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Deafferentation does not disrupt natural rules of action syntax

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Natural rules of action syntax control the sequential order of grooming and ingestive/aversive actions emitted by rats. Grooming and ingestive actions share a common feature in that all are performed with or directed towards the mouth, tongue, and face. This study examined the role of orofacial somatosensory cues and feedback in the generation of natural action syntax. Bilateral deafferentation of the mandibular and maxillary branches of the trigeminal nerve was used to eliminate tactile sensation from the rostral face and mouth while preserving motor function. Neither the overall degree of sequential stereotypy (*H*) of grooming or ingestive sequences, nor the generation of particular natural sequencing rules were affected by trigeminal deafferentation. These natural rules appear to be specified by the brain without need of somatosensory feedback.

INTRODUCTION

A variety of natural actions are emitted by rats during grooming and in response to taste stimuli. These actions include tongue protrusions, forelimb strokes over the face, and a number of other facial and somatic movements^{7,11}. Information analyses of sequential stereotypy have shown that the sequential order of grooming or taste-elicited actions is not random but instead is rule-governed and has a strong degree of Markov and higher-order sequential dependency^{3,7,8}.

We have shown, using computerized techniques of transition tabulation and inspection, that the sequential dependencies revealed by information analysis are the result of at least two types of sequencing rule³. The first type, reflected in transition patterns of perseveration and reciprocity, is a global rule that applies both to

grooming and to ingestive/aversive actions, and that specifies the sequential arrangement of action without constraining which actions will employ it. We have called this global rule 'alternating perseveration'. In the alternating perseveration rule, perseverating repetition of a single action is combined with alternation between two action types to produce an integrated alternation of bouts of the sort AABBAABB or CCDCCD. The identity of A and B, or C and D, is not specified, and many different action pairs may participate in this rule (cf. ref. 3).

The second type of rule, exemplified by linear chaining, is more specific in the sense that the constituents, as well as the order, of a behavioral sequence is specified by the rule. A linear chain is a sequence of the sort ABCDE. This rule is also more specific in that it appears to be used only by grooming sequences and not by, for example, quinine-elicited aversive sequences that share

many of the same individual actions. The linear chain found in grooming consists of a series of tight elliptical strokes over the mystacial vibrissae, followed by a series of slower, downward strokes of successively larger amplitude over the face, followed by head tucking, turning, and terminated by a bout of body licking^{2,3}.

How might rules of action syntax be incorporated into neural mechanisms of behavioral production? One extreme possibility is that rules such as alternating perseveration or linear chaining are imposed by self-contained central neural pattern generators^{5,12,20,21}. Another extreme (but opposite) possibility is that each successive action within a sequential pattern is triggered by the sensory consequences arising from the performance of its predecessors, in a chain reflex fashion¹⁹. An intermediate possibility, which is also sensory-dependent, could be a 'sensory tape' mechanism^{6,13} in which central mechanisms dictate a prespecified sensory goal of particular somatosensory, proprioceptive, etc., inputs, which flexible motor control mechanisms then attempt to achieve. Other interactions between central pattern generators and modulating sensory input also are possible.

These various processes are distinguishable in principle by the different uses they make of sensory information in the production of a sequential pattern of behavior. They can be distinguished empirically by the different consequences they predict to follow from sensory disruption, such as that produced by deafferentation. For instance, if alternating perseveration or linear grooming chains depend crucially upon the presence of adequate tactile eliciting stimuli, as a chain reflex mechanism would imply, or upon the integrity of somatosensory feedback, as a sensory tape mechanism might suggest, then the elimination of such sensory information would be predicted to disrupt the sequential organization of behavior. On the other hand, if syntax rules reflect the operation of central pattern generators that are not dependent on somatosensory cues or consequences, then the sequential organization of action should remain essentially unchanged by manipulations that remove orofacial tactile information.

