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Natural syntax rules control action sequence of rats

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Knowledge of the principles by which behavioral sequences are generated is essential to progress in our understanding of neural mechanisms. We describe here a set of natural principles or syntax rules that organize the components of grooming and feeding. The behavioral stream of facial grooming or of taste-elicited ingestive/aversive consummatory actions of rats can be viewed as a long series of individual movements linked together to form functional sequences. In order to ascertain the syntax rules that determine how these actions are linked together, many thousands of spontaneous grooming and elicited ingestive/aversive actions were videotaped and scored with a microcomputer. Techniques of information analysis of sequential stereotypy, tabulation of the sequential transitions between single actions and between action groups, and visual inspection for linear action chains, were employed to expose underlying rules of behavioral sequencing. These analyses revealed two global patterns: action perseveration and transitional reciprocation between sequential pairs and triplets, which together account for approximately 75% of all sequential transitions during grooming and ingestion/aversion. The pattern of transitional reciprocation could be divided further into patterns of alternation between individual actions on the one hand, and between perseverating bouts of actions on the other. Global syntax rules applied equally to actions emitted during grooming or during taste-elicited ingestion/aversion. In addition, a specific rule of linear chaining was found to apply only to facial grooming. These natural rules of action syntax provide insight into the sequential structure of behavior, and lend themselves well to analyses of neural mechanisms.

INTRODUCTION

The issue of how the brain creates complex behavioral sequences from lawful combinations of simple movements, linked together by implicit rules of action syntax, has received considerable experimental investigation. Peripheral sensory feedback^{16,33}, as well as central neural structures such as orbitofrontal or dorsolateral frontal cortex^{9,18,22,23,25,27}, the corpus striatum with its mesencephalic connections^{3,8,10,12,24,26,30,31} and restricted loci within the caudal brainstem^{11,20}, have been implicated in specifying the order of behavioral sequences.

Although it is clear that neural mechanisms such as these are important to behavioral sequencing, it has often been difficult to specify precisely what aspects are contributed by each to the sequential control of behavior. In part, this may be due to the fact that most measures available for studying sequential patterns (e.g. performance of trained sequences of action, timed or alternating response choice, etc.) can tell us only when control processes have been disrupted to the extent that the measured sequence fails to be completed, but not how or in what way normal action syntax processes have been altered²⁸.

A powerful and different way of identifying

specific changes in syntax rules after neural manipulations may be provided by *natural action sequences* emitted spontaneously or in response to biologically significant stimuli. As will become evident, these actions may possess a rich sequential structure, yet at the same time they are measurable and easily elicited in numbers sufficient to allow their rules of order to be detected.

This study examined two classes of natural action sequences: facial grooming and taste-elicited ingestive/aversive actions. Techniques of information analysis, transition tabulation, and visual inspection of videotape and transcript records were used to identify syntax rules controlling the sequential organization of these actions. We suggest that the identification of such rules is useful both for providing an immediate better understanding of action control at a behavioral level, and for providing a diagnostic assay of sequential control that can be usefully linked to studies of the neural mechanisms that sequence behavior.

MATERIALS AND METHODS

Nineteen male Sprague–Dawley rats (250–350 g) were anesthetized and implanted with chronic oral cannulae to allow infusions of taste solutions into the mouth^{19,29}. These cannulae consisted of flared polyethylene 100 tubing, implanted lateral to the first maxillary molar, attached to 19 gauge steel tubing, and anchored with skull screws and dental cement.

Behavioral categories

Ingestive/aversive actions. Rats show a distinct repertoire of actions when tastes are infused into the mouth¹⁹. Preferred tastes, such as sucrose, elicit rhythmic midline tongue protrusions (6 Hz), non-rhythmic lateral tongue protrusions (approximately 165 ms duration), and bouts of paw licking. Non-preferred tastes, such as quinine, elicit gapes (wide opening of the jaw and retraction of the lips, 125 ms duration), head shakes (at greater than 60 Hz), chin rubs (lowering of the head and pushing of the chin forward along the substrate), forelimb flails (back and forth movement of the forelimbs at greater than 60 Hz), downward forelimb strokes over the face with one

or both paws, locomotion, and stationary paw treading (rhythmic forward and backward extension of the forepaws, generally with the two paws 180° out of phase). Both preferred and unpreferred tastes may elicit rhythmic mouth movements and passive dripping of the solutions (especially at low concentrations).

Grooming actions. Several of the above actions also occur spontaneously following meals^{1,7} or taste infusions⁵ to constitute postprandial face and body grooming^{14,15}. These actions include rhythmic midline tongue protrusions, downward forelimb strokes of varying amplitude over the face, paw and body licking, and forelimb flails.

