

Progressive degradation of serial grooming chains by descending decerebration

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Rule-governed behavioral chains occur predictably within the grooming sequences of rats. Descending levels of decerebration were used to identify the minimum brain substrate needed to generate the sequential structure of a chain that connects up to 25 actions into a stereotyped grooming pattern. Full brain transections in the coronal plane isolated the decerebrate brainstem of rats at one of 3 different levels: mesencephalic (above the midbrain), metencephalic (above the hindbrain), and myelencephalic (above the medulla oblongata). Complete chain sequences were produced successfully by higher decerebrates, demonstrating that brainstem circuitry suffices for the basic generation of this sequential pattern. The pattern of sequential degradation across lower transection levels was gradual and continuous, raising the possibility that the generating circuitry for this chain may not be localized at a single level within the brainstem but rather may be distributed across the hindbrain as a degenerate or parallel network. The competence of this network appears to be reduced merely in increments by descending transections. This possibility is compared to localized generator alternatives.

INTRODUCTION

Natural action is a flow of coordinated movement patterns. When complex sequences are created from simpler behavioral elements, each element must be connected to the next in an ordered fashion. Behavior from the natural species-specific action repertoires of animals provides an especially rich source for obtaining a basic understanding of how the brain organizes elemental actions into patterned sequences^{9,11,18,20,24}. Natural action allows syntactic processes of sequence control²⁶ to be isolated and examined, without the use of training procedures, and relatively independent of the learning and memory processes on which trained action sequences depend.

Rodent grooming contains many natural instances of complex and temporally prolonged sequential patterns^{4,8,15–17,29,31}. The neural control of grooming patterns is also complex, and relevant mechanisms are embedded at many levels of the nervous system. Lesions of rostral forebrain structures, such as the orbital frontal cortex²⁴ or the corpus striatum⁶, can produce alterations in grooming patterns and temporal organization. Yet the individual actions that constitute grooming can be generated by the isolated brainstem, transected below the hypothalamus^{1,2,7,19,20,34} and even decerebrate animals can generate prolonged bouts of grooming^{2,7,19}.

Rule-governed patterns of sequential organization can be discerned within the normal grooming bouts of rodents^{4,15,17,29}. These pat-

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terns include tendencies to direct actions progressively from rostral to more caudal body parts as a bout proceeds²⁹, to make reciprocal transitions among different action types^{4,5}, and to combine elemental actions into larger hierarchical combinations^{4,16,17}, some of which result in tightly structured serial chains of extraordinary stereotypy³⁻⁶. The highest degree of sequential stereotypy is seen in a concatenation of 10–25 separate actions, which combine to form a structured transition between face and body grooming⁴. This pattern, which will be referred to as a syntactic chain, occurs at least 13,000 times more often than chance⁴, and organizes its component actions into four phases. The chain begins with Phase I: a bout of 5–9 rapid elliptical forepaw strokes performed bilaterally over the nose and mystacial vibrissae at a rate of 6–7 Hz. The bout of bilateral ellipses is followed immediately by Phase II: a short series of 1–4 slower strokes of small to intermediate amplitude made unilaterally with one paw or asymmetrically with both paws at different amplitudes. These are followed by Phase III: a series of large amplitude forelimb strokes, bilateral and typically symmetrical with respect to forepaw trajectory, which ascend beyond the level of the ear before being pulled over the face. The chain is then completed with Phase IV: a tucking of the head and shifting of posture to bring the head into contact with the ventral or lateral torso for a bout of body licking, which terminates the chain and transfers the animal to body grooming. Although slight variations in the details of the chain may occur from instance to instance, the basic structure of the chain and the order of its phases are essentially rigid (see Fig. 2A). Once an initiating bout of ellipses has begun, it is possible to predict the serial occurrence of the rest of the phases, leading finally to body licking, with 85–95% certainty for normal rats⁴. The stereotypy of the patterned components indicates a high degree of control, but this control does not depend upon tactile sensory feedback from the trajectory of the paws over the face. Elimination of tactile feedback from the face by trigeminal sensory deafferentation does not impair pattern completion^{3,5}, even though other aspects of grooming may be altered^{3,16}.

The probability of chain completion is reduced by central lesions of the forebrain corpus striatum⁶. The striatum has traditionally been considered to be part of the brain's extrapyramidal motor system, and has been suggested to participate in serial patterning (e.g. refs. 10,14,25,28,32). Striatopallidal lesions appear to disrupt the sequential organization of the chain in a relatively specific fashion. The total number of grooming actions and the rate of *initiation* of chains need not be reduced even in rats that fail to complete a substantial proportion of chain sequences. The interpretation of focal lesion effects is complex, however, and the disruption of patterning by striatal lesions should not be taken to mean necessarily that the pattern itself is *generated* there^{1,6,20,34}. An alternative explanation for the disruption of serial chain completion after striatal damage is that striatal circuits may facilitate the implementation of sequential patterning rules that are generated elsewhere in the brain⁶. This implementation might involve the phasic modulation of sensorimotor systems by the corpus striatum (e.g. refs. 10,23,27,33), in a way that would shift the balance of action control hierarchically between sensory guided and central pattern generating systems. A phasic shift in the sensorimotor vs central patterning control of action has been implicated in the production of stereotyped grooming chains: unlike most grooming actions, forelimb strokes and licks that occur during syntactic chains are relatively immune to certain distortion effects induced by trigeminal deafferentation³.

