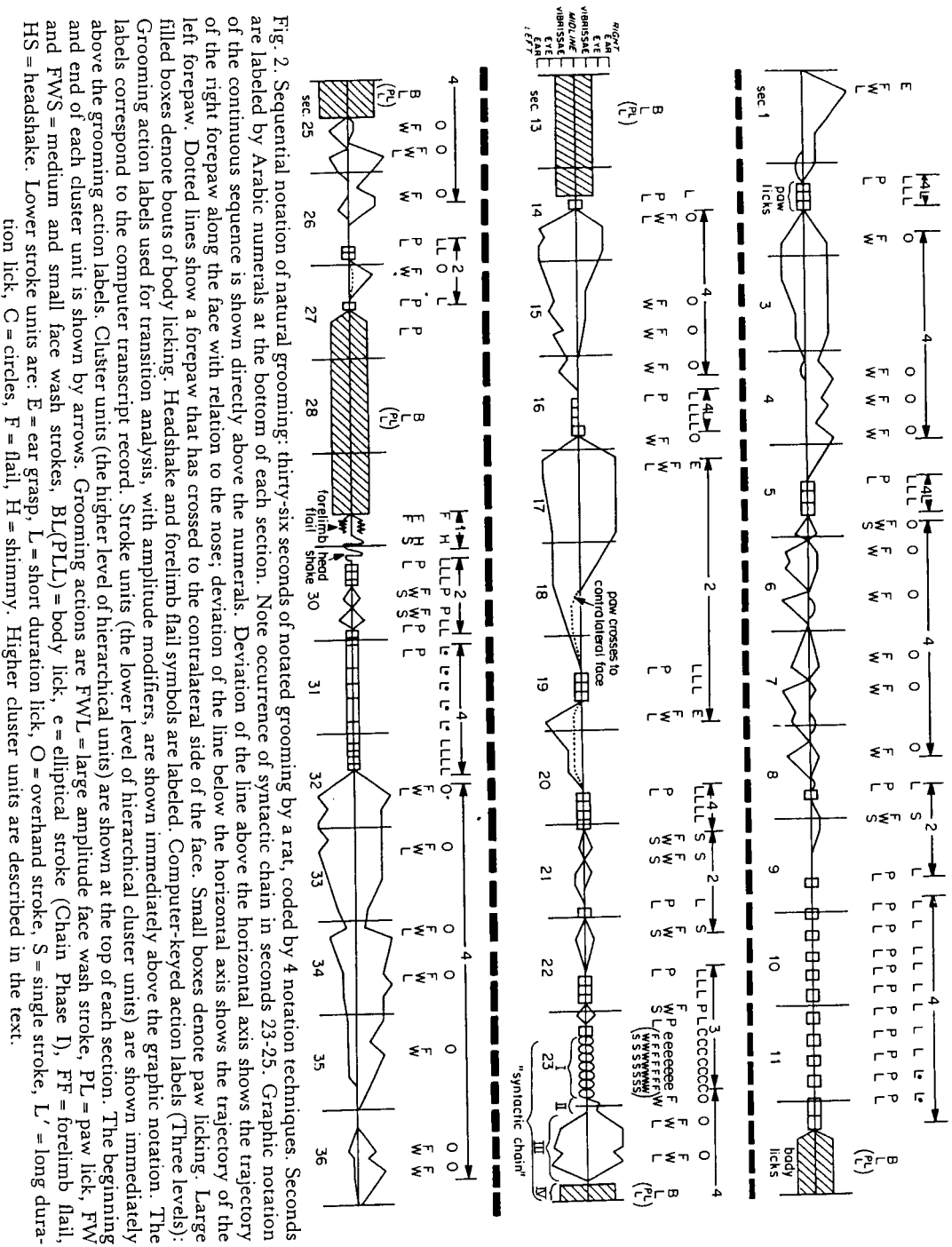
In order to elicit grooming, an animal was sprayed lightly with a water mist and was placed in a transparent testing chamber. A mirror angled beneath the clear floor reflected an image of the face and forelimbs into the close-up lens of a videocamera. A second camera provided a dorsolateral view, which was recorded onto the same videotape. The videotaped record thus allowed clear assessment of stroke trajectories, lick targets, etc., with a temporal resolution of 33 msec (1 frame). This procedure was repeated daily in sessions of 30 min to 2 hrs until at least 100 min of consecutive grooming was taped for each species. Subsequent analyses of the videotaped record were made frame-by-frame or in slow-motion (1/30 speed) and cross-checked by different observers.

Sequential pattern coding.

Two major techniques of fine structure coding were employed in this study: graphic notation of the continuous flow of behaviour, using a modification of the facial grooming graphic notation system of BERRIDGE & FENTRESS (1986), and action labeling, in which each action 'unit' is labeled and the behavioural sequence is represented as a sequential transcript of corresponding units. Two forms of action labeling systems were used. One was the computer-keyed action labeling procedure devised for rat grooming and ingestive sequences by BERRIDGE, FENTRESS & PARR (1987), which yields measures of sequential stereotypy (H: an information measure of the uncertainty versus predictability of sequential elements) and of transition reciprocity (a pattern organization that equates the number of transitions back and forth between two actions or between two action groups). The other system was the 'hierarchical clustering' procedure developed for mice by FENTRESS (1972), which reveals two levels of sequential structure (component elements and larger clusters composed of groups elements). An example of these separate graphic and labeling scoring systems applied to facial and body grooming is shown in Fig. 2.

Graphic notation of syntactic chains.

The graphic notation system for grooming actions, which represents the real-time trajectory of each paw over the face in relation to the tip of the nose (see Fig. 2, first level), was used to identify and describe sequential 'syntactic chains': highly stereotyped behavioral sequences shown by rats (BERRIDGE & FENTRESS, 1986). These chains comprise 4 phases (a phase is defined as a homogeneous series of actions that are of the same type). The phases are chained together with a serial completion probability of 85% in rats, and provide one transition route (though not the only one) between face and body grooming. The syntax of the chain consists of the serial linking of the following phases. Phase I: a



set of 5 to 9 rapid strokes (6-7 Hz) performed bilaterally, forming small elliptical trajectories over the nose. Phase II: a single unilateral (or bilateral asymmetrical) stroke or short series of strokes that ascend to the dorsal border of the mystacial vibrissae. Phase III: a series of repeated, large-amplitude strokes (often over the ear) that typically are bilateral and symmetrical with respect to forepaw trajectory. Phase IV: a tucking of the head and shifting of posture to begin a bout of licking of the ventrolateral torso. For the purpose of identifying this syntactic chain in different species, criteria regarding absolute timing (stroke cycle length and duration) were dropped, and chain candidates were considered to be: 1) any instance of at least three rhythmic elliptical (or small amplitude bilateral) strokes followed consecutively by a series of repetitive large amplitude strokes and then by body licking without interruption or 2) the consecutive occurrence in order of any 3 of the 4 phases defined morphologically (as in BERRIDGE, 1989).

Computer-keyed action labels.

A record of the flow of action was generated by assigning keyed labels to action units, and by pressing each action's key as it began and ended in a videotaped sequence that was played in slow motion (1/10 to 1/20 speed). The computer clock was calibrated to the video playback speed. Unit types were: Facewash Strokes by the paw over the face, which were scored for laterality and amplitude. Laterality was scored either as bilateral, with both paws in simultaneous trajectories, or as unilateral, if the stroke was performed with only the left or right paw. Asymmetrical strokes of unequal amplitude were scored as unilateral strokes of the dominant paw. Amplitude was scored either as small (within the dorsal boundary of the mystacial vibrissae), medium (above the vibrissae but below the level of the eye) or large (extending above the eye). Forelimb Flail forepaw movements (rapid 'back and forth' movement of the forepaw and limb at a speed greater than 30 Hz) were scored as separate units. Headshakes (scored for rhythmic lateral motions of the head at greater than 30 Hz), and Paw or Body Licks were also scored as units. Each stroke, flail, and headshake was counted as a separate unit. In tabulating sequences, continuous paw or body licking was counted by the computer in units of up to 5 sec duration (*i.e.*, a 12 sec bout was considered to occupy three consecutive units). Grooming sequences containing a total of at least 1000 units were scored for each species.

Records of grooming sequences were used to generate transition tables that showed the relative frequencies of particular sequential action pairs and triplets for each species, as in BERRIDGE *et al.* (1987). Transition analysis was extended further in the present study to reveal sequential patterns incorporating the specific laterality and amplitude of strokes. This was done by computing transition frequencies among actions distinguished by laterality (left, right, or bilateral) or, in a separate analysis, by amplitude (small, medium, or large). Finally, a measure of global sequential stereotypy was calculated from the computer transcript for each species using the information statistic of sequential uncertainty (H). Uncertainty (H) expresses the sequential predictability of action as a \log_2 inverse quantity. This value provides an overall measure of the degree to which the emission of an action predicts the actions that follow it (ATTNEAVE, 1959).

Additional unit scoring system.