Test procedure

Each rat received 6 test trials on separate days using 6 different taste-stimulus solutions. These solutions were chosen to ensure that a full range of ingestive, aversive, and grooming actions would be elicited. Taste stimuli were: sucrose (1.0 and 0.03 M), HCl (0.1 and 0.01 M), and quinine HCl (3×10^{-3} and 3×10^{-4} M). The order of presentation was counterbalanced across rats. The oral cannulae of a rat were connected to stimulus delivery tubes and the rat was placed inside the clear plastic test chamber for 5 min habituation prior to stimulus infusion. The transparent floor of the test chamber was positioned above a tilted mirror that reflected a view of the rat's face and mouth into a color video camera.

A 1-ml vol. of the taste solution was infused into the mouth at a constant rate over 1 min. Taste-elicited responses during the infusion were videotaped for subsequent analysis. The rat was allowed to remain in the test chamber for an additional 6 min after the infusion. Rats in this situation often groom postprandially; any spontaneous bouts of grooming during this period were similarly videotaped for subsequent analysis.

Behavioral scoring

A microcomputer was used to score the videotaped behavioral record. Each action corresponded to a key on the computer keyboard. Videotapes were scored at 1/10 to 1/15 actual speed. The computer clock was calibrated to the video speed. As each action occurred, its cor-

responding key was pressed. The termination of the action was signalled either by the onset of the next action or by pressing a terminator key (whichever came first). An additional key signalled 'time-out' periods during which behavior could not be scored due to focus of the camera, movement of the rat out of view, etc. These time-out periods were treated as gaps in the record for the purpose of subsequent sequence analysis, and the two actions bordering such gaps were not considered to constitute an action transition. These procedures created a computer record of the number, duration, and sequential order of each action, which was stored on magnetic disc for subsequent analysis. Discrete actions such as tongue protrusions, gapes, headshakes, and face washing strokes were recorded each time they occurred. Continuous actions such as paw licking, mouth movement, locomotion or passive dripping of the solution were recorded in 5-s bins or parts thereof (thus 6 continuous seconds spent paw licking was recorded as two occurrences). This reflects the fact that continuous actions typically persist for several seconds. The use of bins minimizes the possibility that 'artificial bouts' might be created by the use of inappropriately small units of measurement.

Sequence analysis

A. Information analysis

Information analysis provides a measure of the degree of stereotypy or predictability of a behavioral sequence². A predictable sequence is one in which the next action can be successfully predicted if one knows the *preceding* action or actions, based upon lawful sequential dependencies between actions. An uncertain sequence is one in which the occurrence of an action is unrelated to preceding actions; that is, in which there are no sequential dependencies between actions. Information analysis measures the degree to which a sequence is predictable or uncertain as a whole and expresses the uncertainty (H) as a set of statements regarding particular levels of knowledge. At the lowest level, the uncertainty of a sequence where one knows only which actions *can* occur is H_0 . The potentially lesser uncertainty

of a sequence where one knows the relative frequencies at which different actions *actually occur* is H_1 . If the sequence is governed by a second-order sequential dependency, that is, if the probability of the next action is influenced by the action *immediately prior* to it, then uncertainty may be reduced still further by knowing that prior action (H_2). If different pairs of action have different probabilities of being followed by a third action, then knowledge of the *two* preceding actions may reduce uncertainty even further (H_3), and so on. Information analysis expresses the degree of uncertainty as a base two logarithm. A value of $H = 1.0$ implies that a behavior can be predicted with 50% accuracy; $H = 2.32$ means that an action can be predicted correctly one out of five times; $H = 3.58$, one out of twelve times, etc. Uncertainty reflects the weighted probability of emission for all possible behavioral groups. The value of H_0 is simply the \log_2 value of the number of different actions that can occur. $H_1 = \sum P_i (\log_2 1/P_i)$, where P_i is the observed probability of each action. $H_2 = (\sum P_{\text{pair}} (\log_2 1/P_{\text{pair}})) - H_1$, where P_{pair} is the observed probability of each possible sequential pair of actions. Similarly, $H_3 = (\sum P_{\text{triplet}} (\log_2 1/P_{\text{triplet}})) - H_2$, where P_{triplet} is the observed probability of each possible sequence of three actions².

Information uncertainty values (H_0 , H_1 , H_2 , H_3) were calculated separately for each rat and for each taste stimulus and grooming condition. To avoid the mathematical problem of having to take the logarithm of zero, particular actions, action pairs, or action triplets that never occurred in a given data set were arbitrarily deemed to have occurred once. Since $\log_2 1 = 0$, the resulting H values are unlikely to be distorted.

Fagen and Young¹³ recommend that a sample size of at least $5 R^2$ to $10 R^2$ behavioral transitions be obtained for Markov analyses, where R is the number of action types. This implies a requirement of 720 to 1,440 behavioral transitions for the present analysis. The H values below are based upon sample sizes ranging from 920 to 6,798 observed transitions, depending upon the test condition (each taste and grooming condition was analyzed separately). The mean sample size was 3,326 transitions per stimulus condition.