The present study examined the contribution of oral and facial tactile information to the sequential structure of natural action syntax. A trigeminal deafferentation procedure was used to remove somatosensation from the face and mouth. This preparation preserves all motor function as well as all proprioceptive and gustatory sensory function, while eliminating orofacial pain and tactile sensitivity^{14,17,22-24}. The sequential structure of grooming and of taste-elicited ingestive/aversive sequences was then analyzed and compared to the sequential structure found in intact rats. Our analysis revealed the sequential organization of grooming and taste-elicited ingestive/aversive actions to be essentially unchanged after deafferentation, suggesting that tactile input is not crucial to the implementation of these action syntax rules.

MATERIALS AND METHODS

Eleven male Sprague-Dawley rats (275–350 g), which had been previously implanted with chronic oral cannulae and examined for the sequential organization of grooming and taste-elicited actions³, were reanesthetized and subjected to bilateral trigeminal deafferentation (section of the inferior alveolar, lingual, and auriculo-temporal nerves of the mandibular branch, and of the anterior superior alveolar and infraorbital nerves of the maxillary branch) using the procedure of Jacquin and Zeigler¹⁴. This deafferentation procedure removes tactile somatosensation and pain from the upper and lower lips, gums, and incisors, anterior tongue, oral mucous membrane, chin, cheek, vibrissae, and facial pads. Chorda tympani gustatory function and trigeminal motor function are spared^{14,17,22-24} (the lingual nerve was transected proximal to the divergence of the chorda tympani in order to preserve lingual taste function). Mandibular nerves were exposed by blunt dissection using the ventral neck approach of Richter¹⁸. The individual nerves were visually identified under 15 × magnification by comparison with Green¹⁰, hooked, and sectioned with microscissors. Maxillary nerves were exposed in the orbital canal by gentle orbital deflection, visually identified by

comparison with Gregg⁹, hooked, and sectioned (cf. Jacquin and Zeigler¹⁴ for details).

Following deafferentation, rats were maintained on commercial baby cereal mixed with water to form a loose mash. In addition, they were intubated with 10 ml of water twice daily for 3 days after surgery to prevent dehydration. If body weight fell below 85% of its presurgical value (2 rats), intubations of a milk diet (equal parts sweetened milk and water) were substituted until body weight recovered (which occurred within 1 week). To prevent incisor overgrowth or tongue biting after deafferentation, rats were briefly anesthetized once weekly for clipping and sanding of the incisors. Testing began 48 h after deafferentation and was completed within 2 weeks, before recovery of function can be expected to occur¹⁴ (this was confirmed by repeated testing for recovery of facial responsiveness to blunt and sharp probes).

The behavioral testing, scoring, and sequence analysis procedures were identical to those described previously for neurologically intact rats by Berridge et al.³. Briefly, spontaneous postprandial grooming sequences and ingestive/aversive sequences elicited by 1 ml volume–1 min duration infusions of sucrose (1.0 and 0.03 M), HCl (0.1 and 0.01 M), and quinine HCl (3×10^{-4} and 3×10^{-5} M) into the mouth were videotaped. The videotaped records were subsequently scored in slow-motion by an observer who keyed each action into a computer. Scored actions were: rhythmic mouth movements and midline tongue protrusions, non-rhythmic lateral tongue protrusions, paw and body licking, passive dripping of the solution, gapes, head shakes, chin rubs, downward forelimb strokes of varying amplitude across the face, forelimb flails, locomotion, and stationary paw treading. The resulting transcript was analyzed by computer for sequential stereotypy and for transition patterns and by human observer for the occurrence of linear chains³. The computer analysis calculated information statistics (H_0 , H_1 , H_2 , and H_3) for each rat in each condition, and tabulated two-way and three-way transitions for all sequential pairs and triplets. Human observers examined the computer transcripts and videotaped records of identified linear

grooming chains in a frame-by-frame analysis, and recorded the number, timing, and order of each component.