FENTRESS (1972) and FENTRESS & STILWELL (1973) used a 'unit labeling' system, different from the one described above, to demonstrate that sequential actions could be empirically clustered into hierarchical groupings (based upon inspection of unit transcripts), which were sequentially ordered themselves (see FENTRESS & STILWELL, 1973 for criteria and rationale of hierarchical grouping). In order to replicate this finding and to extend it beyond a single species, and to establish the compatibility of this unit scoring system with the one described above, grooming sequences from rats and mice (at least 1000 units

each) were rescored using criteria modified from FENTRESS & STILWELL (1973), and analyzed for transition patterns and for sequential stereotypy. Subsequently, the transcript of molecular action units was categorized into larger hierarchical units or clusters, again using criteria modified from FENTRESS & STILWELL (1973). Approximately twice as many seconds of grooming were coded for higher cluster units as were coded for lower action units, in order to keep the total number of each type of unit near 1000. The resulting sequence of 'clusters' was also analyzed for transition patterns and for stereotypy(H). Lower action units were: Circles (rapid small amplitude paw movements over the nose (equivalent to small bilateral strokes or ellipses above); Licking of paws (classed as either of duration greater than or less than 0.5 sec); Parallel strokes (bilateral strokes of small or medium amplitude); Shimmy (head or body shake); Single strokes (unilateral or asymmetrical bilateral strokes of small or medium amplitude); Overhand stroke (a bilateral or unilateral stroke of large amplitude); Ear grasp (a unilateral stroke of large amplitude in which the ear or fur is grasped and pulled towards the mouth); and Pause. Hierarchical units, based upon the sequential clusters defined empirically by FENTRESS & STILWELL (1973), were: Unit 1 (any occurrence of Shimmy); Unit 2 (alternating series of Overhand strokes and Licks); Unit 3 (one or more Licks followed immediately by one or more Circles); Unit 4 (a perseverating run of 3 or more strokes of the same type (except for runs of Circles that qualified as Unit 3); Unit 5 (any occurrence of a Forelimb Flail); and unit 6 (a default unit for series of strokes and licks that did not fall into any of the above patterns).

Ellipse and chain timing relations.

Finally, for each species, a frame-by-frame analysis of timing (1/30 sec temporal resolution) was made of the stereotyped elliptical strokes that initiate syntactic chains, of the other chain components, and of the duration of chains themselves. A further analysis was made, in which the timing of ellipses in chains that were completed syntactically was compared to the timing of ellipses that initiated uncompleted chains (*i.e.*, chains in which Phases I and II were not followed syntactically by Phases III and/or IV, but instead either reverted to facial grooming that was sequentially flexible or else interrupted grooming). This was done in order to learn whether ellipse timing was related to the probability that the sequence would be completed.

For the purpose of analysis, statistics were calculated separately for each animal. Twenty to 50 observations per animal were combined into a single mean value for that individual for each of the quantitative parameters described above. These "individual means" were then averaged to obtain mean values for each species and were also used for statistical comparisons of species. An exception to this procedure was made for ground squirrels because only two individuals were available for observation. To allow statistical comparison of squirrels to other species, observations from each squirrel contributed four values for each parameter to ANOVA and post hoc analyses, based upon a random division of the total observations of that squirrel into four equal groups.

Results

Physical size.

Mean body weights and nose-rump lengths for each species were: guinea pig (958 ± 30 g; 31 ± 0.4 cm), rat (379 ± 17 g; 24 ± 1 cm), Belding ground squirrel (360 ± 2 g; 23 ± 1 cm), hamster (148 ± 6 g; 18 ± 1 cm), gerbil

(88 ± 7 g; 14 ± 0.2 cm), and mouse (30 ± 1 g; 11 ± 0.1 cm). Each species differed from all others on both traits, except for rats and squirrels which were alike on both (Newman-Keuls, $p < 0.05$ each). The correlation between body weight and length was 0.92 (Pearson's r ; only correlations in which $p < 0.05$ are reported).

Syntactic chains.

Just as the physical anatomy of different rodents shows variation along a shared rodential pattern, so the 'behavioral anatomy' of grooming by each species showed variation along a shared syntactic chain pattern (Fig. 3). The ten examples of syntactic chaining shown for each species in Fig. 3 illustrate the range of variability within and across individuals. Inter-individual variation within a single species typically was not greater than the variation shown by a single individual across successive trials. Every one of the four sequential phases that have been defined previously for rats was found in the syntactic chains of other rodents. The first occurrence of each chain phase is labeled for every species in Fig. 3 in order to aid the reader. It should be noted that the stability of this pattern across species is not the trivial result of a lack of alternative ways to make transitions from face to body grooming. In fact, there are alternatives (see secs 12 and 27 in Fig. 2). The pattern of a syntactic chain instead reflects an active serial ordering process.

Species variations.

In spite of their common adherence to this syntactic pattern, the species' chains differed by a number of qualitative and quantitative parameters. Distinctive qualitative features of the chains of each species are labeled in Fig. 3. Both gerbils and ground squirrels, for example, often exhibited chains containing 'novel' sequential phases not seen in the chains of rats. The novel phase of gerbils appeared to be a combination of Phase I bilateral ellipses with Phase II small unilateral strokes, resulting in a hybrid I-II transitional phase of small amplitude, bilateral strokes. These hybrid strokes lacked the circular trajectory and fast rhythmic timing of ellipses. The novel phase of Belding ground squirrels was a truly unique pattern in which both paws moved together in describing a 'figure 8' trajectory, traveling together first on one side of the face and then crossing the midline together to move on the other side. The two squirrels also tended to combine Phase II and Phase III patterns into a series of asym-

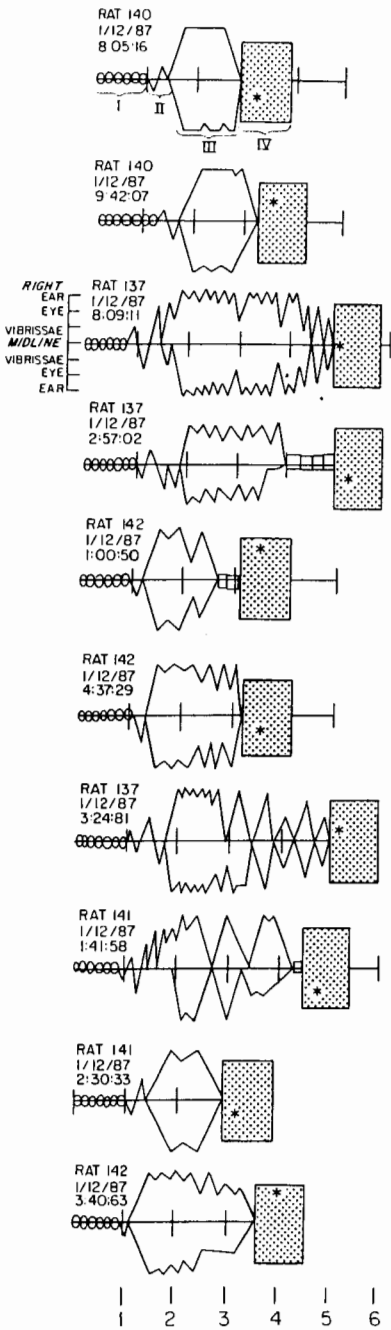
metrical, large amplitude, bilateral strokes in which the left and right paws took turns in performing the dominant trajectory.

Within Phase I, the form, timing, and symmetry of elliptical strokes was often distinctive for a particular species. Ground squirrels, for example, showed a distinctive form in the performance of ellipses. Squirrels elongated each elliptical stroke into a slide along the longitudinal axis of the chin, and restricted the zone of lateral movement in comparison to the other species. Guinea pigs displayed a unique temporal spacing of ellipses, momentarily pausing between each stroke before continuing on to the next (mean ellipse cycle = 226 msec stroke + 90 msec pause). Mice lacked the strong bilateral symmetry of rat ellipses, showing instead a strong alternating asymmetry, in which each jaw took turns performing the dominant stroke.