B. Transition tabulation

Information analysis can tell us of the existence and strength of sequential dependencies, but cannot define or identify those sequencing rules. To identify particular patterns of sequential dependency we must construct a transition matrix that shows the frequency with which particular actions or action pairs are followed by other actions. A two-way transition matrix shows the transitions between individual actions. With 12 separate actions there are 144 possible transitions. If there is no sequential dependency between individual actions ($H_1 = H_2$), then the transition distribution would be random and depend only upon the relative frequency of each action. Deviations from a random distribution reflect the presence of particular sequential couplings. Similarly, a three-way transition matrix shows the frequency with which a particular pair of actions is followed by every other action to form a triplet. With 12 actions there are 1,728 possible three-way transitions. Two-way and three-way transitions were tabulated separately for each rat and for each taste and grooming condition. These individual matrices were then added together across rats to form group tables for each stimulus condition.

C. Inspection for sequence chains

Both information analysis and transition tabulation detect sequential patterns that characterize the entire behavioral sequence. However, they are poor detectors of sequence rules that operate only during particular portions of the sequence. Repeated visual inspection of videotaped sequences and their computer transcripts by three observers was therefore employed to try to identify particular linear chain sequences that occurred regularly. The number, timing, and order of each action occurring within identified chains was recorded in a frame by frame analysis.

RESULTS AND DISCUSSION

A. Information analysis

High and low concentrations within a taste elicited equivalent stereotypy with all 3 tastes. For that reason, the averaged H values for only the high concentrations of each taste, plus grooming,

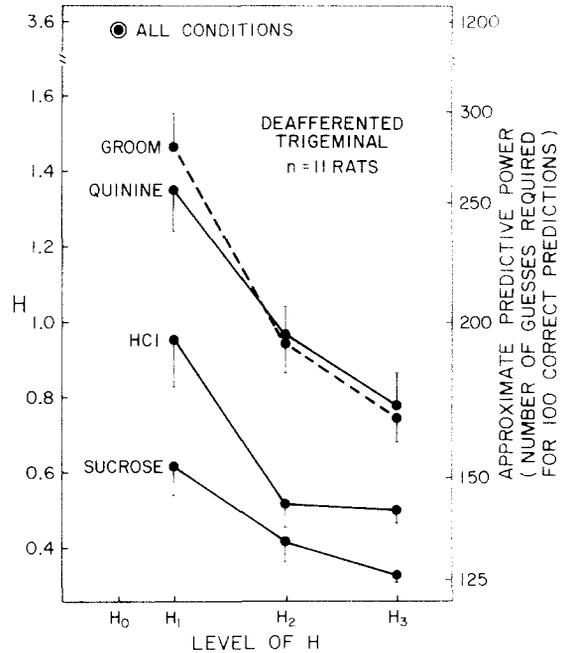


Fig. 1. Information analysis of grooming and ingestive/aversive sequences at different levels of H . Reduction of sequential uncertainty (H) at higher levels implies a proportional increase in stereotypy. Approximate predictive power of H values is shown on the right vertical axis.

are shown in Fig. 1. The actual mean number of each action that was observed in each condition (reflecting relative frequencies) is shown in Fig. 2.

Two trends are immediately apparent. First, all taste-elicited sequences show the same overall changes in sequential dependency from H_1 to H_3 , regardless of taste. Grooming also conforms to this pattern, suggesting that this pattern of dependency reflects a fundamental sequencing process. Knowing the relative frequencies of each action increases one's ability to predict correctly the next action from an accuracy of one out of twelve (based on simply knowing the list of possible behaviors without knowing the relative frequencies) to one out of two or three, a considerable reduction of uncertainty. Knowledge of the immediately preceding action (H_2) further increases the ability to predict by approximately 25–50% ($P < 0.01$ for each condition, paired t -test). Sucrose-elicited ingestive actions, for example, at $H_2 = 0.65$ can be predicted at $1/1.57$. That is, one could predict correctly 100 out of 157 guesses, nearly two out of three. Thus the occurrence of any action is related to the action that

immediately preceded it during both taste-elicited and grooming sequences. A further reduction of uncertainty can be gained at H_3 through knowing the preceding pair ($P < 0.05$ for HCl; $P < 0.01$ for quinine and grooming), albeit this is a weaker uncertainty reduction than was gained at H_2 . Knowing the preceding pair of actions increases one's ability to predict the next action by 5–10% over knowing the preceding action alone.