RESULTS

Information analysis

The sequential stereotypy of deafferented grooming and ingestive/aversive sequences was very similar to that of sequences made by intact rats (Fig. 1). Just as for intact rats³, knowing the relative frequency of each action was by itself sufficient to reduce uncertainty from $H_0 = 3.6$ (allowing a 1/12 chance of correct prediction) to a maximum $H_1 = 1.5$ (increasing the chance of correct prediction to 1/3). Knowing which action occurred immediately preceding reduced uncertainty further by approximately 30% ($P < 0.01$; paired *t*-test) to a maximum $H_2 = 1.0$. Uncertainty was reduced still further by approximately 5–10% ($P < 0.05$) over that of H_2 by knowing the preceding pair of actions (H_3). Only HCl-elicited sequences, which contain both inges-

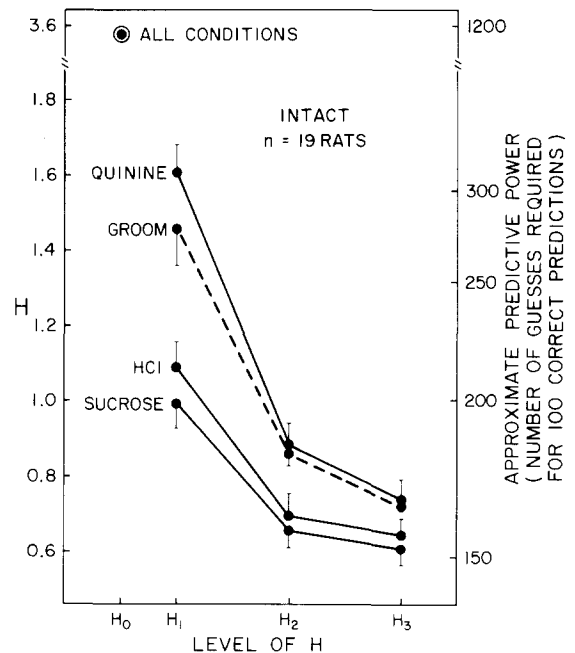


Fig. 1. Information analysis of deafferented grooming and ingestive/aversive sequences at different levels of H . Reduction of sequential uncertainty (H) at higher levels implies a proportional increase in stereotypy. Approximate predictive power of H values is shown on the right vertical axis.

tive and aversive actions, failed to show this higher-order sequential dependency, just as in intact rats³.

A second trend shared by deafferented and intact rats was the difference in absolute stereotypy among the different taste-stimulus and grooming conditions. The uncertainty of grooming sequences and of aversive sequences elicited by quinine was reliably higher at all levels of *H* than the uncertainty of ingestive sequences elicited by sucrose ($0.001 < P < 0.05$). The uncertainty of mixed HCl-elicited sequences was also lower than that of grooming or of quinine-elicited sequences at H_2 ($P < 0.01$) and remained lower than quinine-elicited aversion at H_3 ($P < 0.01$). Quinine-elicited and grooming sequences never differed significantly from each other in stereotypy; similarly, HCl- and sucrose-elicited sequences never differed.

The only difference in stereotypy observed between the sequences of deafferented and intact rats was in the absolute level of uncertainty of sucrose-elicited sequences. The uncertainty of deafferented sequences elicited by sucrose was significantly below that of sequences of intact rats at all levels of *H* ($P < 0.02$ at each level; two-sample *t*-test). The lower uncertainty of deafferented sucrose-elicited sequences may perhaps be accounted for by the facts that (a) sucrose elicits predominantly ingestive actions such as paw licks, lateral tongue protrusions, rhythmic midline tongue protrusions, and (less ingestive) rhythmic mouth movements, and (b) bilateral trigeminal deafferentation changes the relative frequencies of these responses, so that the number of paw licks and tongue protrusions are reduced while mouth movements are enhanced¹. Thus the response of a deafferented rat to sucrose consists mostly of rhythmic mouth movements. This distortion of individual response probabilities would reduce H_1 directly and might also reduce H_2 and H_3 by promoting bouts of perseveration.

Transition tabulation

Tabulation of two-way transitions between single actions in intact rats reveals two patterns: *perseveration*, the repetition of a single action in bouts, and *transitional reciprocation*, a tendency

for transitions from action A to action B to be matched by an approximately equal number of transitions from B to A³.