The 'hierarchical controller' explanation of striatal control of syntactic chaining can remain plausible, however, only if the basic sequential structure of chains can be shown to be generated by non-striatal neural systems. Since mesencephalic decerebrates have been shown to be capable of engaging in prolonged grooming bouts of coordinated appearance^{2,3,19}, it is reasonable to ask whether caudal brainstem systems possess the capacity to generate syntactic chain sequences without assistance from striatal or related forebrain circuits. A 'levels of transection' approach was used here to identify the minimum neural substrate needed to generate the syntactic struc-

ture of stereotyped serial chains. The brainstem was isolated by transection at one of three levels, and the capacity to produce syntactic grooming chains was assessed beginning two weeks later. Decerebration levels, named by reference to the highest structure remaining, were: mesencephalic (transection at the caudal border of the diencephalon; leaving midbrain, pons, cerebellum, and medulla), metencephalic (transection at the midbrain-pontine junction; leaving pons, cerebellum, and medulla), and myelencephalic (transection at the pontine-medullary junction, severing most cerebellar connections; leaving an isolated medulla oblongata).

MATERIALS AND METHODS

Surgery

Decerebration was accomplished by spatula transection in the coronal plane. Mesencephalic and metencephalic decerebrations were performed in two unilateral stages 1 week apart, in order to promote recovery and survival. Myelencephalic decerebrations were performed in a single bilateral procedure, because pilot observations had shown that unilateral myelencephalic recovery was poor and that a 2-stage procedure had no advantages at this level.

Male Sprague-Dawley rats (300–400 g), pretreated with atropine sulfate (0.3 mg) and bicillin (30,000 μ), were anesthetized with ketamine (100 mg/kg) and xylazine (10 mg/kg). The dorsal skull was exposed, and bregma and lambda arranged in a level horizontal plane. Mesencephalic transections were made using the procedure of Grill and Norgren²⁰. Metencephalic and myelencephalic transections were made using a modification of this procedure.

Mesencephalic transections. A unilateral transverse slit was drilled in a plane that lay 40% of the distance from lambda to bregma, beginning medially 1 mm from midline and proceeding laterally to the rim of the skull. The dura mater was opened. An L-shaped spatula (base 3 mm [bottom length] \times 4 mm [height] \times 1.5 mm [top length]) was lowered into the slit at the medial point, with the foot of the L facing medially. This spatula was moved up-and-down and laterally in a continuous

motion until the spatula reached the lateral rim. The spatula was reversed, so that the L pointed laterally, and the procedure was repeated. This procedure produced a complete hemispheric transection but spared the sagittal sinus along the medial dorsal surface, so that bleeding was minimal. The spatula was removed, the skull slit filled with saline-soaked gelfoam, and the wound was sutured. This procedure was repeated on the opposite side after 7 days recovery.

Metencephalic transections. A unilateral transverse slit was drilled in a plane that lay 9.5 mm posterior to bregma, from midline to the lateral rim, and the dura was opened. This procedure typically resulted in piercing of the transverse sinus, and bleeding was controlled with gelfoam. A hemispheric transection was made as above, and repeated on the contralateral side after 7 days. Artificial respiration was not generally needed after mesencephalic or metencephalic transections.

Myelencephalic transections. After bregma and lambda were arranged horizontally, a bilateral slit was drilled in a plane 12.2 mm posterior to bregma. The mouth bar was then lowered 3 mm, to keep the plane of transection perpendicular to the longitudinal axis of the hindbrain. The rat was respirated artificially (Harvard small animal respirator) beginning immediately prior to transection. The dura was opened, and a complete transection was performed bilaterally. Breathing typically recovered within 5 min after transection, and the rat was removed from the respirator. All decerebrates were warmed and kept at a minimum body temperature of 31 °C for the first 12 h after surgery.

Surgical control group. Ten intact control rats were pretreated and anesthetized. Skull slits were drilled and the dura was opened as above (4 rats at the mesencephalic level, 3 at the metencephalic level, and 3 at the myelencephalic level) to form a single control group for comparison.