The second trend shown by Fig. 1 is that, although the relative uncertainty of H_1 , H_2 , and H_3 is equal over all conditions, the absolute uncertainty is not. Uncertainty is always higher for grooming and quinine-elicited (aversive) sequences than for sucrose-elicited (ingestive) or HCl-elicited (mixed) sequences. In general, the presence of ingestive actions in a sequence seems to entail a greater degree of predictability of that sequence. Grooming and quinine do not differ from each other at any H ; similarly, sucrose and HCl do not differ. However, grooming and quinine both have higher uncertainty at H_1 than either sucrose or HCl ($P < 0.01$ in every case). Grooming and quinine-elicited sequences also show higher uncertainty at H_2 than sucrose-elicited sequences ($P < 0.05$), and quinine is similarly higher than HCl ($P < 0.05$). At H_3 , the uncertainty of quinine-elicited sequences remains higher than either sucrose-elicited or HCl-elicited sequences ($P < 0.02$). The fact that grooming and quinine-elicited sequences share a number of actions, such as forelimb flails and forelimb strokes over the face (face washing), may in part account for the grooming/quinine similarity if similar sequencing rules are used in all contexts for a given set of actions. An inspection of the relative action frequencies elicited by each taste (Fig. 2), suggests that actions are more equiprobable in response to quinine than to either sucrose or HCl, perhaps accounting for the higher level of H_1 seen in aversive sequences. Whether this will fully account for the elevation of grooming or aversive sequences at H_2 and H_3 is unclear.

B. Transition tabulation

As would be expected from the values of H_2 and H_3 , transitions between individual actions

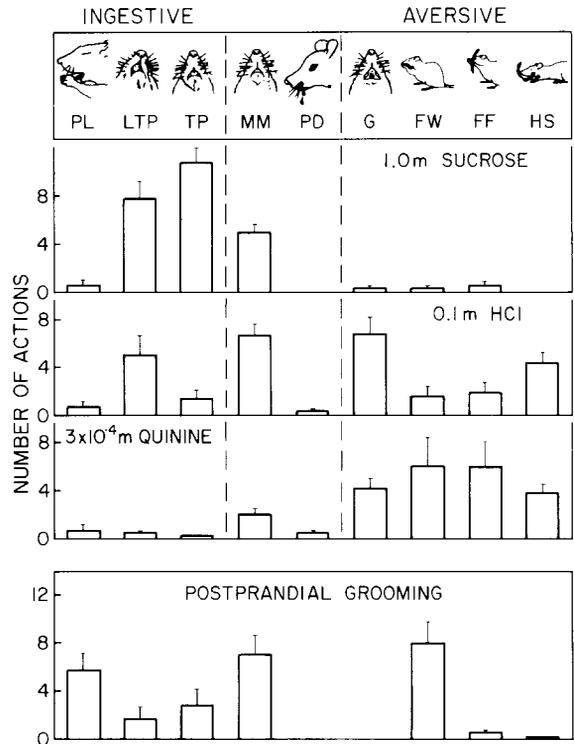


Fig. 2. Relative frequencies (mean \pm standard error) of each action type emitted to tastes and during grooming. Abbreviations: PL, paw licking; LTP, lateral tongue protrusions; TP, rhythmic midline tongue protrusions; MM, mouth movement without tongue protrusion; PD, passive dripping of the infused solution; G, gapes; FW, face washing; FF, forelimb flails; HS, headshakes.

shown in Table I clearly are non-random. Of the possible 144 transition types, many do not occur at all even when several thousand actual transitions are observed. Actually occurring transitions tend to follow one of two rules: *perseveration*, in which an action follows itself in sequence, and *transitional reciprocation* between pairs, in which the number of transitions from action A to action B tend to be closely matched by the number of transitions from action B to action A (Table I). Perseveration is reflected by the large number of transitions clustered along the left-right downward diagonal (see boxes). Transitional reciprocation is seen strikingly in the circled pairs, which in these combined matrices carry a correlation coefficient of 0.99.

Perseveration could be caused by a sequencing rule that produced actions in repetitive bouts:

TABLE I

Two-way transitions: frequency of particular sequential pairs occurring during sucrose ingestion (top) and postprandial grooming (bottom)

Column at left shows first action; row at top shows subsequent action. Boxed numbers denote instances of repeated action (simple perseveration). Circled pairs denote reciprocal numbers of transitions AB and BA. Abbreviations: TP, rhythmic tongue protrusion; LTP, lateral tongue protrusion; G, gape; CR, chin rub; FW, face wash stroke; FF, forelimb flail; HS, headshake; PT, paw tread; PL, paw or body licking; MM, rhythmic mouth movement; PD, passive dripping of solution; LO, rapid locomotion about the chamber.