These two patterns are also seen in the two-way transition matrices of deafferented rats (Table I). Large numbers of transitions tend to cluster along the descending left-right diagonal, indicating that many actions are most likely to be followed by themselves. Other large values in the transition matrix tend to conform to the reciprocation pattern (see the circled pairs in Table I), indicating matching transitions between sequential pairs of the sort AB and BA.

TABLE I

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

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; bilateral trigeminal Grooming during infusion

	TP	LTP	G	CR	FW	FF	HS	PT	PL	MM	PD	LO	Total
A TP	887	-	-	-	-	-	-	-	-	43	11	-	941
n LTP	-	1	-	-	-	-	-	-	-	12	-	-	13
t G	-	-	-	-	-	-	-	-	-	-	-	-	0
e CR	-	-	-	-	-	-	-	-	-	-	-	-	0
c FW	-	-	-	-	-	-	-	-	-	-	-	-	0
d FF	-	-	-	-	-	-	-	-	-	-	-	-	0
e HS	-	-	-	-	-	-	-	-	-	-	-	-	0
d PT	-	-	-	-	-	-	-	-	-	-	-	-	0
e PL	-	-	-	-	-	-	-	-	-	-	-	-	0
n MM	47	12	-	-	-	-	-	-	-	1250	5	1	1315
t PD	11	-	-	-	-	-	-	-	-	5	-	-	16
t LO	-	-	-	-	-	-	-	-	-	-	-	-	0
Totals:	945	13	-	-	-	-	-	-	-	1310	16	1	
Grand total:	2285												

Postprandial grooming

	TP	LTP	G	CR	FW	FF	HS	PT	PL	MM	PD	LO	Total
A TP	191	-	-	-	14	4	2	-	3	59	-	-	273
n LTP	-	-	-	-	-	-	-	-	-	15	-	-	15
t G	-	-	-	-	-	-	-	-	-	-	-	-	0
e CR	-	-	-	-	-	-	-	-	-	-	-	-	0
c FW	14	-	-	-	55	45	-	-	17	4	-	-	135
d FF	5	-	-	-	56	10	-	-	10	10	-	-	91
e HS	2	-	-	-	-	-	1	7	-	5	-	-	15
d PT	-	-	-	-	-	-	-	-	-	-	-	-	0
e PL	4	-	-	-	9	15	1	-	2	2	-	-	33
n MM	61	15	-	-	5	11	4	-	1	363	1	1	462
t PD	-	-	-	-	-	-	-	-	-	1	-	-	1
t LO	-	-	-	-	-	-	-	-	-	1	-	-	1
Totals:	277	15	-	-	139	86	14	-	33	460	1	1	
Grand total:	1026												

Three-way transition tabulation in intact rats, showing the frequency with which a sequential pair of actions is followed by a third action, suggests that the two patterns of perseveration and transitional reciprocation actually reflect 3 types of sequence: simple perseveration of a single action, rapid alternation between a pair of actions, and the combination of the two into a third, integrated syntax rule of alternating perseveration³. By this third rule, alternation occurs between whole repetitive bouts of two action