Postsurgical maintenance

All decerebrates were nourished by 3 daily intragastric feedings of a liquid diet (equal parts sweetened condensed milk and water, with a vitamin supplement). Meal volume began at 6 ml

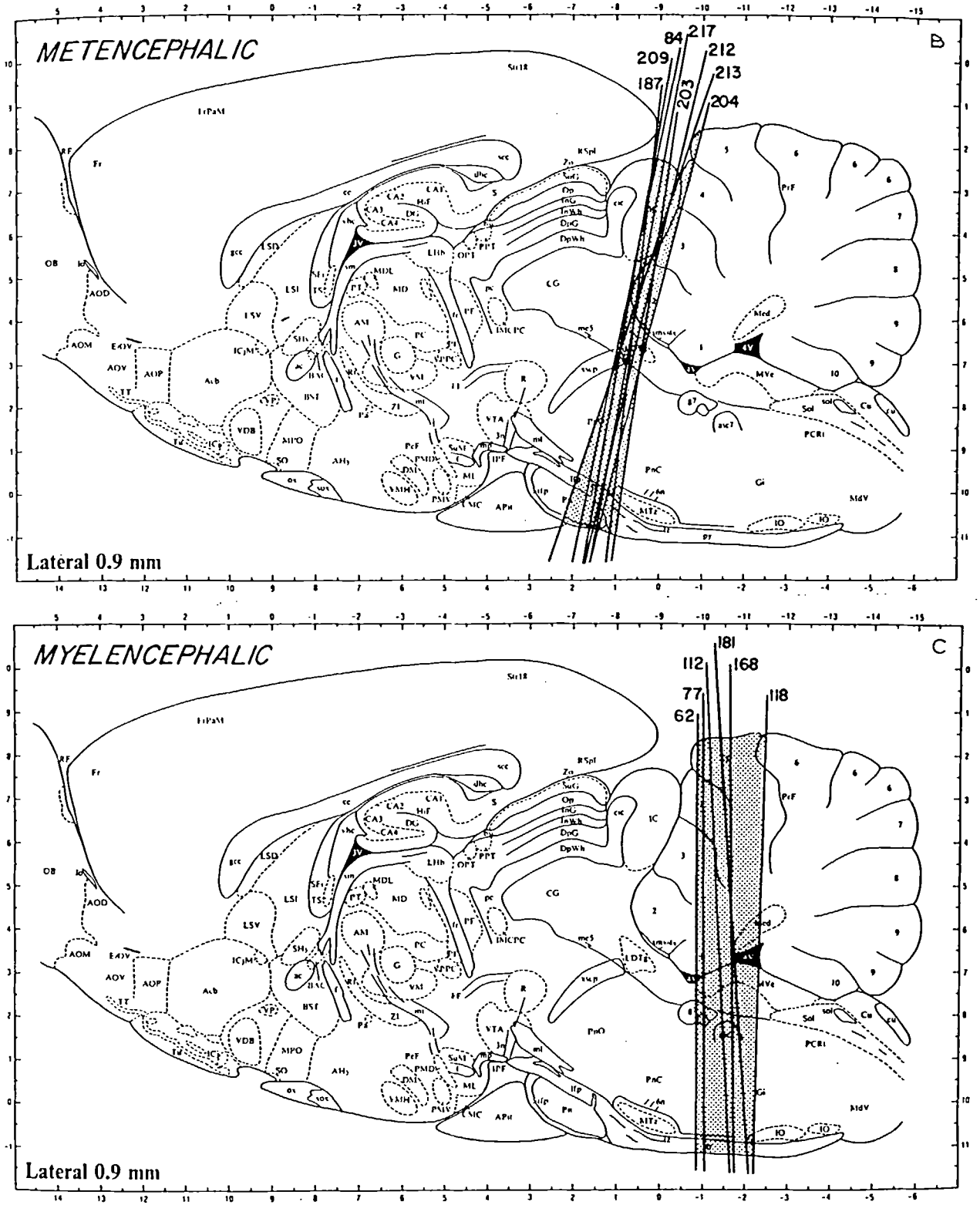


Fig. 1. Descending levels of transection. A: range and individual transections for mesencephalic decerebrate brains. Numbered lines denote the level of transection for individual rats. B: metencephalic transections. C: myelencephalic transections.

stroke over the nose and mystacial vibrissae at a speed faster than 7 Hz (i.e. a stroke duration of less than 140 ms), or else of the sequential occurrence of Phase II (unilateral, small amplitude stroke), Phase III (bilateral, large amplitude stroke), and Phase IV (body lick) actions in consecutive order with no intervening non-chain actions. This criterion was more liberal than that used in earlier studies (e.g. refs. 5,6) in order to allow the inclusion of myelencephalic sequences. Chains were analyzed for frequency, duration, component action number, and completion rates, and notated chains from each group were visually compared.

Histology

Decerebrates that survived to the end of testing were deeply anesthetized and perfused intracardially. Their brains were removed, frozen, sectioned in the sagittal plane (50 μ m), and stained with Cresyl violet. The heads of rats that died during the experiment were removed and immersion perfused for two weeks before sectioning. The level and completeness of transection was verified for each brain (Fig. 1).