2-way transition matrix; 1.0 M sucrose; intact
Grooming during infusion

| | TP | LTP | G | CR | FW | FF | HS | PT | PL | MM | PD | LO | Total |
|--------------|------|-----|---|----|----|----|----|----|----|------|----|----|-------|
| TP | 3640 | 13 | - | - | - | - | - | - | 6 | 428 | - | - | 4087 |
| A LTP | 10 | 8 | - | - | - | 1 | - | - | 3 | 140 | - | - | 162 |
| n G | - | - | 1 | - | - | - | - | - | - | - | 1 | - | 2 |
| t CR | - | - | - | - | - | - | - | - | - | - | - | - | 0 |
| e FW | - | - | - | - | 1 | - | - | - | 1 | - | - | - | 2 |
| d FF | - | - | - | - | - | - | - | - | 2 | 2 | - | - | 4 |
| e HS | - | - | - | - | - | - | - | - | - | - | - | - | 0 |
| d PT | - | - | - | - | - | - | - | - | - | - | - | - | 0 |
| e PL | - | 2 | - | - | 1 | - | - | - | 8 | 13 | - | - | 24 |
| n MM | 450 | 141 | 1 | - | 3 | - | - | - | 7 | 1915 | - | - | 2517 |
| t PD | - | - | - | - | - | - | - | - | - | - | - | - | 0 |
| LO | - | - | - | - | - | - | - | - | - | - | - | - | 0 |
| Totals: | 4100 | 164 | 2 | - | 2 | 4 | - | - | 27 | 2499 | - | - | |
| Grand total: | 6798 | | | | | | | | | | | | |

Postprandial grooming

| | TP | LTP | G | CR | FW | FF | HS | PT | PL | MM | PD | LO | Total |
|--------------|-----|-----|---|----|-----|----|----|----|----|-----|----|----|-------|
| TP | 149 | 4 | - | - | 2 | - | - | - | - | 40 | - | - | 195 |
| A LTP | 2 | 24 | - | - | 2 | - | 1 | - | 2 | 101 | - | - | 132 |
| n G | - | - | - | - | - | - | - | - | - | - | - | - | 0 |
| t CR | - | - | - | - | - | - | - | - | - | - | - | - | 0 |
| e FW | 1 | 1 | - | - | 86 | 4 | - | - | 43 | 4 | - | - | 139 |
| d FF | - | 1 | - | - | 5 | 1 | - | - | 1 | 1 | - | - | 9 |
| e HS | - | 1 | - | - | - | - | - | - | - | - | - | - | 1 |
| d PT | - | - | - | - | - | - | - | - | - | - | - | - | 0 |
| e PL | - | 3 | - | - | 42 | 1 | - | - | 26 | 2 | - | - | 74 |
| n MM | 34 | 102 | - | - | 1 | 4 | - | - | 2 | 257 | - | - | 400 |
| t PD | - | - | - | - | - | - | - | - | - | - | - | - | 0 |
| LO | - | - | - | - | - | - | - | - | - | - | - | - | 0 |
| Totals: | 186 | 136 | - | - | 138 | 10 | 1 | - | 74 | 405 | - | - | |
| Grand total: | 950 | | | | | | | | | | | | |

AAAAAA. Transitional reciprocation could be caused by a sequencing rule that produced action in alternation: ABABABAB. The simplest way to account for the two phenomena of perseveration and transitional reciprocation, then, would be to posit two sequencing rules which take turns in producing separate phases of alternation and repetitive bouts: AAAAA-ABABA-BBBBB. A slightly more complex alternative to this 'separate phases' system would be to combine perseverating bouts and reciprocal alternation into a single integrated 'alternating perseveration' rule:

AAABBBAAABBB. This is essentially an alternation of perseverating bouts, and is a more complex sequencing rule because it requires that a previous transition from A to B, for example, be remembered through a string of Bs and then followed reciprocally by a transition back to A (rather than on to C or to D).

The two-way transition matrix shown in Table I does not allow us to choose between a 'separate phases' and an 'alternating perseveration' rule because it is compatible with both. A three-way matrix, however, can discriminate between the two rules. By the separate phases rule, transitions between A and B occur especially during single action alternations ABABAB. Three-way transitions between different actions should therefore be found to cluster mainly in triplets of the sort ABA and BAB. By the alternating perseveration rule, on the other hand, we expect transitions between bouts of A and bouts of B. Transitional reciprocation between action triplets should therefore be expected to exist between triplets of the sort AAB and BAA, and similarly between ABB and BBA.

Table II shows a sample three-way transition matrix for spontaneous grooming after sucrose infusion. There are 1,728 possible transition types. To conserve space, only those action pairs that occurred at least once are listed in the column. Although alternation between single actions does exist (see hexagons in Table II), it appears that transitional reciprocation between circled triplets ($r = 0.98$) of the sort suggested by the alternating perseveration hypothesis (e.g. LTP-MM-MM and MM-MM-LTP, PL-FW-FW and FW-FW-PL, etc.) accounts for approximately 60% of the two-way reciprocation between actions. The reciprocating action pairs seen in two-way transition matrices thus appear to involve alternation between action bouts as well as between single actions. The participation of both bouts and single actions in alternation suggests that the key rule being followed may be one of alternation between action types, where the number emitted of each type is under independent control. This number is variable: it may be truncated to a single emission of that action or expanded into a repetitive bout.