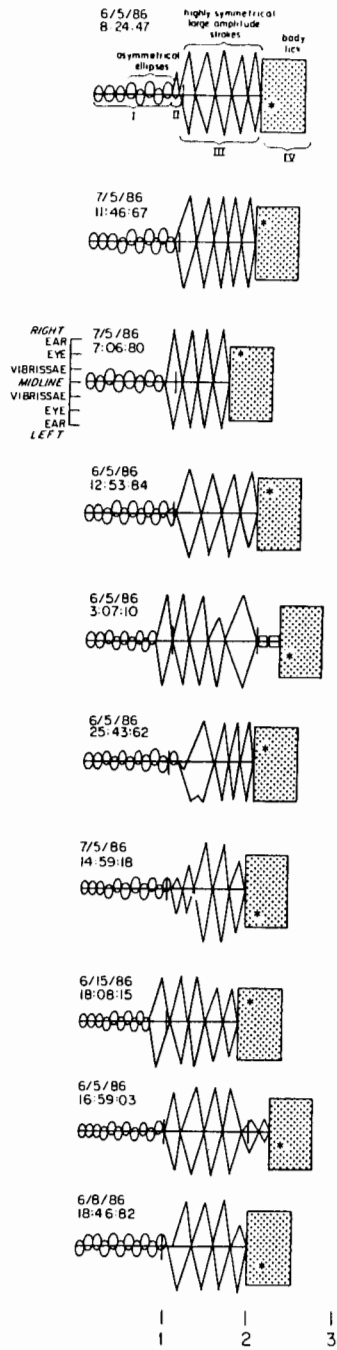
Lateral symmetry proved to be a signature feature for species in Phases III and IV as well. Unlike mouse asymmetrical ellipses, the Phase III large amplitude strokes of mice were extraordinarily symmetrical in the trajectory or the two paws. Guinea pigs, conversely, were unique in showing only unilateral Phase III strokes. A given guinea pig could use either paw to perform Phase III strokes, but would use only one paw at a time during a chain. The other paw was planted on the floor for postural support during Phases III and IV (though neither forepaw touched the floor during Phase I). The two paws could switch roles in the middle of a series of Phase III strokes. Further, guinea pigs invariably initiated their Phase IV bout of body licking on the side of their body ipsilateral to the paw used for the last Phase III stroke (denoted by asterisks in Fig. 3). Equally invariably, but at the opposite extreme, Phase IV body licking was always initiated on the ventral midline by ground squirrels. Myomorph species tended to be intermediate and more variable in Phase IV initiation (Fig. 3).

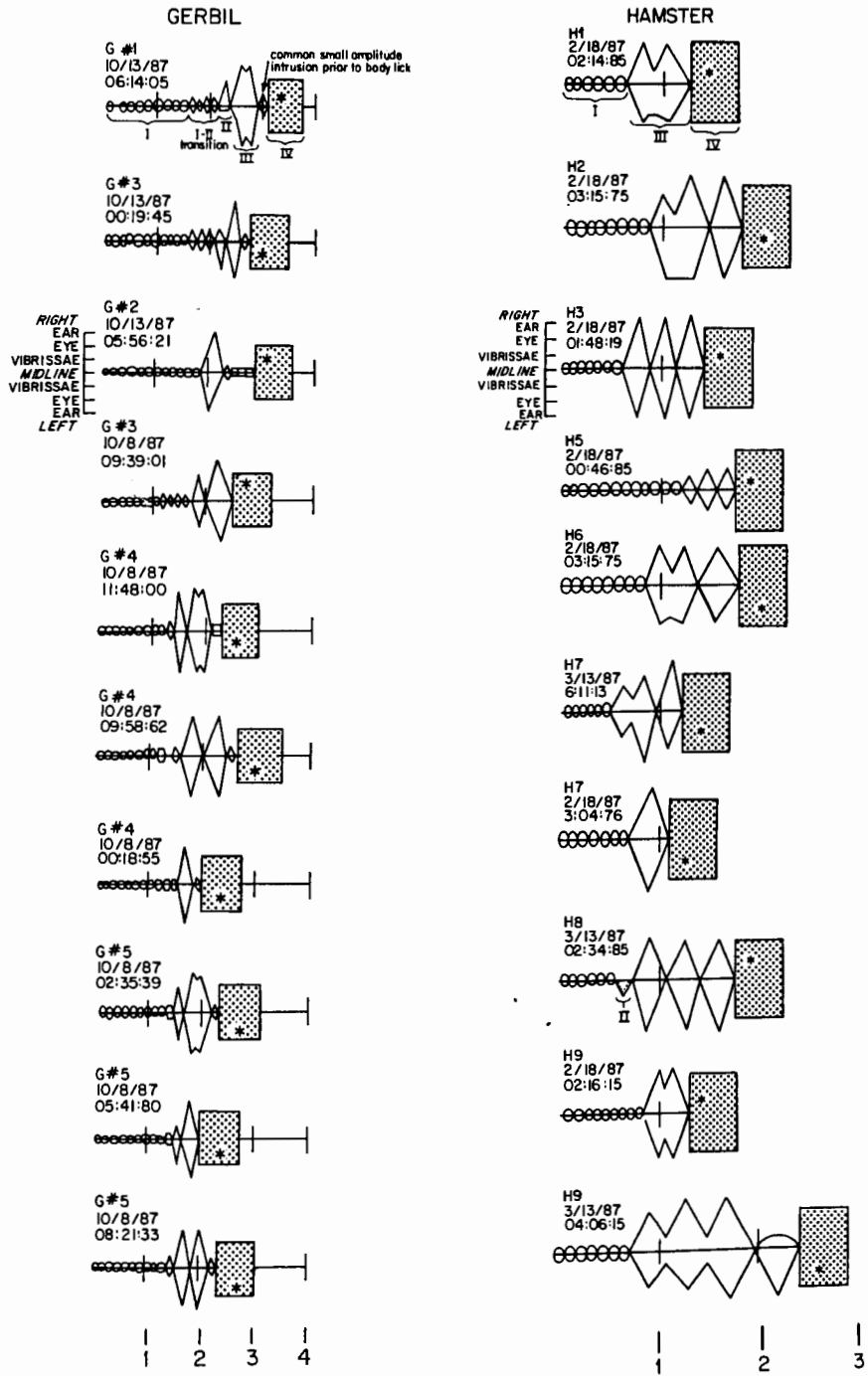
Fig. 3. Syntactic chains. The first occurrence of each syntactic phase is labeled for every species in order to aid the reader. Stars denote the lateral placement on the ventral torso of initial Phase IV body licks. Novel phases, unique transition phases, and other distinctive species-specific features are labeled the first time they occur. Note especially the novel phase of ground squirrels, in which both paws travel together on first one side of the face and then on the other side, and the transition phases of ground squirrels and gerbils, in which aspects of two phases are combined together. Also note the alternating asymmetry of mouse Phase I ellipses; the 'spacing' of guinea pig Phase I ellipses; the strong symmetry of mouse Phase III strokes; the unilateral form of guinea pig Phase III strokes; the invariable initiation of guinea pig Phase IV body licks ipsilateral to Phase III strokes; and the equally invariable initiation of ground squirrel Phase IV licks on the ventral midline.

RAT

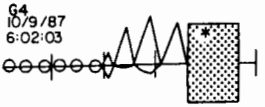
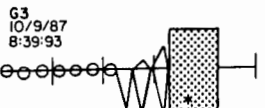
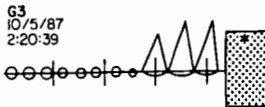
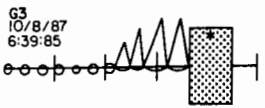
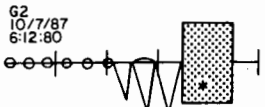
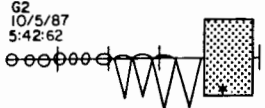
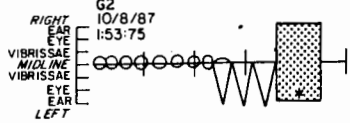
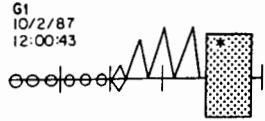
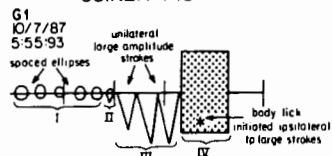


MOUSE



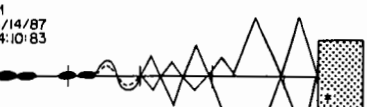
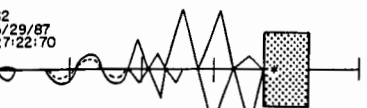
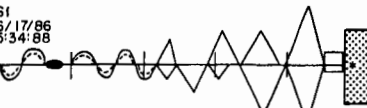
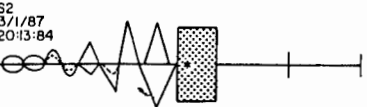
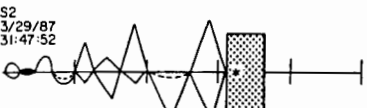
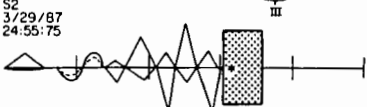
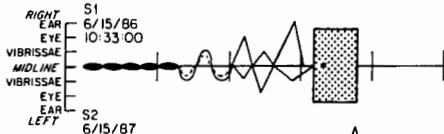
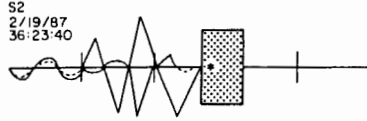
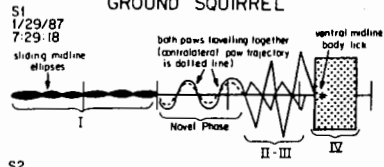


GUINEA PIG



1 2 3 4 5

GROUND SQUIRREL



1 2 3 4 5 6

Quantitative variations.

Quantitative comparisons were performed for chain stroke number and for chain duration (latency from first ellipse to initiation of Phase IV body lick), and separately for Phase I elliptical stroke number, Phase II-III stroke number, and the cycle length of Phase I ellipse. Stroke number was ascertained by counting the number of acceleration zero crossings from ascent, to descent, represented by 'peaks' in the notated graphs. For the purpose of this analysis, strokes were counted separately for each paw: bilateral motions of both paws simultaneously were counted as two strokes.