RESULTS

General

Ten mesencephalic decerebrates, 8 metencephalics, and 6 myelencephalics survived to complete testing. The longest surviving mesencephalic and metencephalic decerebrates lived for 13 and 10 weeks respectively, when they were sacrificed. The appearance of these rats was generally good: they often sat upright or rested in a hunched or relaxed crouch on 4 paws, could right themselves when placed on their side, engaged spontaneously in grooming bouts, and would orient and walk a few steps in response to a light tapping, sound, or to tail pinch^{1,2,20,34}. Metencephalic decerebrates showed a slight but detectable extensor rigidity, especially in the hindlimbs, that was lacking in mesencephalics. Metencephalic decerebrates also failed to orient to sound, although they would startle to a loud noise. Myelencephalic decerebrates, in comparison, were impaired much more dramatically. These decerebrates showed

pronounced forelimb extensor rigidity, which resulted in the paws being held in a 'crossed' left/right reversed position, and hindlimb rigidity that was even more severe. Rigidity declined somewhat over recovery in both metencephalic and myelencephalic decerebrates, but hindlimb rigidity never disappeared even in the myelencephalic that lived longest (6 weeks). Myelencephalic decerebrates never attempted to right themselves, but lay on their side on their bedding (which was always kept clean). Nonetheless, if they were supported and their forelimbs freed, even myelencephalic decerebrates showed vigorous and coordinated strokes and headshakes to a water mist.

Grooming

As other studies have shown, mesencephalic decerebrates engaged in extended bouts of face and body grooming, with bout frequencies and durations similar though not identical to intact rats^{2,19}. The general rostrocaudal progression in the distribution of grooming actions over the face and body, which characterizes normal grooming bouts^{29,31}, could also be discerned to varying degrees in mesencephalic and metencephalic decerebrates^{2,19}. Myelencephalic decerebrates never groomed spontaneously in the home cage, though they would occasionally emit a short series of unilateral paw swipes. When postural support was provided, however, myelencephalics would engage in bouts of grooming of up to 30 s duration, with good bilateral coordination between the two forepaws.

Production of syntactic grooming chains: initiation and completion

Syntactic grooming chains were initiated by intact control rats at a rate of roughly 4 chains per 5 min of grooming (0.87 chains per min). Mesencephalic and metencephalic decerebrate rats initiated syntactic chains at similar rates (mesencephalic = 0.60, metencephalic = 0.66), which did not differ significantly from normal (Kruskal-Wallis $H = 1.8$, $P > 0.1$). The rate of chain initiation did vary across groups when myelencephalic decerebrates were considered ($H = 6.3$, $P < 0.001$), however, and myelence-

phalic decerebrates had significantly lower chain initiation rates (0.26 per min) than controls (Mann–Whitney U , $P < 0.02$).

Although the chain *initiation* rates of mesencephalic and metencephalic decerebrates were comparable to normal, the percentages of those initiated chains that were completed syntactically were not (ANOVA $F_{2,23} = 8.6$, $P < 0.002$). Syntactic chain completion was below the normal 85% rate for both mesencephalic (completion rate 59%; Newman–Keuls $P < 0.05$) and metencephalic (completion rate 43%; Newman–Keuls $P < 0.01$) decerebrates. This degree of impairment is comparable to that produced by large lesions of the corpus striatum⁶.

The central question for this study, however, was whether the isolated brainstem retained the capacity to generate the basic sequential structure of syntactic grooming chains. Fig. 2 shows that the answer to this question is unequivocally yes for both mesencephalic and metencephalic decerebrates. Myelencephalic decerebrates, in contrast, never produced a complete syntactic chain with all 4 phases in proper serial order.

Structural detail of syntactic chains

Inspection of the notated microstructure of actual syntactic chains produced by each group (Fig. 2) allows a more complete understanding of the effects of decerebration on action sequence.

The completed chains of mesencephalic decerebrates (Fig. 2B) included a number of sequences that appeared to be within the normal range of chain variation shown by intact rats. Completed mesencephalic chains did not differ from the completed chains of normal controls either in duration latency from Phase I initiation to Phase IV (body lick) consummation (mesencephalic mean \pm S.E.M. = 4.3 ± 1.2 s; intact = 3.7 ± 0.5 s) or in the total number of forelimb strokes constituting the sequence (mesencephalic = 23.4 ± 2.6 ; intact = 25.7 ± 3.1 [a bilateral stroke made with two paws was counted as two separate strokes for this analysis]).

The completed chains of metencephalic decerebrates, on the other hand, did tend to be distorted both structurally and temporally. Metencephalic chains lacked the strong bilateral sym-

metry that characterized the structure of normal syntactic chains, and included many prolonged runs of unilateral strokes in Phase III (Fig. 2C). Metencephalic chains also differed in latency to Phase IV completion (Kruskal–Wallis, $P < 0.02$). Specifically, metencephalic chains tended to be prolonged in duration compared to intact ones (5.2 ± 0.5 ; Mann–Whitney, $P < 0.05$), and included many instances of over twice normal duration. Although Fig. 2C appears to show that these longer metencephalic chains also contained more strokes, this is an illusion resulting from temporal expansion and actually is not the case. Counting strokes in terms of acceleration ‘zero-crossings’ (i.e. a change from an ascending to a descending stroke, represented by peaks in the notated graphs), total stroke number did not differ among intact, mesencephalic, and metencephalic groups (Kruskal–Wallis, $P > 0.1$). Instead the shorter duration of intact chains appears to compress strokes together and superimpose peaks into ‘blips’ on a continuous plateau of Phase III strokes, while the same peaks stand apart as separate mountains in the expanded metencephalic chains.