TABLE II

Three-way transitions: frequency of particular sequential triplets during grooming

Column at left denotes preceding pair of actions; row at top denotes third action (only those pairs that actually occurred are shown in the column). Boxes denote simple perseveration. Hexagons denote triplets of the sort ABA, as predicted by a paired alternation rule. Circles denote reciprocal transitions between triplets of the sort AAB and BAA, as predicted by an alternating perseveration rule. Abbreviations as for Table I.

3-way transition matrix; postprandial; intact

| | Subsequent | | | | | | | | | | | Total | |
|--------------|------------|-----|---|----|-----|----|----|----|----|-----|----|-------|-----|
| | TP | LTP | G | CR | FW | FF | HS | PT | PL | MM | PD | | LO |
| TP/TP | 122 | 2 | - | - | 1 | - | - | - | - | 21 | - | - | 146 |
| TP/LTP | - | 1 | - | - | - | - | - | - | - | 3 | - | - | 4 |
| TP/FW | - | - | - | - | 2 | - | - | - | - | - | - | - | 2 |
| TP/MM | 14 | 4 | - | - | - | - | - | - | 1 | 19 | - | - | 38 |
| LTP/TP | 1 | 1 | - | - | - | - | - | - | - | - | - | - | 2 |
| LTP/LTP | 21 | 3 | - | - | - | - | - | - | 1 | 18 | - | - | 23 |
| LTP/FW | - | - | - | - | - | - | - | - | - | 2 | - | - | 2 |
| LTP/HS | - | 1 | - | - | - | - | - | - | - | - | - | - | 1 |
| LTP/PL | - | 2 | - | - | - | - | - | - | - | - | - | - | 2 |
| LTP/MM | 2 | 43 | - | - | - | - | - | - | 1 | 49 | - | - | 95 |
| FW/TP | - | - | - | - | - | - | - | - | - | 1 | - | - | 1 |
| FW/LTP | - | 1 | - | - | - | - | - | - | - | - | - | - | 1 |
| FW/FW | 1 | - | - | - | 58 | 3 | - | - | 20 | 2 | - | - | 84 |
| FW/FF | - | - | - | - | 2 | 1 | - | - | 1 | 2 | - | - | 3 |
| FW/PL | - | - | - | - | 24 | - | - | - | 14 | - | - | - | 38 |
| FW/MM | - | 1 | - | - | - | - | - | - | - | 3 | - | - | 4 |
| FF/LTP | - | - | - | - | - | - | - | - | - | 1 | - | - | 1 |
| FF/FW | - | - | - | - | 4 | - | - | - | 1 | - | - | - | 5 |
| FF/FF | - | - | - | - | 1 | - | - | - | - | - | - | - | 1 |
| FF/MM | - | - | - | - | - | - | - | - | - | 1 | - | - | 1 |
| HS/LTP | - | - | - | - | - | - | - | - | - | 1 | - | - | 1 |
| PL/LTP | - | 1 | - | - | - | - | - | - | 1 | 1 | - | - | 3 |
| PL/FW | - | - | - | - | 19 | - | - | - | 22 | - | - | - | 41 |
| PL/FF | - | - | - | - | 1 | - | - | - | - | - | - | - | 1 |
| PL/PL | - | 1 | - | - | 13 | - | - | - | 9 | - | - | - | 23 |
| PL/MM | - | 1 | - | - | - | - | - | - | - | 1 | - | - | 2 |
| MM/TP | 17 | 1 | - | - | 1 | - | - | - | - | 14 | - | - | 33 |
| MM/LTP | 1 | 17 | - | - | 2 | - | - | - | - | 75 | - | - | 96 |
| MM/FW | - | - | - | - | - | 1 | - | - | - | - | - | - | 1 |
| MM/FF | - | 1 | - | - | 2 | - | - | - | - | 1 | - | - | 4 |
| MM/PL | - | - | - | - | - | - | - | - | - | 1 | - | - | 1 |
| MM/MM | 14 | 53 | - | - | 1 | 3 | - | - | - | 167 | - | - | 238 |
| Totals: | 173 | 134 | - | - | 130 | 8 | 1 | - | 71 | 381 | - | - | |
| Grand total: | 898 | | | | | | | | | | | | |

It should be noted that we are unable to discern from the present data whether bouts alternate in the strong sense proposed by the alternating perseveration rule (AAABBBAAA) or in a slightly weaker form (AAABAAA). If it is the weaker form that tends to predominate, however, then we can be sure from the fact that reciprocating action triplets of the sort ABB-BBA are often matched by reciprocation between AAB-BAA (e.g. MM-TP-TP and TP-TP-MM matched by TP-MM-MM and MM-MM-TP, etc. in Table II) that AAABAAA sequences must be commonly matched by BBBABBB. This reinforces the conclusion that we are observing a