TABLE II

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

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; bilateral trigeminal

	TP	LTP	G	CR	FW	FF	HS	PT	PL	MM	PD	LO	Total
TP/ TP	139	-	-	8	1	2	-	1	37	-	-	-	188
TP/ FW	4	-	-	5	2	-	-	1	-	-	-	-	12
TP/ FF	-	-	-	2	-	-	-	-	1	-	-	-	4
TP/ HS	-	-	-	1	-	-	-	-	1	-	-	-	2
TP/ PL	1	-	-	1	-	-	-	-	1	-	-	-	3
TP/ MM	27	1	-	1	1	-	-	-	29	-	-	-	59
LTP/LTP	-	3	-	-	-	-	-	-	7	-	-	-	10
LTP/ MM	-	14	-	-	-	-	-	-	27	-	-	-	41
FW/ TP	7	-	-	5	-	-	-	1	-	-	-	-	13
FW/ FW	5	-	-	58	18	-	-	13	5	-	-	-	99
FW/ FF	2	-	-	38	5	-	-	7	6	-	-	-	58
FW/ PL	2	-	-	12	6	1	-	7	-	-	-	-	28
FW/ MM	-	-	-	3	-	-	-	-	5	-	-	-	8
FF/ TP	2	-	-	1	2	-	-	-	-	-	-	-	5
FF/ FW	5	-	-	26	32	-	-	6	2	-	-	-	71
FF/ FF	-	-	-	13	3	-	-	2	-	-	-	-	18
FF/ PL	1	-	-	2	6	-	-	1	-	-	-	-	10
FF/ MM	2	-	-	1	6	-	-	-	3	-	-	-	12
HS/ TP	2	-	-	-	-	-	-	-	-	-	-	-	2
HS/ FF	1	-	-	-	-	-	-	-	-	-	-	-	1
HS/ HS	1	-	-	-	-	5	-	-	1	-	-	-	7
HS/ MM	1	-	-	-	-	-	-	-	3	-	-	-	5
PL/ TP	2	-	-	-	-	-	-	1	1	-	-	-	4
PL/ FW	-	-	-	10	5	-	-	7	-	-	-	-	22
PL/ FF	1	-	-	10	2	-	-	2	1	-	-	-	16
PL/ HS	-	-	-	-	-	-	-	-	1	-	-	-	1
PL/ PL	-	-	-	5	2	-	-	-	1	-	-	-	8
PL/ MM	1	-	-	-	1	-	-	-	-	-	-	-	2
MM/ TP	34	-	-	-	-	-	-	-	22	-	-	-	57
MM/LTP	-	7	-	-	-	-	-	-	37	-	-	-	44
MM/ FW	-	-	-	4	1	-	-	-	2	-	-	-	7
MM/ FF	1	-	-	7	5	-	-	-	3	-	-	-	16
MM/ HS	1	-	-	-	-	2	-	-	1	-	-	-	4
MM/ PL	-	-	-	-	1	-	-	-	-	-	-	-	1
MM/ MM	27	27	-	5	4	3	-	1	403	1	-	-	471
MM/ PD	-	-	-	-	-	-	-	-	1	-	-	-	1
MM/ LO	-	-	-	-	-	-	-	-	1	-	-	-	1
PD/ MM	-	-	-	-	-	1	-	-	-	-	-	-	1
LO/ MM	1	-	-	-	-	-	-	-	-	-	-	-	1
Totals:	270	52	-	214	108	14	-	51	602	1	1	-	
Grand total:	1313												

types, rather than between single emissions of each type. This rule is reflected by the observation that three-way matrices for intact rats show transitional reciprocation between triplets of the sort ABB and BBA and between AAB and BAA (consonant with sequences of the sort AABBAABB) rather than simply between ABA and BAB (which would have suggested ABABAB).

All of these transition patterns endure after trigeminal deafferentation (Table II), implying that orofacial somatosensory information is not required for the execution of this rule. Table II shows a sample three-way transition matrix for deafferented grooming; this pattern was also seen in the transition matrices of deafferented ingestive/aversive actions. The 3 patterns of simple perseveration (boxes in Table II), simple alternation (hexagons), and alternating perseveration (connected circles), together account for over 75% of all three-way transitions in Table II. The persistence of reciprocating ABB and BBA triplets after deafferentation is especially striking since deafferentation does alter the relative frequencies at least of individual ingestive and grooming actions^{1,2}. The failure of this change in probabilities of emission to abolish transitional reciprocation provides further evidence that the alternating perseveration rule is imposed despite individual action probabilities, rather than arising fortuitously from them.

Grooming chains

Both increases⁷ and decreases²² in time spent grooming have been reported to follow trigeminal deafferentation in mice⁷ and rats²². We found no change in the total number of postprandial grooming strokes emitted before and after deafferentation, although the distribution of stroke types was altered⁶. Time spent grooming presumably is affected by species and test differences, as well as by factors such as dehydration and debilitation (which we attempted to minimize by our postsurgical maintenance regimen).