Stroke number: Species differed in total stroke number contained within the chain (Phases I, II, and III combined; $F(5,47) = 6.60$, $p < 0.001$). Mean (\pm standard error) values were guinea pig: 17.2 ± 0.9 , squirrel: 19.9 ± 2.1 , hamster: 20.0 ± 1.6 , gerbil: 25.6 ± 1.8 , rat: 26.7 ± 2.8 , and mouse: 27.9 ± 0.9 . This pattern suggested that smaller rodents in general, and perhaps muroid myomorphs especially, tend to include more strokes in their chains than do other species (Fig. 1b), and *post hoc* tests confirmed that rats, mice, and gerbils emitted significantly more strokes than all others (Newman-Keuls, $p < 0.05$ each). An analysis of separate phases showed that species distributed their strokes differentially among the different phases. Of the three species emitting chains with the greatest number of strokes, rats tended to emit more during phases II-III (14 ± 3 compared to gerbils 4 ± 1 ; $p < 0.05$), while gerbils and mice emitted significantly more Phase I ellipses (11 ± 1 and 10 ± 1 , respectively) than all other species (mean = 6.7 ± 2.1 ; Newman Keuls, $p < 0.05$ each). A moderate inverse correlation existed between ellipse number and body size ($r = -0.65$ for body length; $r = -0.38$ for weight ($p < 0.05$ for all correlations reported in this study).

Timing features and allometry.

Phase I Ellipse Timing. A strong positive correlation existed between ellipse cycle duration and body weight ($r = 0.90$). This allometric relation is shown in Fig. 4. The allometric power function ($y = a \cdot x^b$) was calculated for the relation $y_{time} = a \cdot x_{mass}^b$, by taking the common logarithmic transform of all weight and duration values, and solving the linear regression equation $\log y = \log a + b \log x$ (SCHMIDT-NIELSEN, 1984). Conversion to linear values gave the allometric relationship of ellipse cycle length to body mass: $y_{time} = 17.4421 \cdot x_{mass}^{0.3928}$. Thus, ellipse cycle duration in msec increases in direct proportion to a value

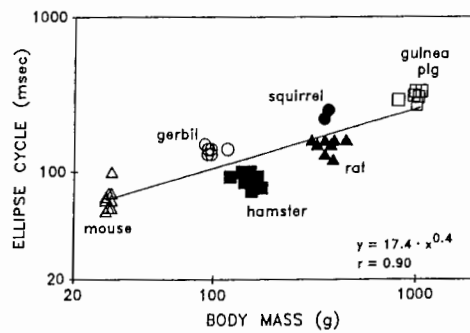


Fig. 4. Allometric relation of action timing to body mass. Cycle duration (interval between the initiation of two successive strokes) of syntactic chain Phase I ellipses is plotted against body weight for individuals from each species. Each variable is represented on a logarithmic axis. The allometric power function, $y_{time} = a * x_{mass}^b$, and the $x:y$ Pearson's correlation, are shown at lower right.

($2.5\sqrt{\text{mass}}$) that lies between the value of the square root and the value of the cube root of body mass in grams. The correlation between ellipse cycle duration and body length ($r = 0.86$) was only slightly weaker than that between duration and mass. Ellipse stroke duration was identical to ellipse cycle duration (*i.e.*, the interval between the initiation of successive ellipses), and therefore showed a similar relation to body mass, for all species except guinea pigs.

Chain duration.

The latency from chain initiation to completion was also positively, though more weakly, correlated with body length ($r = 0.53$) and weight ($r = 0.39$). This weaker correlation reflects the interaction of differences in stroke number, mentioned above, with the effect of mass on stroke duration. When a multiple correlation was performed between the latency to chain completion and the combined factors (body weight, height, the mean duration of Phase I ellipses, and the total number of strokes within the chain) a correlation value of $r = 0.70$ was obtained.

Syntactic efficacy.

Chaining rule strength, or syntactic efficacy, refers to the tendency of the syntactic pattern to resist fragmentation. Syntactic efficacy can be measured by ascertaining the likelihood that initiated chains, which meet



Fig. 5. Syntactic efficacy of chaining. The percentage of chains completed syntactically to Phase IV, out of the total of chains begun by Phase I ellipses, is shown for each species. Different bar types indicate completion rates that differed significantly from other types.

criterion 1 described in Methods for Phase I initiation, will be completed syntactically through to Phase IV. Completion rate is expressed as a percentage score. The syntactic efficacy of chaining, as measured by completion rate, varied among the different species ($F(5,47) = 10.79$, $p < 0.01$). Chaining efficacy ranged from 100% for guinea pigs to 46% for ground squirrels (Fig. 5). All myomorph species were characterized by intermediate completion rates, which generally were both significantly higher than that of squirrels and significantly lower than that of guinea pigs ($p < 0.05$, Least Significant Difference *post hoc* tests). Murid rats and mice, and cricetid gerbils, showed completion rates within the same 80% to 90% range that has been reported previously for rats (BERRIDGE & FENTRESS, 1987; BERRIDGE, in press b). Cricetid hamsters completed chains syntactically at a rate of 66%, significantly different from all other species except gerbils and ground squirrels ($p < 0.05$ each, LSD test).

Effect of timing upon syntactic efficacy.

In order to discover whether events exist early in a chain that predict success or failure at syntactic completion of that same chain, a separate analysis was performed on the timing of ellipses in chains that either were or were not completed to Phase IV. Guinea pigs emitted only complete chains, and so were not used in this comparison. For each of the other species, the average Phase I frequency of ellipses per second was ascertained for complete chains, and separately for Phase I ellipses of chains that were incomplete (which typically reverted to sequentially flexible grooming during Phase II or III). The ellipses of complete and incomplete chains did not differ for gerbils, hamsters, or ground squirrels. For rats, however, ellipses performed during Phase I of complete

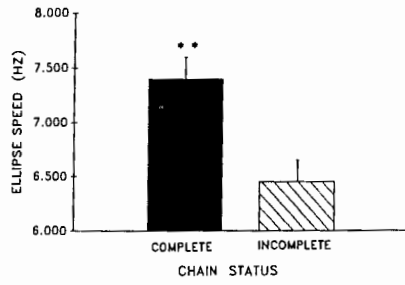


Fig. 6. Speed of Phase I ellipse cycles in chains that either were or were not completed syntactically to Phase IV by rats. Stars denote statistical significance.

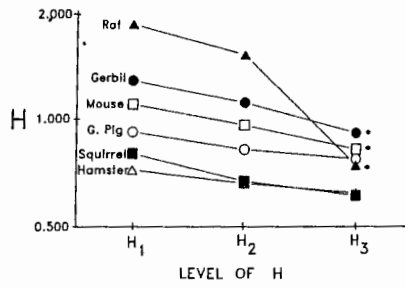


Fig. 7. Values of the information statistic (H) of sequential uncertainty at H_1 , H_2 , and H_3 levels. Smaller H values indicate greater predictability. Stars denote species that reduced uncertainty significantly from H_2 to H_3 .

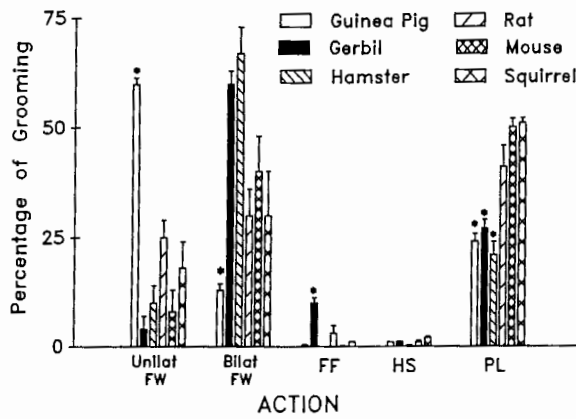


Fig. 8. Relative frequency of grooming components for each species. Species with stars differed significantly from all species without stars. Component actions are: *Unilat FW* = unilateral or asymmetrical face wash stroke; *Bilat FW* = bilateral face wash stroke; *FF* = forelimb flail; *HS* = headshake; *PL* = paw or body lick.

chains were found to be nearly 1 Hz faster than those of syntactically incomplete chains ($F(1,8) = 8.52$, $p < 0.02$; Fig. 6) and the ellipses of complete chains were nearly 0.5 Hz faster for mice ($F(1,14) = 7.6$, $p < 0.02$). Thus, for murid rodents, parameters of events in Phase I of this chain appear to predict aspects of the sequential structure that will be seen several phases later.

Overall sequential stereotypy.