general syntax rule (as does the fact that many different actions seem to participate in reciprocal relations) rather than simply the haphazard intrusion of occasional single actions into long bouts of other actions. It can be noted that this sequencing rule does not result as an emergent property from fortuitously matched individual action probabilities. Strong reciprocal relations can be seen even between actions with widely disparate individual probabilities of occurrence, as for example between mouth movements (MM) and lateral tongue protrusions (LTP). Rather than arising from the chance combination of aleatory probabilities, transitional reciprocation appears to characterize action transitions despite the different probabilities of individual actions. This strongly suggests the imposition of a general sequencing rule. Transition patterns suggesting alternating perseveration, similar to that shown in Table II, were observed in the transition matrices for every behavioral condition: ingestive, aversive, and grooming. The three rules of simple perseveration, paired alternation, and alternating perseveration together appeared to account for approximately 75% of all transitions observed during grooming and taste-elicited sequences.

C. Inspection for linear chains

Linear chains are relatively fixed sequences of the sort ABCD. Unlike the alternating perseveration rule described above, where sequential structure is a general rule that is independent of which actions use it, a linear chain requires that specified actions occur in a specified order. For ingestive/aversive actions, Grill and Norgren²⁰ reported that a modal chain of aversive actions (gape/chin rub/face wash/paw tread) could be elicited reliably by 50 μ l infusions of all tastes in thalamic rats, in which all neural structures rostral to the thalamus (neocortex, hippocampus, basal ganglia) had been ablated. In contrast, the present study could identify no reliable linear chains occurring to any taste, either ingestive or aversive, in neurally intact rats. The absence of ingestive/aversive chains is consistent with other evidence suggesting that taste-elicited actions may be activated by a probabilistic, rather than deterministic, mechanism⁶.

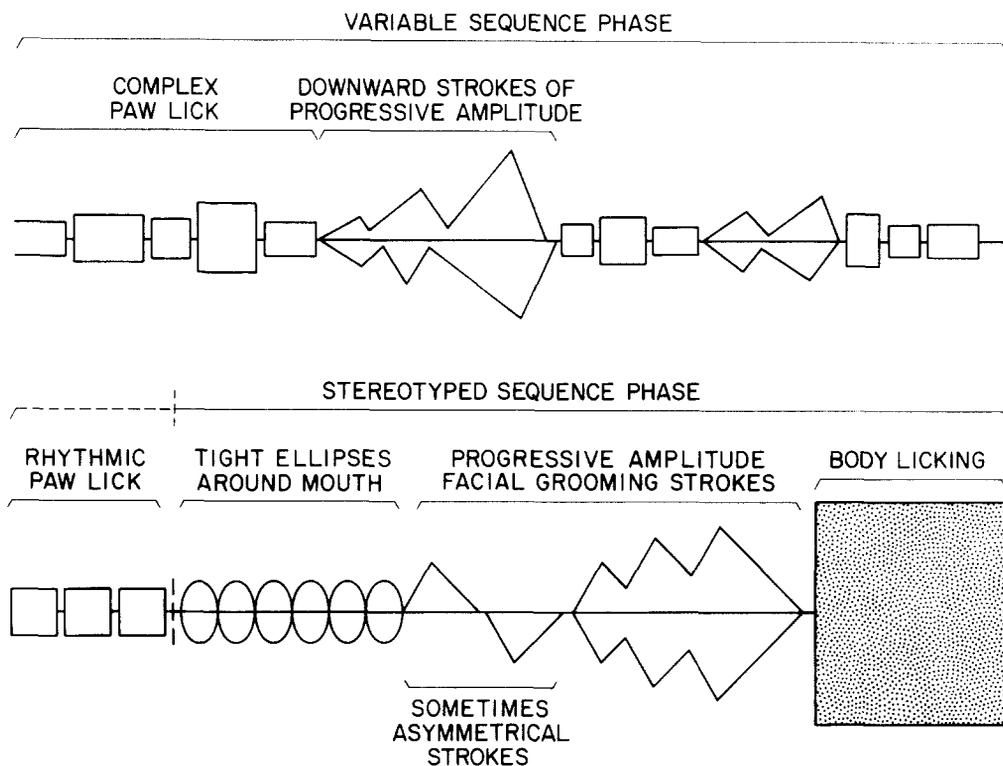


Fig. 3. Idealized schematic representation of facial grooming leading to a linear chain. Deviations of the lines above and below the horizontal axis denote movements of the two forepaws upward along the face away from the nose. The chain is depicted on the bottom.