A specific linear chaining rule characterizes portions of spontaneously occurring sequences of grooming by intact rats (5-9 rapid elliptical forepaw strokes over the mystacial vibrissae at

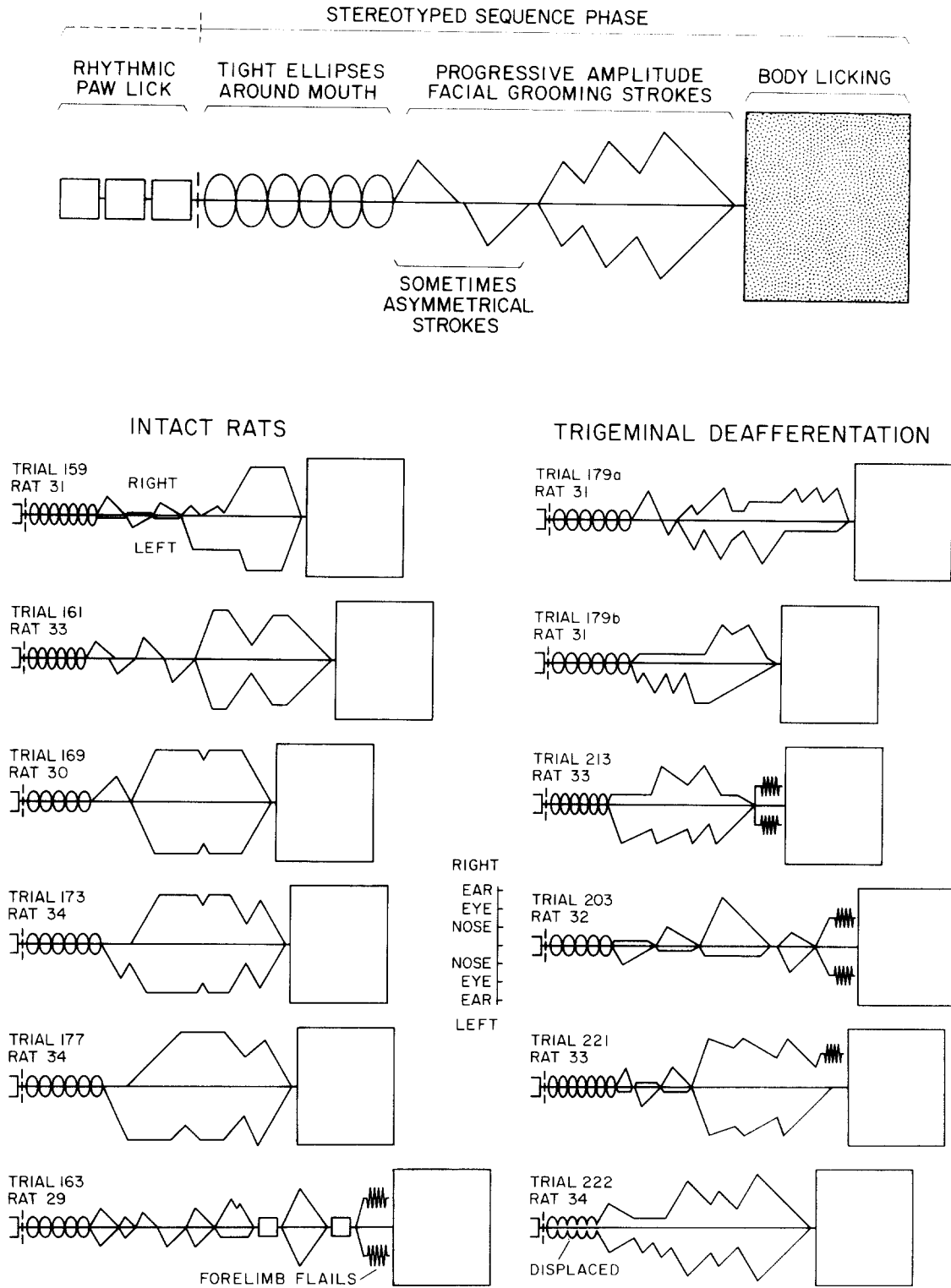


Fig. 2. Schematic and sample individual linear grooming chains observed in intact (left) and deafferented (right) rats. Deviations of the lines above and below the horizontal axis denote movements of the two forepaws upward along the face away from the nose. Forelimb flails intrude occasionally into the grooming chains especially of deafferented rats, typically after the series of forelimb strokes and before the bout of body licking.