The isolated medulla of the myelencephalic decerebrates never produced a complete chain with all 4 Phases in order, even in a structurally or temporally distorted form. On the other hand, sequential chain organization was not lost completely in myelencephalic decerebrates, or even simply fragmented (in the sense that only one or two phases might have persisted). Instead, myelencephalic rats showed an extremely variable array of partial and whole chain skeletons, which were degraded sequentially as well as in form (Fig. 2D). Each separate phase was observed at different times in the grooming of these rats, and syntactic combination of phases occurred often. The syntactic combinations produced by myelencephalic rats included frequent coupling of Phases 1 \rightarrow 2, 2 \rightarrow 3, and even 1 \rightarrow 2 \rightarrow 3, and ‘omission’ couplings such as 1 \rightarrow 3, or 1 \rightarrow 2 \rightarrow 4. Perhaps most intriguing was an instance of a complete but ‘inverted’ or sequentially backwards chain (4 \rightarrow 3 \rightarrow 2 \rightarrow 1; Fig. 2D). A complete sequential inversion of this sort has never been observed by us in an intact rat. The generation of syntactic

couplings persisted despite the postural deficits and severe extensor rigidity of myelencephalic decerebrates, which often caused the left and right forepaws to cross and to execute strokes on the opposite sides of the face. The persistence of

residual syntactic organization, despite the disruption of proprioceptive and tactile feedback that such crossing would produce, attests to the strong degree of pattern generation remaining even in the myelencephalic decerebrate.