During grooming, however, a reliable chain was identified. Although the majority of grooming actions are emitted in sequentially flexible sequences, there are occasional phases during which a relatively stereotyped linear order is followed⁵ (Fig. 3). These chains typically follow bouts of rhythmic paw licking and are initiated by a set of 5–9 rapid elliptical forepaw strokes (6–7 Hz), 1 cm in diameter, over the nose and mystacial vibrissae. The elliptical strokes are followed by a short series of slower strokes (2–4 Hz) of generally ascending amplitude, with the final strokes passing usually above and caudal to the pinnae. The downward strokes are followed by a tucking of the head and twisting of the torso, and the chain is terminated by a bout of licking of the ventrolateral body surface. This entire stereotyped chain was observed in virtually every rat (with occasional minor variations in forepaw bilateral symmetry and in the amplitude of the ascending series of strokes) and typically was completed by body licking within 3 s of initiation. Based upon

the probability of occurrence of each component action (unpublished observations), it was calculated that the probability of an entire chain being formed by chance from 9 consecutive grooming actions was roughly 7.1×10^{-10} . The actual observed rate of occurrence (based upon a total observation pool of 2,988 grooming actions) was calculated to be at least 13,000 times greater than expected by chance. The chain was seen often during spontaneous grooming but very rarely during taste-elicited aversive sequences employing similar action components.

The appearance of this chain marked a shift in sequential control from a flexible rule, characterized by alternating perseveration, to a fixed specified chain. To ascertain whether reliable predictors of this shift in sequential control precede the shift itself, the chains were examined closely in a frame-by-frame video analysis. Chains were typically preceded by a bout of paw licking during which the paws made irregular elliptical strokes around the mouth, rarely passing above the nose.

These strokes differed from the elliptical strokes that marked the initiation of a chain in that the earlier strokes were (a) irregular, not rhythmic, and of a slower speed, (b) spatially focused on the mouth rather than the mystacial vibrissae, and (c) less 'tight' or constant in their trajectory. The differences were not quantal, however, but appeared to vary continuously between the two types of strokes. For a chain to begin, *each* of these features had to assume the proper value. Thus a bout of ellipses that moved up to the vibrissae and tightened in trajectory, but did not increase in frequency per second, would not be followed by a chain. Similarly, a bout of strokes that did increase in frequency and tightness, but spatially moved too far caudally or dorsally along the face, would not lead to a chain. But if the elliptical strokes (a) increased in frequency, (b) increased the tightness of the trajectory, and (c) focused spatially upon the vibrissae, a chain could be predicted with more than 90% certainty.

The predictive power of these criteria suggests that, as these 3 features vary continuously, their configuration is continually assessed for a 'trigger threshold', which, once surpassed, initiates the chain. This configural trigger could be supplied by somatosensory or proprioceptive feedback from the face and paws or it could arise centrally from the motor outputs themselves (e.g. von Holst's efferent copy)^{21,22}. In either case, it is of interest to note that the critical frequency, 6–7 Hz, is very similar to the frequency of taste-elicited rhythmic mouth movements and midline tongue protrusions^{4,19,32}, perhaps suggesting the existence of a central oscillator which can be employed in a variety of neurobehavioral systems¹⁷.

CONCLUSIONS

A variety of sequencing rules appear to be obeyed by the nervous system as grooming and ingestive/aversive actions are produced. Information analysis demonstrates that these actions are not emitted in random order but instead show a marked sequential dependency. On average, the occurrence of any action exerts a strong Markov influence over the action that immediately follows it, and a weaker but significant higher-order influence over which action will follow its successor.

Transition and inspection analyses show fur-

ther that there are at least two different types of sequencing rules contributing to this sequential dependency. The first is a global strategy of sequencing which applies both to ingestive/aversive and to grooming actions. Two-way transition matrices reveal the two trends of perseveration, or repetitive single-action bouts (AAAA), and transitional reciprocity between AB and BA pairs, consonant with paired alternation (ABAB). Three-way matrices show transitional reciprocity exists also between action triplets, suggesting reciprocity and perseveration both reflect a single, integrated rule that produces an alternation (AABBAABBCCDDCCDD) [or, conceivably, a nesting (AABBCCDDCCBBAA)] of bouts. We have called this complex pattern of alternation between bouts 'alternating perseveration'. Many different actions of widely disparate individual probabilities participate in this rule, suggesting it is a general rubric controlling the pattern but not the constituents of a behavioral sequence.

A specific, second class of syntax rule, linear chaining (ABCDE), was found only during grooming. In this rule both the order and the constituents of a sequence are specified. The transition from sequentially flexible grooming sequences, characterized by alternating perseveration, to linear chains may be initiated by a configural trigger sensitive to the trajectory, spatial focus, and frequency of forelimb strokes over the face.

The discovery of particular rules of behavioral sequencing raises a number of questions regarding underlying brain mechanisms. Are these patterns the products of stimulus or feedback guided 'reflex systems', producing particular patterns in response to sensory cues, or do they reflect a central control imposed independent of feedback? Do the caudal brainstem mechanisms that have been shown to produce the individual actions involved in these sequences²⁰ also dictate the complex sequential patterns we have observed or are rostral brain structures involved? What are the neural mechanisms that switch behavior from one sequencing rule to another? The identification of natural sequences of emitted action, which have rules of syntax that can be objectively measured and identified, provides a practical means of addressing these and other related issues.

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