Calculations of sequential uncertainty (versus stereotypy) were performed separately for each individual rodent. Mean values of uncertainty were obtained for each species at three levels (Fig. 7): H_1 (a \log_2 index of uncertainty where only the observed relative frequencies of each action (Fig. 8) are known), H_2 (where observed sequential dependencies resulting in the formation of action pairs (Table 1) are incorporated to reduce uncertainty), and H_3 (where higher level sequential dependencies that result in the formation of action triplets (Table 2) may reduce uncertainty further (ATTNEAVE, 1959). Values of H were determined by: $H_1 = -\sum P_1 (\log_2 1/P_1)$; $H_2 = (\sum P_2 (\log_2 1/P_2)) - H_1$; and $H_3 = (\sum P_3 (\log_2 1/P_3)) - H_2$, where P_1 = the observed probabilities of individual actions, P_2 = the observed probabilities of sequential pairs, and P_3 = the observed probabilities of sequential triplets (ATTNEAVE, 1959).

A 2-way ANOVA (species X H level) showed that the overall stereotypy of grooming sequences varied across the different species ($F(5,53) = 6.20$, $p < 0.001$), and across the different levels of H ($F(2,106) = 16.42$, $p < 0.001$), and that a significant interaction existed between these two factors ($F(10,106) = 2.92$, $p < 0.01$ (Fig. 7). Knowing the immediately prior action (H_2) has been reported to reduce the sequential uncertainty of grooming actions from H_1 in both mice (FENTRESS, 1972; FENTRESS & STILWELL, 1973) and rats (BERRIDGE *et al.*, 1987). This finding was replicated here and seen to apply also to all of the other rodent species (Newman Keuls, $p < 0.05$ each). Knowing the preceding two actions has been reported to reduce H_3 uncertainty still further for rat grooming (BERRIDGE *et al.*, 1987). This was replicated also and seen to apply as well to both mouse and gerbil grooming sequences ($p < 0.05$ each). A significant reduction from H_2 to H_3 was not found for squirrels, guinea pigs, or hamsters. This may reflect the fact that these species begin from baseline H_1 values of below 1.0 (Fig. 7), indicating that the grooming sequences of these species may be predicted with better than 50% accuracy based merely on relative action frequencies alone.

TABLE 1. Transition reciprocity among pairs of actions

Table shows sequential transitions for all pairs of computer-keyed actions. Circled pairs denote AB—BA sequential pairs that showed significant reciprocity (*i.e.*, that correlated significantly across individuals within the species). Boxes denote perseveration of a single action. Abbreviations are *FW* = face wash forelimb stroke; *FF* = forelimb flail; *HS* = headshake; *PL* = paw or body lick.

SEQUENTIAL PAIRS

RAT						MOUSE							
A n t e c e d e n t		Subsequent				Total	A n t e c e d e n t		Subsequent				Total
		FW	FF	HS	PL				FW	FF	HS	PL	
FW		602	18	5	239	864	FW		354	-	10	699	1063
FF		28	1	2	3	34	FF		2	-	-	1	3
HS		5	5	-	2	12	HS		17	-	-	15	32
PL		227	8	6	445	686	PL		686	3	23	644	1356
Total		862	32	13	689	1596	Total		1059	3	33	1359	2454

GERBIL						HAMSTER							
A n t e c e d e n t		Subsequent				Total	A n t e c e d e n t		Subsequent				Total
		FW	FF	HS	PL				FW	FF	HS	PL	
FW		935	148	9	249	1341	FW		791	-	-	143	934
FF		194	21	4	7	226	FF		-	-	-	-	0
HS		8	7	1	-	16	HS		2	-	1	-	3
PL		201	48	1	408	658	PL		139	-	1	147	287
Total		1338	224	15	664	2241	Total		932	0	2	290	1224

GUINEA PIG						SQUIRREL							
A n t e c e d e n t		Subsequent				Total	A n t e c e d e n t		Subsequent				Total
		FW	FF	HS	PL				FW	FF	HS	PL	
FW		799	-	4	230	1033	FW		398	1	-	130	529
FF		1	-	-	-	-	FF		1	1	-	-	2
HS		9	-	1	3	14	HS		-	-	-	-	0
PL		202	-	8	133	343	PL		128	-	1	454	582
Total		1011	0	13	366	1390	Total		527	2	-	584	1113

TABLE 2. Transition reciprocity among sequential triplets

The first two members of each triplet are shown in the column at left (only sequential pairs that actually occurred are shown in the column). The final member of each triplet is shown by the top row. Circled transitions denote AAB—BAA sequential triplets that showed significant reciprocity (*i.e.*, that correlated significantly across individuals within the species). Abbreviations are as in Table 1.

SEQUENTIAL TRIPLETS			
RAT			
FW	FF	HS	PL Total
FW/FW	474	13	5
FW/FF	15	1	109
FW/HS	3	1	1
FW/PL	88	6	4
FF/FW	16	5	7
FF/FF	1	-	-
FF/HS	-	2	-
FF/PL	-	1	-
HS/FW	4	-	2
HS/FF	4	-	1
HS/PL	7	-	2
PL/FW	104	-	121
PL/FF	6	-	1
PL/HS	2	-	1
PL/PL	139	-	2
Total	856	32	13

MOUSE			
FW	FF	HS	PL Total
FW/FW	204	-	1
FW/FF	5	-	49
FW/HS	335	-	6
FW/PL	-	1	-
FF/FW	-	1	-
FF/FF	3	-	1
FF/HS	5	-	13
FF/PL	143	-	7
HS/FW	-	8	531
HS/FF	2	-	1
HS/PL	12	-	10
PL/FW	635	-	15
PL/FF	1045	-	3
PL/HS	-	32	1346
Total	2426	3	22

GERBIL			
FW	FF	HS	PL Total
FW/FW	764	33	8
FW/FF	129	13	3
FW/HS	4	4	1
FW/PL	113	16	-
FF/FW	51	101	-
FF/FF	16	4	-
FF/HS	2	2	-
FF/PL	1	4	-
HS/FW	5	2	-
HS/FF	6	-	-
HS/HS	1	1	-
HS/PL	11	1	-
PL/FW	113	11	1
PL/FF	42	2	1
PL/HS	1	-	-
PL/PL	87	28	1
Total	1334	221	15

SQUIRREL			
FW	FF	HS	PL Total
FW/FW	339	-	59
FW/FF	-	1	-
FW/PL	30	-	96
FF/FW	1	-	-
FF/FF	1	-	-
FF/HS	55	-	71
FF/PL	97	-	349
Total	523	2	575

HAMSTER			
FW	FF	HS	PL Total
FW/FW	663	-	109
FW/PL	71	-	67
HS/FW	2	-	2
HS/HS	1	-	1
PL/FW	106	-	33
PL/HS	1	-	1
PL/PL	67	-	1
Total	911	1	285

GUINEA PIG			
FW	FF	HS	PL Total
FW/FW	666	-	3
FW/HS	2	-	1
FW/PL	147	-	71
HS/FW	9	-	2
HS/HS	-	-	1
PL/FW	96	-	1
PL/HS	5	-	1
PL/PL	53	-	7
Total	978	-	13

Transition reciprocity between action pairs.

In rats, overall sequential stereotypy arises at least in part from particular patterning rules that describe specific aspects of the grooming sequence. One such rule is transition reciprocity. Reciprocity between the frequencies of matched sequential pairs is a widespread pattern, in which many different actions may participate during both grooming and feeding (BERRIDGE *et al.*, 1987). Reciprocity between action pairs was found here for every species, and is visible in tables representing the frequencies of transitions between particular actions (Table 1).

The general pattern of reciprocity is that, for particular actions A and B, the number of transitions AB is matched by a similar number of transitions BA. A and B are open roles: various action types may enter them, and follow the reciprocity rule, as seen in Table 1. Significant correlations (Pearson's r (based upon matched pair transition scores for each individual animal, which were used as data to produce a correlation and probability value for the species)) between matched pairs are denoted by connected circles. Reciprocity, as defined by significant correlation between matched AB-BA transition values, was seen in every rodent species. As a "control group", random sequences were obtained from random number tables, and entered into the computer as 1200 successive 'behavioral' digits. Random sequences did not produce significant reciprocity among any transition pairs. This suggests that natural reciprocity among behavioral transitions does indeed reflect the imposition of a sequential ordering rule. A second sequential pattern shown in the table is perseveration, namely, the tendency for actions to be emitted in repetitive bouts (denoted by boxes in Table 1).

These patterns of reciprocity and perseveration have been shown in rats to be different aspects of a single, larger pattern. This larger pattern can be seen more clearly in a tabulation of sequential triplets (BERRIDGE *et al.*, 1987). Transition tables of action triplets reveal that reciprocity and perseveration of A and B transitions are combined together to result in a further reciprocity between triplets of the sort ABB and BBA and, conversely, between AAB and BAA. Reciprocity between matched triplets was found to apply here for every species (Table 2; matched triplets showing significant correlations are circled). Again, this appears to reflect a natural lawfulness within rodent grooming sequences; sequences generated by random number tables showed no significant correlations between matched triplets.

Conservation of reciprocity across subcategories.