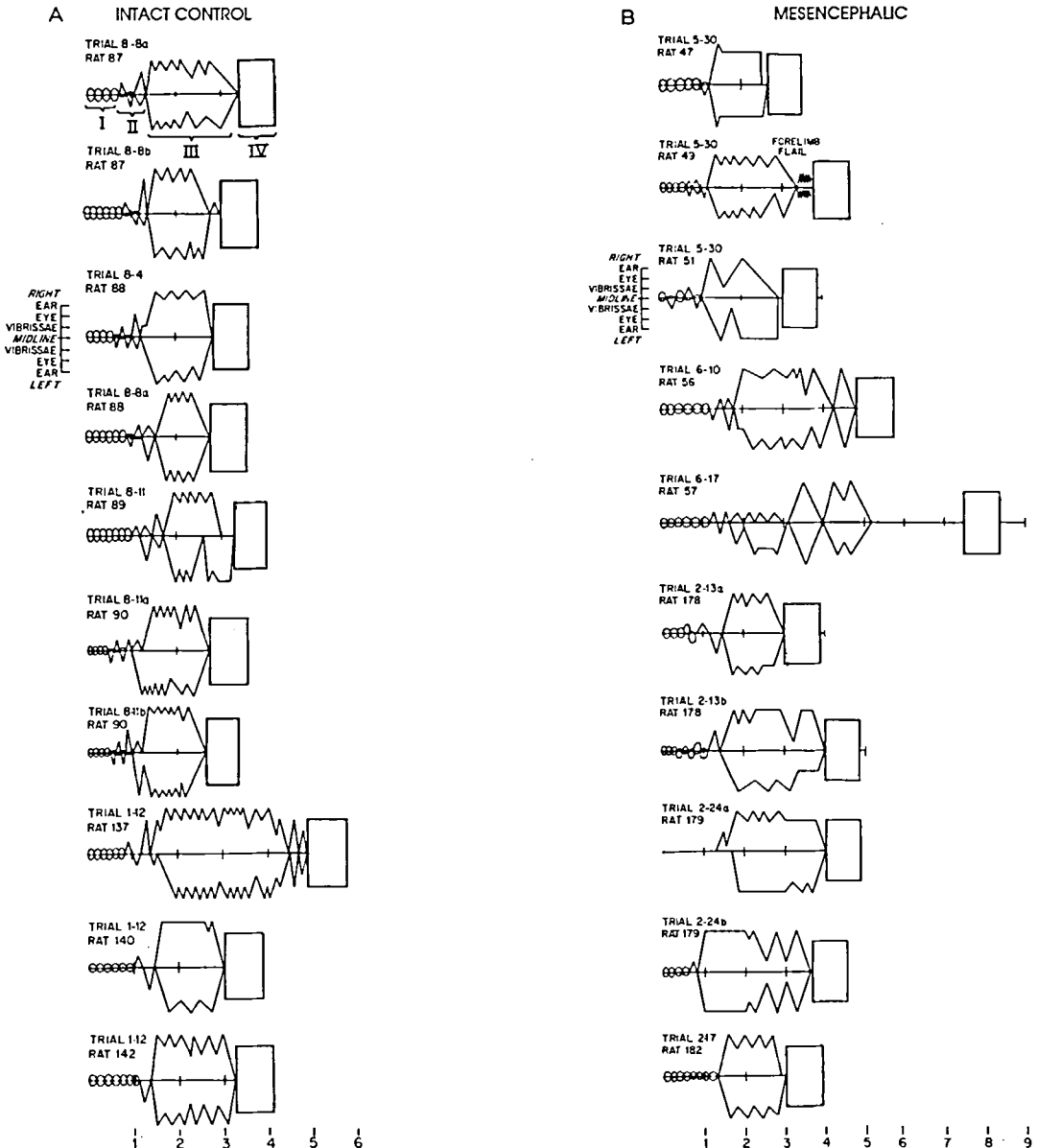


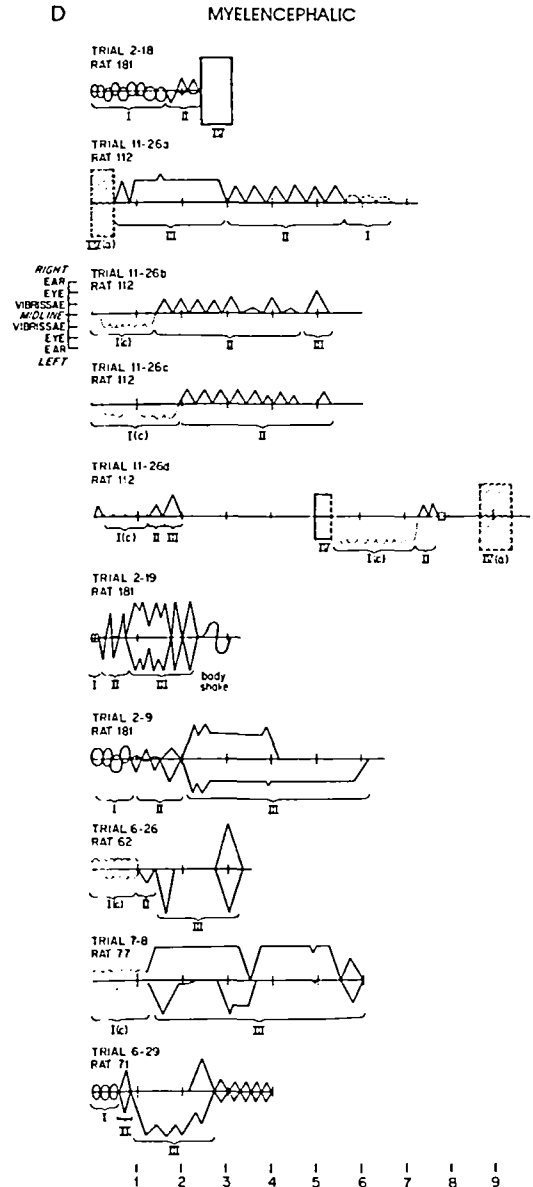
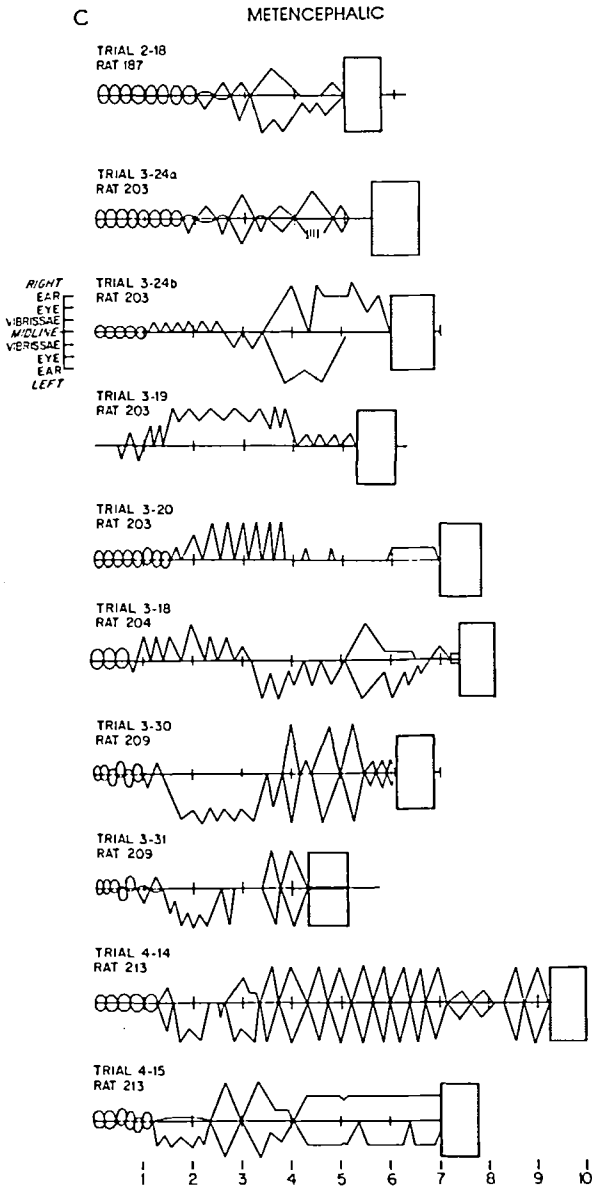
Fig. 2. Notated syntactic chains. Time proceeds from the left to right (seconds noted beneath). A: intact control chains: forepaw trajectories along the face are depicted relative to the position of the nose midline. The tip of the nose is represented by the horizontal axis. Deviation of the line above the axis depicts the shape, amplitude and duration of right paw movements upwards and downwards along the face (see legend at left for degrees of amplitude); deviation of the line below the horizontal axis depicts the same information for the left paw. Large boxes denote instances of body licking. Phases I, II, III, and IV are labeled for the chain at the top. Decerebrate chains: the 10 best chains from each group are represented. B: mesencephalic – note the intrusion of a bilateral forelimb flail (rapid shaking of forepaws, represented by zigzag line) after Phase III [rat 49], the intrusion