6–7 Hz, followed by a series of slower forepaw strokes of generally ascending amplitude, followed by head tucking, turning, and body licking)^{2,3}. This chaining rule persisted after trigeminal deafferentation (Fig. 2). Neither the order, speed, number, nor amplitude of the component strokes within this sequence were altered significantly by deafferentation, although a number of changes in the amplitude and number of grooming strokes *outside* of this stereotyped linear chain have been found after trigeminal deafferentation². Once begun by the initial series of elliptical strokes at the proper frequency and location, one can predict the completion of this linear action chain with more than 90% certainty for both intact and deafferented rats.

While no changes were seen in the normal sequence components after deafferentation, however, there was a significant increase in the proportion of chains in which *new* actions intruded (Fig. 2). Approximately 25% of deafferented chains were marked by the intrusion of a pause or an action not normally seen in this sequence. A brief forelimb flail was the most common intruder. These intrusions virtually never disrupted the sequence, however, which proceeded to its normal conclusion.

The fact that the removal of somatosensory feedback does not eliminate or terminate this sequence chain shows clearly that the chain is not produced by a series of linked reflexes to somatosensory cues. The additional fact that even the improper intrusion of 'extra' actions into the chain does not terminate it suggests further that a series of *proprioceptive* reflexes cannot be the mechanism, since the performance of extra acts such as a forelimb flail must produce proprioceptive cues alien to the usual sequence. This linear chain, once begun, thus appears to reflect a strong degree of sequential central programming, which can proceed to completion in the face of a wide range of somatosensory and proprioceptive stimulus patterns.

DISCUSSION

The sequential structure of grooming and of taste-elicited ingestive/aversive actions in rats ap-

pears to be largely independent of orofacial somatosensory feedback. The overall degree of sequential stereotypy, as measured by information analysis, was essentially unchanged after bilateral trigeminal deafferentation. Similarly, the general sequencing rule of alternating perseveration, which characterizes both ingestive/aversive and grooming actions, and the specific linear chaining rule seen only in grooming, continued to remain in force after deafferentation.

These results rule out a cascading series of action reflexes to orofacial somatosensory cues as a candidate production system for these action syntax rules. They also eliminate the possibility that a 'sensory tape' system¹³ operating on orofacial tactile cues could be the mechanism that generates sequential structure. Although we have previously reported tactile feedback to be important to the control of individual action *form*², as well as to the activation of certain responses¹, the *sequential* organization of these actions appears to be characterized by a strong degree of central patterning, which does not require orofacial somatosensation. The relative independence of these emitted sequences from trigeminal tactile cues is especially interesting given that the sequential organization of *appetitive-to-consummatory*⁴ sequences involved in the approach and consumption of food and water by rats and pigeons, and in predatory capture and killing by cats, may be profoundly disrupted by trigeminal deafferentation^{14,16,22–24}.

Of course, the persistence after deafferentation of behavioral sequencing rules for grooming and taste-elicited actions should not be taken to mean that orofacial somatosensation is irrelevant to the sequential patterning of these actions. The presence of intrusions into deafferented linear chains is proof that somatosensory feedback contributes something to normal action syntax, even if that contribution is merely to inhibit the intrusion of extraneous actions into an otherwise programmed sequence. Also, it is possible that manipulations which produced orofacial somatosensory cues inappropriate to the sequence would prove more disruptive than simply eliminating somatosensation altogether: the mechanisms responsible for these sequencing rules might be more affected by

the presence of an unexpected somatosensory signal than by the mere absence of expected feedback. Whatever the hidden role of trigeminal afferent signals in guiding sequences of action, however, it is clear from these results that central neural pattern generators must exert a prime influence upon the organization of these natural actions into rule-governed sequences. A better understanding of how central structures impose these specific rules of order upon the stream of behavior will provide insight to the longstanding problem¹⁵ of how the brain organizes functional sequences of action.

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