Subcategories of forelimb strokes can be defined on the basis of lateral symmetry (symmetrical bilateral *versus* asymmetrical unilateral or dominant) and stroke amplitude (small, medium, or large). In order to ascertain whether sequencing rules persist across action subcategories, the transition analysis was extended, and computer transcripts were retabulated to show transitions among paired actions incorporating either laterality (Table 3) or amplitude (Table 4) action subcategories. Transition reciprocity between action pairs was determined as above. Significant reciprocity was conserved in both subtype analyses, both for transitions within FW strokes of different subtypes (masked as simple FW stroke perseveration in Tables 1 and 2), and for transitions between strokes and other actions. Thus, transitions appear to be lawfully structured by the reciprocity rule even across action subcategories.

Reciprocity summary.

These observations indicate that transition reciprocity reflects a fundamental property of grooming sequences. The pattern represents a global rule: a variety of different actions (paw lick, forelimb stroke, headshake, forelimb flail) can participate in a variety of paired combinations. Although different species emit grooming actions with different relative frequencies (Fig. 8), such changes in relative emission probabilities appear not to eliminate the rule, but simply rearrange the actions that participate. Reciprocity exists as a strong characteristic of natural grooming sequences, extending even to transitions among action subtypes. Reciprocity was never seen, however, within random 'control' sequences of comparable length.

Hierarchical levels.

FENTRESS & STILWELL (1973) showed that the individual actions of mouse grooming could be grouped into hierarchical units or 'clusters' based on empirically defined sequences. They found that H_2 values of sequential uncertainty tended to be lower for sequences of hierarchical cluster units than for sequences of the constituent actions themselves, and concluded that the stereotypy of sequential patterns was greatest at hierarchically higher levels. In order to replicate and extend this finding beyond a single species, videotaped mouse and rat grooming sequences were rescored using the modified FENTRESS & STILWELL criteria described

earlier, re-entered into the computer record separately as low unit and as high unit transcripts, and analyzed for uncertainty (H_1 , H_2 , and H_3) and transition patterns.

Sequential dependency upon preceding actions and action pairs was exhibited by mice and rats at both levels of units (Fig. 9). A 3-way mixed

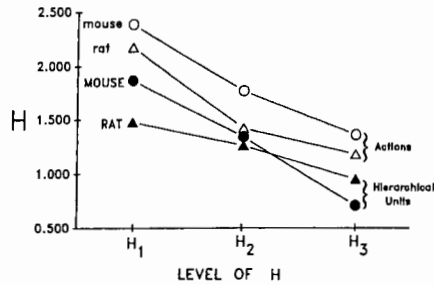


Fig. 9. Values of the uncertainty information statistic (H) for lower and higher hierarchical units in mice and rats. Open symbols show H values for component action units ('lower' units); filled symbols show H values for hierarchical cluster units ('higher' units).

ANOVA (species \times unit level \times H level) showed significant overall uncertainty reduction as H level increased ($F(2,28) = 223.98$, $p < 0.001$), and a significant overall difference between the uncertainty of lower and higher hierarchical units ($F(1,14) = 189.48$, $p < 0.001$). Rats and mice differed only marginally overall ($F(1,14) = 4.20$, $p < 0.057$), but showed significant species 2-way interactions with unit level ($F(1,14) = 5.33$, $p < 0.05$) and H level ($F(2,28) = p < 0.05$). In addition, rats and mice showed a 3-way species \times unit level \times H level interaction ($F(2,28) = 7.92$, $p < 0.01$). For both species, the level of sequential uncertainty for individual actions was reduced by knowing the preceding action, and reduced further by knowing the action before that (Newman Keuls, $p < 0.01$ each), just as in the earlier analysis of stereotypy. At the level of hierarchical units, too, uncertainty was reduced for both species by knowing the preceding unit, and reduced further by knowing the preceding two hierarchical units (Newman Keuls, $p < 0.05$ each). Finally, uncertainty was lower for hierarchical cluster units than for component action units at all H levels, excepting H_2 for rats ($p < 0.05$ each).

Of course, the reduced uncertainty for sequential 'clusters' compared to individual actions arises at least in part from the fact that there are fewer types of clusters than of actions, and so hierarchical units are more

TABLE 5. Hierarchical action and cluster unit transitions in mice and rats

Circles denote sequential unit pairs that showed significant reciprocity. Action units are S = single stroke, L and L' = short and long licks, O/L = overhand stroke combined with paw lick, O = overhand stroke, H = shimmy, C = circular stroke, N = undefined action, P = parallel stroke, and F = flail. Higher cluster units are defined in the methods.

MOUSE: INDIVIDUAL ACTION UNITS (LOWER)												
A	S	L	L'	O/L	O	H	C	N	P	E	F	Total
n	48	135	6	15	3	9	237					
i	144	78	6	129	3	9	63	483				
e												
c	21	150	3	3	3	6	18	24				
d												
e												
n	21	51	3	9	6	87	12	189				
i	3	66	3	3	3	6	6	78				
F	3	6	18	3	3	15	48					
Totals	246	492	18	6	231	15	24	186	75	48	1341	

MOUSE: CLUSTER UNITS (HIGHER)												
A	1	2	3	4	5	6	Total					
								Subsequent				
n	1	21	14	14	7	56						
i	2	288	70	56	56	74	565					
e	3	21	49	7	77							
c	4	144	29	28	171							
d	5	14	7	7	21	77						
e	6	14	107	16	14	30	181					
Totals	49	579	77	171	84	167	1127					

RAT: INDIVIDUAL ACTION UNITS (LOWER)												
A	S	L	L'	O/L	O	H	C	N	P	E	F	Total
n	29	2	6	4	2	72						
i	40	424	9	2	174	7	5	6	20	43		
e												
c	19	79	28	4	2	2	1	135				
d												
e	1	55	270	33	3	1	1	16	518			
n	2	18	1	1	4	27						
i												
F	1	1	3	1	2	1	9					
Totals	73	733	561	516	21	69	19	28	63	8	1722	

RAT: CLUSTER UNITS (HIGHER)												
A	1	2	3	4	5	6	Total					
								Subsequent				
n	1	8	32	40								
i	2	212	28	220	4	24	500					
e	3	28	36	64								
c	4	28	244	8	332	20	44					
d	5	8	16	4	28							
e	6	28	40	68								
Totals	40	500	36	676	24	72	1348					

predictable based simply upon the relative frequencies of each unit (low unit $H_1 = 2.3$, high unit $H_1 = 1.7$ overall). Still, the hypothesis that higher or more abstract sequential units may be more organized or stereotyped than the components they contain (FENTRESS, 1972) is consistent with this result. Stronger support for the hypothesis comes from the observation, noted earlier, that the presence and order of phases in syntactic chains appears more constant and stereotyped across species than the characteristics of the separate actions which make up each phase.

Strong reciprocity was found between matched pairs and triplets for both species at the level of lower action units (r values = 0.76 to 0.99). Reciprocal matched pair transitions are shown in Table 5. Reciprocity did not obtain for transitions between higher cluster units for either rats or mice. Reciprocity thus appears to be a rule that applies strongly to action elements, and does not effectively describe transitions among higher-level packages of action.

Discussion

These observations support the proposition that rodent grooming is characterized by strong syntactic organization, in which identifiable patterns and rules occur. Specific rules for the sequential fine structure of action were found to be shared by species from all of the classical suborders of Rodentia. This conclusion could be rephrased slightly, in recognition that the classical tripartite suborder division is considered to be archaic by many authors (*e.g.*, EISENBERG, 1981; LUCKETT & HARTENBERGER, 1985), to state that rules are shared by species ranging across highly diverse superfamilial groups.

These shared rules produce sequential patterns of behavior that are remarkably similar across species (although there is no obvious necessity that grooming should follow such patterns). The similarity exists despite the wide divergence in the evolutionary histories of these species, which has occurred since the massive radiation of Rodentia during the Eocene (EISENBERG, 1981). These six species have evolved separately on continents ranging from Eurasia (mouse, rat, hamster, gerbil), to North (ground squirrel) and South America (guinea pig) for periods ranging from perhaps 20 million years, for division of the *Rattus-Mus* branch, to up to 65 million years for the differentiation of the basic suborder or superfamilial groups (EISENBERG, 1981; SHOSHANI, GOODMAN, CZELUSNIAK & BRAUNITZER, 1985). Yet both the stereotyped patterns, such as syntactic chaining, and the more abstract organizing principles,

such as transition reciprocity, are easily distinguishable within the behavioral sequences of each of the six species tested here. The broad extent of these sequential patterns throughout Rodentia raises the question whether these specific syntactic patterns might not extend even to other related orders? It also supports the notion that syntactic principles of behavioral order, in general, may be a fundamental property of neurobehavioral organization. Mammalian brains, as producers of action, are constrained to pattern behavioral sequences in a rule-governed fashion (LASHLEY, 1951; VOWLES, 1970).

Nature of sequential rules.

A number of descriptive rules or patterns were documented by this study: syntactic chaining; general sequential stereotypy (H); transition reciprocity among action pairs and triplets; organization into a compositional hierarchy; and the preservation of stereotypy patterns among hierarchical cluster units. Although these patterns are inter-related (H₃ stereotypy, for example, results in part from clustering and reciprocity rules), no single explanatory account of action production can be expected to cover all of the patterns. The principles and mechanisms involved in the production of short and stereotyped syntactic chains, for example, may be quite different from those that produce the abstract patterns of reciprocity and hierarchical clustering, which operate throughout the entire sequence.