DISCUSSION

Forebrain vs brainstem systems of chaining

These observations demonstrate that the brainstem below the midbrain contains mecha-

nisms sufficient for specifying the basic sequential structure of syntactic grooming chains. Both mesencephalic and metencephalic decerebrate rats were capable of generating complete chain sequences, containing dozens of actions organized



of a unilateral stroke into the Phase I series of ellipses [rat 51], and the asymmetry of certain Phase I ellipses [rat 178]. C: metencephalic – note the temporal prolongation of most chains, the marked asymmetry of many Phase III strokes [rats 203, 204, 209], and the continued asymmetry (and one omission) of Phase I ellipses [rats 203, 209, 213]. C: myelencephalic – all sequential phases are labeled to aid the reader. Note the Phase I (c) ‘crossed ellipses’, where left and right paws execute strokes on the opposite sides of the face (crossed trajectories depicted by dotted lines [rats 62, 77, 112]), and the Phase IV (a) ‘attempted’ body licks, where the head is lowered and the tongue protruded but no contact is made, depicted by large hatched boxes [rat 112]. Also note instances of ‘omission couplings’ [rats 77, 112, 181] and sequential ‘inversion’ [rat 112].

syntactically into 4 serial phases. Forebrain circuits are clearly not *required* for the basic specification of this sequential pattern.

This claim for brainstem competence in sequencing is based narrowly upon the *best instances* of decerebrate sequential patterns, rather than upon their typical products, and should not be taken to mean that forebrain systems are not involved in syntactic chaining. Although midbrain and hindbrain decerebrates can generate this basic sequential pattern, the normal implementation of the pattern requires forebrain systems. The efficiency of pattern completion in mesencephalic and metencephalic rats was reduced to roughly 50% the normal rate. Equivalent disruptions of chain implementation have been produced merely by restricted forebrain lesions of the corpus striatum⁶ or of the nigrostriatal dopamine projection (in preparation). A major challenge remaining is to formulate and identify ways that forebrain systems could contribute to syntactic rule implementation beyond mere sequence generation. One possible way might involve the dynamic modulation of hierarchical sensorimotor controls (see ref. 6) but other alternatives are possible. One alternative would be for forebrain circuits to act as auxiliary pattern generators within a larger degenerate system (see below).

Nature of brainstem syntactic chain generation

The concept of a 'neural pattern generating center' has traditionally provided a powerful explanatory device for mammalian behavioral patterns that are relatively stereotyped and independent of sensory guidance¹¹. Whether conceived as a localized, discrete center or as a distributed, serial circuit, the concept of a distinct set of neurons that are dedicated to the task of generating a particular movement pattern has guided investigators and proven useful in understanding the neural basis of actions ranging from swallowing to locomotion (e.g. refs. 11,21).

The concept of a dedicated sequential patterning center applied to syntactic grooming chains translates straightforwardly into a prediction for this descending transection study: if the central patterning circuit lies within the brainstem, then transections above it should preserve the ability to

generate the essential structure of the chain. Transections that intrude below the patterning circuit and isolate it from spinal systems, conversely, should eliminate the ability of the circuit to execute the pattern. Transections that encroach upon but do not entirely disrupt a localized patterning circuit might be expected to produce intermediate effects; however, a shift to a slightly more caudal transection ought then to resolve into a complete disruption. Even if we expand the list of possible outcomes by imagining a cascade of connected subcircuits, in which each subcircuit is responsible for generating only a portion of the chain's detailed structure, the above predictions hold true with only slight modifications. Descending transections ought to be able to fragment the sequential structure of grooming chains generated by a serial cascade of component sequences but only by removing segments as 'all-or-none' entities, as their respective subcircuits are successively interrupted.