Yet the different patterns do share many features. In terms of formal organization, each of these patterns appears to be characterized by certain aspects of structure, represented by LASHLEY's (1951) concept of action syntax: the notion of a schema of order which is relatively independent of the motor units it contains. Aspects of pattern structure, which are reminiscent of linguistic syntax rules (in the sense that the structural rules actively organize their component elements rather than emerge fortuitously from chance combinations of those lower elements (CHOMSKY, 1957; GARDNER, 1985)), can be seen in these patterns in several ways. Even the stereotyped syntactic chain can be noted to have a pattern, in the sense of its phase structure, that is more stable across species than are the component actions it contains. The component actions used by different species for each phase may differ in form, symmetry, number, and timing. Yet each major sequential phase can be found in every species, and the phase order I->II->III->IV is never altered, even for species that occasionally insert novel elements along the

way (gerbil, ground squirrel). A related aspect of organization is demonstrated by the recursive dependence of murid sequential completion late in the chain upon the properties of ellipses that happened many actions earlier. In order for chains to be completed syntactically through phase IV, an apparent 'threshold' of ellipse speed must be met in phase I (Fig. 6). Although it is not yet possible to say whether faster ellipses actually contribute to, or simply reflect, the syntactic integrity of the chain, this finding suggests the conclusion that the entire pattern is produced as one structure, whose parts are interdependent, and that it is generated with a single degree of activation which can be measured in different ways (*i.e.* by ellipse speed or by completion efficacy).

Structure is seen even more clearly in the prolonged and abstract sequential pattern such as reciprocity, perseveration, and hierarchic clustering. Reciprocity characterized the transition relations among grooming action for all six species. The pervasiveness of this patterning rule is shown by its persistence even when the stream of action is recoded in a variety of ways (*i.e.*, in ways that are sensitive to laterality or to amplitude, or that employ different molecular units). The persistence of reciprocity, even when different actions are involved, supports the argument that the pattern does not arise simply out of the chance combination of particular actions. The widespread appearance of reciprocity does not imply that it is a trivial or necessary feature of action sequences. Although all species displayed the reciprocity rule, they applied it differently to different behavioral elements. For example, only murid mice and rats displayed significant reciprocity between transitions among forelimb facewash strokes and headshakes. Reciprocity among action pairs and triplets appears to reflect a general rule that can be applied to any selection of elements, even when those elements occur with a variety of relative frequencies. Candidates for this rule include alternating perseveration (which could produce action sequences of the sort: AAAB-BAAABBB or CCCDDDCCDDDD) and bout 'nesting' (which would produce sequences of the sort: AAABBBCCBBBAAA; see BERRIDGE *et al.*, 1987). A production algorithm: 1. Select action pair, A_i and B_i . 2: Emit A_i . Then either (weighted decision) repeat 2, go to 3 or to 4a. 3: Emit B_i . Then either (weighted decision) repeat 3, repeat from 2, or go to 4b. 4a: Select new action A_{i+1} . Repeat from 3. 4b: Select new action B_{i+1} . Repeat from 2. could easily generate a pattern such as alternating perseveration. Of course, this is only one of many possible algorithms capable of generating reciprocity. An important point shared by all such algorithms, however, is that A and B can be many different actions (forelimb strokes, flails, headshakes, and

paw licks in various pairs), just as many different nouns and verbs may be organized by rules of linguistic syntax. It is clear that here are limits to this flexibility in practice, however, since all species exhibited reciprocity between particular combinations of actions, such as paw licks and facewash strokes. This suggests that the algorithm which generates reciprocity must constrain A and B connections to specific sets of action units (again perhaps similar to the constraints on participation by words in linguistic syntax rules).

Species differences.

Despite the consistency of patterning rules, the six species differed in a variety of details and in the quantitative parameters of each pattern. For example, the graphic notation system that was used to record syntactic chains allows each species to be recognized at a glance by its distinctive 'signature': the configuration of special features regarding the symmetry, timing, *etc.* of chain constituents (Fig. 3).

Allometric control of pattern.

Where differences in sequential pattern and timing existed among species, lawful regularities could be found. Some quantitative regularities appeared to depend straightforwardly upon phenotypic properties such as physical size. Temporal parameters such as ellipse cycle length (and to a lesser inverse degree, stroke number and total chain duration), for example, were directly related to body mass. It is possible to discern the likely source of this relationship. One possible source, which probably can be ruled out, is the physical difference among species in limb inertia and momentum that would be produced as weight increased. Although the ratio of body mass to body surface is higher in heavier species, thus altering aspects of the physics of movement (SCHMIDT-NIELSEN, 1984), the allometric relationship between timing and mass may be better explained by neural mechanisms than by motion physics. This can be deduced by considering the difference that is found between the duration of ellipse strokes and ellipse cycles of guinea pigs compared to other species, and the principles that might operate to produce this difference.

Guinea pigs showed a dissociation between ellipse stroke and cycle durations due to the inclusion of a post-stroke pause in every cycle. Although guinea pigs weighed roughly three times as much as ground squirrels, the duration of ellipse strokes did not differ between the two

species. The duration of ellipse cycles, however, did. Guinea pigs paused between ellipses for a period that was sufficient to cause the cycle to conform to the allometric power function, $y_{time} = a \cdot x_{mass}^b$, where a was approximately 17.4 and b was approximately 0.4. Since limb inertia would affect movement duration (*i.e.*, the stroke itself) more directly than it would affect intermovement intervals, and since allometry requires the contribution of interstroke pauses, we may rule out forces arising from the physics of motion as a complete explanation of the allometric relationship. An alternative hypothesis that may be more plausible is that allometric timing relationships are generated within the brain: that a 'neural clock' controls the timing of action, and that this clock runs at a rate that is inversely proportional to the average adult body size of the species. If it were the case that each species possessed an allometric neural clock for action timing that was calibrated inversely to average adult mass, then one could predict that even representatives of different species which were compared when of equal size would still fail to equate cycle timing. Thus a 'rat-sized' juvenile guinea pig weighing 250 g would be expected to emit ellipses of a cycle duration more similar to that of a conspecific adult guinea pig weighing 1 kg than to that of an adult rat of its own 250 g size. Similarly, a 30 g 'mouse-sized' rat pup should resemble the timing of adult rats more closely than the timing of a 30 g adult mouse. Preliminary observations in my laboratory suggest that these predictions are true: juvenile guinea pigs and rats appear to possess cycle durations that conform to the body mass they will have as adults rather than to the durations that the allometric equation would predict based upon their own small sizes. These preliminary observations support the hypothesis that differences in stroke timing arise endogenously from a 'neural clock' rather than directly from body size. The speed of the clock appears to be set by a principle of interspecific allometry (GOULD, 1966).

Phylogenetic relationships.

Many of the parameters of syntactic chains, of transitional reciprocity, and of other sequential patterns that differed among species could not be accounted for by differences in physical traits. A second source for behavioural variation among species, separable from differences in their current physical phenotype, arises from their phylogenetic history and from different degrees of similarity in their genotype (*e.g.*, LORENZ, 1941; HINDE, 1971; DEWSBURY, 1978; PELLIS, 1988). Many of the specific dif-

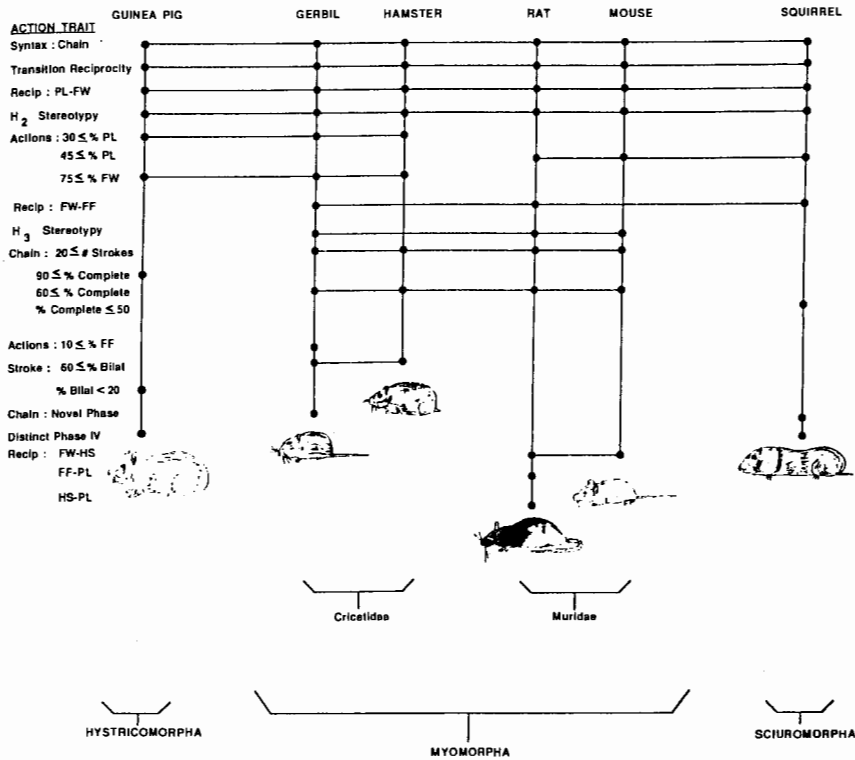


Fig. 10. Behavioral taxonomy of species based upon the behavioural grooming traits described in text. Compare to Fig. 1. Dots denote the presence of a particular trait for that species. Shared action traits, common to more than one species, are represented by the horizontal lines that connect different species. Note the progressive differentiation from a common pool of traits shared by all the rodents, into suborder, family, and species groups.