With these predictions in mind, it becomes somewhat difficult for a 'single center' or 'serial circuit' generator hypothesis to account for the observed pattern of changes in sequential organization produced by descending decerebration. The gradually increasing degree of structural and sequential degradation produced by more caudal transections, the extreme range of serial variability of myelencephalic chains, together with the survival of constituent couplings and even of a loose global structure evidenced by omission couplings and by inversion, all point to a gradual and general degradation of the chain pattern as the available neural substrate shrinks, rather than to an elimination of any specific sequential portion. A 'generating center' hypothesis is somewhat challenged to reconcile these observations. Consider, for example, the ability of the metencephalic decerebrate to generate chains with each phase serially ordered. This demonstrates that a fundamental generating circuit for this pattern is contained within the hindbrain. The increased incidence of structural and temporal irregularities, however, indicates that the ability of pontine-medullary circuits to control the pattern is limited. The temporal prolongation of the metencephalic pattern suggests a reduction of efficiency, and the

relative loss of symmetry among Phase III strokes indicates a further deterioration of control. One interpretation of the irregularities of metencephalic chains might have been that the pattern-generating circuit had been disrupted marginally at the pontine level, and that the deteriorated metencephalic performance was a direct reflection of a degraded sequencing signal. But if the pattern-generating circuit lay substantially within the rostral pons and was slightly impaired by the metencephalic 'suprapontine' transection, then one would expect myelencephalic decerebrates that lacked a pons to also lack completely the global structure of the sequential pattern. Yet this does not seem to be the case. Myelencephalic decerebrates retained not only separate chain phases, but also syntactic couplings among most phase combinations. Myelencephalic decerebrates even showed a tendency to produce 'omission' sequences with missing phases but with preserved syntactic relations among those segments present, indicating a degree of global syntactic structure able to cope with missing elements. These observations strongly favor the conclusion that even the isolated medulla oblongata retains a degraded but significant capacity for specifying diverse aspects of chain structure, even though not a single entire chain was generated by myelencephalic decerebrates in many hours of observation.

This paradox raises the possibility that the neural generation of sequential chains might not be best explained by positing a discrete generating circuit that can be completely localized or interrupted at any single level of the neuroaxis. It may be reasonable to consider other alternatives. A very different alternative to a localized center or dedicated serial circuit concept of pattern generation is offered by 'degenerate' or 'parallel distributed processing' models of pattern specification^{12,13,22,30}. These models hold that patterns are coded not by the serial activation of distinct and dedicated elements, but instead by large pools of many patterning circuits, connected more or less in parallel. The population of elements is viewed as highly homogeneous, each circuit partly but not fully redundant with the next, and patterning is accomplished by the population as a whole

rather than by assigning specific sequencing functions to separate elements. Although these models have focused especially on pattern *recognition*, rather than production, and have had greatest success with non-sequential patterns²², the essential model may be applicable also to the production of complex action syntax. As Edelman argues, 'The units of action are not muscles or joints or simple feedback loops but functional complexes or synergies (patterns of movement)... such gestures must be considered as *patterns to be recognized* by somatic selection in the nervous system,'¹³ (pages 220-221). Adapting a degenerate model to grooming, one would posit that the generation of sequential chains could be controlled by a hindbrain population network of partially redundant circuits connected in parallel, rather than by a single command circuit. If the population of parallel circuits were distributed along the rostral-caudal axis of the brainstem, then this system would not be halted by a discrete neural transection so long as a portion of the population of generating circuits remained intact. The output of the system would be globally degraded, however, to a degree proportional to the quantity of degenerate circuits lost. This prediction appears to accurately describe the consequences of descending decerebration. If this means that a degenerate model may be true for sequential patterning by the hindbrain, then it should be noted that it opens the way also for an extension of the distributed system rostrally into the forebrain: even striatal circuits relevant to chaining might participate in such a parallel patterning network (but see ref. 6 for an alternative interpretation).

Although the effects of decerebration on sequencing are consistent with a degenerate model of sequential patterning, they do not yet compel such a view. One can also imagine a compromise between these two different models in which each might apply to different aspects of pattern control. It is conceivable, for instance, that a localized pattern-generating circuit might exist largely within the myelencephalic medulla but have only reduced and ineffective control of motor output in the absence of rostral structures. Just as the degree of decerebrate motor rigidity appears in-

versely proportional to the level of transection, it might be that lower transections entail greater loss of control of secondary execution or 'motor tone' mechanisms required to translate a patterned signal from a localized medulla generating center into a corresponding pattern of spinal activity and muscular contraction. This 'secondary motor' account retains an aspect of distributed processing, which would be degraded only gradually by descending decerebration, but it assigns this aspect to a secondary or 'clutch' stage that translates the motor signal into action rather than to the generation of the signal itself (which would be assigned entirely to the myelencephalon). While it is not clear which of these explanations more closely approximates the truth, it is reasonable to believe that an adequate explanation will share some features with both the central patterning circuit and the degenerate system model. Future investigations of pattern generation within the hindbrain may help to identify the features that are described by each.

Summary

The production of syntactic grooming chains by mesencephalic and metencephalic decerebrates demonstrates that the minimum neural circuitry required for the basic specification of this serial action pattern is contained within the sub-mesencephalic hindbrain. The progressive degradation of chaining by descending metencephalic and myelencephalic transections, together with the preservation of a primitive global structure even in chain-like myelencephalic sequences, suggests that some aspect of this circuitry may be better described by degenerate or parallel principles of organization than by traditional concepts of local or serial-circuit pattern-generating centers. In broader perspective, these observations indicate a sophisticated hindbrain capacity for sequential behavioral organization and they are consistent with recent contentions that degenerate neural networks may play an important role in the production of behavior.

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