Trait definitions. *Syntax Chain*: the presence of syntactic chains containing all 4 phases. *Transition Reciprocity*: the existence of significant correlations between AB and BA transitions during grooming. *Recip PL-FW, FW-FF, FW-HS, FF-PL, HS-PL*: significant reciprocity between these particular AB pairs of actions (PL = paw lick; FW = face wash forelimb stroke; FF = forelimb flail; HS = head shake). *H₂* or *H₃ Stereotypy*: significant reduction of sequential uncertainty at H₂ level (from H₁) or H₃ level (from H₂). *Actions %*: the relative frequency of each type of grooming action. *Chain # Strokes* are the number of component strokes contained within Phases I, II & III. *% Complete*: syntactic efficacy of chaining expressed as the rate of completion through Phase IV. *Stroke % Bilat*: the proportion of symmetrically bilateral forelimb strokes (versus asymmetrical or unilateral strokes). *Chain Novel Phase*: the presence of a new syntactic phase within chains, in addition to the four defined ones. *Unique Phase IV Initiation*: the presence of a highly stereotyped pattern of Phase IV initiation (e.g., always ipsilateral to the last Phase III stroke (guinea pig), or always on the midline (ground squirrel)).

ferences in a) the relative frequencies of grooming actions, b) the percentage of bilateral *vs* unilateral forelimb strokes, c) chain parameters such as completion rates or stroke number, d) sequential stereotypy (H), and e) the participation of particular actions in the reciprocity rule, did appear to coincide with phylogenetic relationships. These behavioural traits can be arranged to form a taxonomy of similarity (Figure 10) based upon the number of species that share each trait. This behavioural taxonomy parallels the phylogenetic relationships of these species (Fig. 1). The behavioral taxonomy shows both a common pool of traits shared across the Rodentia order, and a progressive separation of suborder, family, and genus/species groups as additional traits are considered. The four myomorph species share more similarities with each other than with the hystricomorph or sciuricomorph representatives. Within the myomorph order, the two members of the cricetid family are more similar to each other than to the two members of the murid family and, conversely, the two members of the murid family are more similar to each other than to the members of the cricetid family.

There is one interesting exception to the pattern of progressive differentiation of phylogenetic groups. This exception is the linking of cricetids to the caviomorph guinea pig, and the linking of murids to the sciuricomorph ground squirrel, based upon the relative frequencies of grooming actions. The link occurs in place of a link between myomorph families for this trait. This anomalous grouping of ostensibly separate suborder or superfamilial groups (EISENBERG, 1981; HARTENBERGER, 1985) might simply reflect an evolutionary parallelism or convergence between the members of these phylogenetically distinct groups (LUCKETT & HARTENBERGER, 1985). It is interesting in this regard, however, that a recent analysis of phylogenetic relationships based upon molecular amino acid sequence also has suggested a linking of cavia and cricetid (*Ondatra*) groups (SHOSHANI *et al.*, 1985).

Neural substrates of syntax control.

Both brainstem and forebrain systems have been implicated in the control of the sequential patterns described here. The structure of syntactic chains and of global reciprocity and stereotypy appears to be characterized by a strong degree of central patterning in the rat, it does not reside in any one brain structure, even for the most stereotyped syntactic pattern: the structural integrity of these patterns remains essentially unimpaired after removal of sensory tactile cues from the face (BERRIDGE & FENTRESS,

analysis systems used here (graphic notation, the labelling analysis of BERRIDGE *et al.* (1987), and the modified labelling analysis of FENTRESS & STILWELL (1973), a strong degree of correspondence existed. Fig. 2 shows that the grooming units designated by the two systems of action labelling are sufficiently similar so that general translation rules might be devised to convert one into the other. Similarly, patterns such as pair and triplet reciprocity, that arise from the computer-assisted action labeling procedure, also can be derived from FENTRESS & STILWELL (1973) units, when these units are used as inputs for the computer-assisted tabulation. Additional information is encoded in the graphic notation system, which is not reducible to the 'unit' analysis of action labelling systems. However, translation in the opposite direction should be possible. Future analyses may be able to make use of this correspondence to develop a parsimonious but comprehensive coding and analysis procedure for the sequential fine structure of natural behavior.

Summary

The phylogenetic constancy of a set of syntactic patterning rules for grooming was examined in six rodent species: guinea pig, Belding's ground squirrel, gerbil, hamster, rat, mouse. Species were chosen to allow comparisons of separate suborders of Rodentia (Hystricomorpha, Sciuromorpha, Myomorpha) and of separate families within suborders (Cricetidae and Muridae). Each species was examined for possession of the syntactic patterns of chaining, transition reciprocity, sequential stereotypy, and hierarchical clustering. These syntactic patterns were detected and quantified using videoanalysis, graphic notation, and a variety of computer-assisted action coding and analysis techniques.

Each syntactic pattern or sequencing rule mentioned above was found to obtain in all six of the species tested. The wide applicability of these rules suggests that they reflect a fundamental feature of neurobehavioral organization, which was established relatively early in rodent evolution. Syntactic organization appears to be a basic property of action production by mammalian brains.

The techniques used in this study also allowed a quantitative comparison to be made across species of syntactic pattern strength, form, stereotypy, and timing parameters. This comparison showed that many differences in behavioral patterns among species could be explained by one of two principles. The first explanatory principle was phylogenetic relationship: the behavioral traits of species from within a single family tended to be more similar than were traits of species from separate families, and species from a single suborder tended to be more similar than species from separate suborders. The second principle, which applied especially to temporal parameters, was programmed allometric control by physical size. The timing of patterns (for example, the cycle duration of certain highly stereotyped forepaw strokes performed on the face) was related to the average size of the species by an allometric power function.

The nature of these syntactic patterns and of the rules that generate them, the nature of their neural substrates, and the origin of parameters differences between species, is discussed.

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Zusammenfassung

Die phylogenetische Gültigkeit einer Anzahl von Ordnungsregeln im Ablauf des Körperpflegeverhaltens wurde in sechs Nagetierarten untersucht. Verwendet wurden *Cavia porcellus*, *Spermophilus beldingi*, *Meriones unguiculatus*, *Mesocricetus auratus*, *Rattus norvegicus* und *Mus musculus*, um einen Vergleich zwischen den verschiedenen Unterordnungen der Rodentia (Hystricomorpha, Sciuromorpha, Myomorpha) sowie verschiedenen Familien innerhalb einer Unterordnung (Cricetidae und Muridae) zu ermöglichen. Jede Art wurde in Hinsicht auf die Anwesenheit der Ordnungsregeln Verknüpfung, Umkehrung, Vorhersagbarkeit und hierarchische Gruppierung in der Folge der Elemente des Körperpflegeverhaltens untersucht. Zur Beschreibung und Quantifizierung des Verhaltens wurden Videoanalyse, graphische Notation und verschiedene computergesteuerte Aktivitätskodierungs- und Analysetechniken verwendet.

Jede der erwähnten Regeln im Ablauf des Pflegeverhaltens wurde in allen sechs Arten aufgefunden. Die weite Verbreitung dieser Regeln ist ein Hinweis darauf, daß sie einen grundlegenden Aspekt neuronaler Verhaltensorganisation beschreiben, der schon früh innerhalb der Nagetierevolution entwickelt wurde. Diese Ordnungsregeln entsprechen somit einer Grundeigenschaft der neuronalen Verhaltenssteuerung im Säuger.

Die in dieser Studie benutzten Techniken erlaubten einen quantitativen Artenvergleich in Bezug auf Gestalt, Ausprägung, Uniformität und Zeitfolge der Körperpflegeverhaltens. Dieser Vergleich zeigte, daß zwei Erklärungsprinzipien ausreichen, um viele Artunterschiede im Reinigungsverhalten zu erklären. Das Prinzip der phylogenetischen Verwandtschaft besagt, daß Arten innerhalb einer Familie oder Unterordnung mehr Verhaltensähnlichkeiten aufzeigen als Arten von einer anderen Familie oder Unterordnung. Das zweite Prinzip besagt, daß die Zeitdauer eines Verhaltensablaufs, wie etwa eines stereotypen Wischens der Vorderpfote über das Gesicht, in einer exponentiellen allometrischen Beziehung zur Körpergröße steht.

Die Eigenschaften der Organisation des Körperpflegeverhaltens und die Regeln, die diese Organisation generieren können, die neuronalen Grundlagen, sowie der Ursprung von Artunterschieden werden in dieser Studie diskutiert.

