

ONTOGENY OF ACTION SYNTAX IN ALTRICIAL AND PRECOICIAL RODENTS: GROOMING SEQUENCES OF RAT AND GUINEA PIG PUPS

by

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Summary

Behavior occurs as coordinated patterns of serial order, with rules of 'action syntax'. Grooming behavior of adult rodents provides several striking examples of action syntax rules. The most stereotyped of these is a 'syntactic chain' pattern, which organizes up to 25 facial strokes and licking movements into a predictable sequence. This pattern previously has been found to be emitted by diverse rodent species from all major suborders: myomorph, sciurormorph, and caviomorph. In this study, we compared the postnatal ontogeny of grooming syntax in two rodent species: rat *versus* guinea pig. Rats are relatively altricial at birth, whereas guinea pigs are precocial. A day-by-day study of the fine-grain structure of sequential patterns was carried out during the first three weeks after birth, using slow-motion videoanalyses and a choreographic notation system for scoring behavioral grooming sequences. The results showed that substantial action syntax rules exist in guinea pig grooming even on the day of birth. For guinea pigs, postnatal grooming syntax development was limited to minor increments in the strength of the syntactic pattern and in postural control. By contrast, for rat pups, action syntax did not begin to appear until the second postnatal week, and developed gradually into the third week. The development of rodent syntactic patterns in both species appeared to be independent of the maturation

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of the movements that composed the pattern. Our results indicate that action syntax rules develop as hierarchical entities independent from constituent movements.

Keywords: neonatal, development, rat, guinea pig, grooming, movement, ontogeny, sequence, syntax, neostriatum, dopamine, action.

Introduction

Serial organization is a pervasive feature of behavior. In order to be functionally effective, action must be organized into efficient sequences. Species-typical patterns of behavior, such as self-grooming by rodents, provide a useful source for the study of serial organization and control because of their often strong degree of sequential lawfulness.

Grooming by rodents comprises many types of movement. Forelimb strokes over the face and body, postural adjustments, coordinated licking of the paws, limbs, and body, are linked together into various sequences (*e.g.* Moore & Rogers, 1984; Fentress, 1988; Sachs, 1988). The sequential organization of grooming movements is organized by pattern-generating rules (Fentress, 1972; Fentress & Stilwell, 1973; Richmond & Sachs, 1980; Berridge, 1990; Fentress, 1992). These rules can be viewed as a 'syntax of action' (Lashley, 1960). They are generalized schemas of sequential coordination that can be imposed on a wide variety of specific acts.

Some grooming syntax rules are anatomically-based. These may arise as a relatively passive consequence of physical body shape. For example, adjoining body parts are groomed in series, and contiguous body parts are groomed sequentially in a cephalocaudal direction (Richmond & Sachs, 1980; Ferron & Lefebvre, 1982; Thiessen *et al.*, 1983; Moyaho *et al.*, 1995). Other rules do not appear to arise obviously from the anatomy of body parts, but rather are imposed on the flow of action as relatively arbitrary yet predictable patterns. These endogenous patterns of action syntax range from abstract rules, such as perseveration and bout alternation, to stereotyped syntactic chains whose particular moment-to-moment serial pattern can be predicted with great accuracy (Fentress, 1972; Fentress & Stilwell, 1973; Berridge & Fentress, 1986; Berridge, 1990; Fentress, 1992). Endogenous syntax patterns are especially valuable for studies of how the brain imposes sequential patterns upon action. Endogenous patterns must be actively imposed, despite available alternatives, upon the flow of action.

The presence of endogenous patterns in behavioral sequences thus reveals the nervous system's competence to actively impose sequential order. For developmental studies, they thus serve as a useful indicator of maturational competence of systems that impose sequential coordination.

Syntactic chains of grooming actions

The most predictable and stereotyped grooming sequence is a 'syntactic chain' pattern (Berridge & Fentress, 1986), which occurs during grooming 13 000 times more often than would be expected by chance based on the relative frequencies of component actions (Berridge *et al.*, 1987). This stereotyped sequence is only one of many aspects of grooming syntax, but its 'tip of the iceberg' visibility makes it especially valuable for studies of sequential competence. Syntactic chains connect 15 to 25 distinct stroke and lick components into a concatenation of four phases (Fig. 1). As orig-

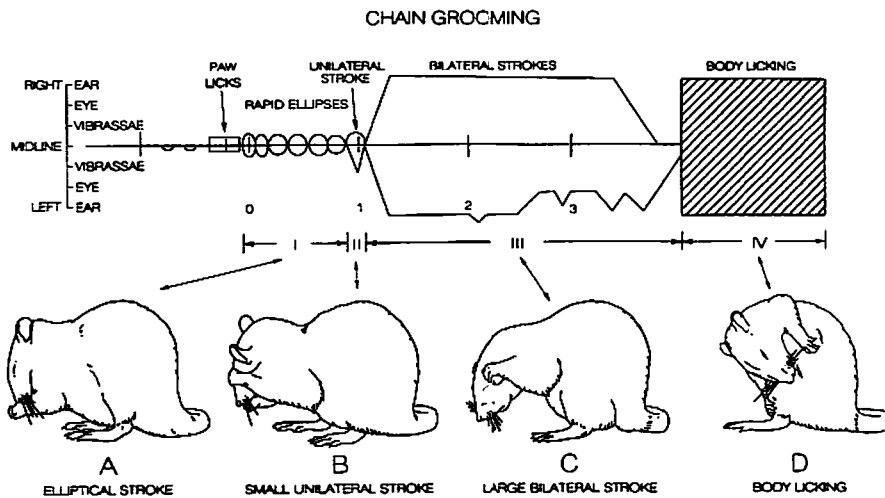


Fig. 1. A syntactic grooming chain performed by an adult rat. Choreographic notation (top) depicts the moment by moment trajectories of component paw strokes over the face and the occurrence of other grooming movements. Drawings (bottom) depict a 'snapshot' of the representative actions that compose the four syntactic phases. Time proceeds from left to right. The horizontal axis of the choreographic notation represents the center of the nose. The line above the horizontal axis denotes trajectory of the right forepaw along the face; the line below the axis denotes trajectory of the left forepaw. Small rectangles denote paw licks. Large rectangle denotes body licks. Adapted from Aldridge *et al.* (1990).

inally described for rats. Phase I consists of 5-7 elliptical paw trajectories traced around the tip of the nose, usually at a rate faster than 6 Hz. Phase II consists of 1 to 3 small strokes traced by a single paw over the lower half of the face. The paw not performing the stroke will often continue to trace out an ellipse more tightly around the nose. Phase III consists of a series of many large amplitude strokes performed symmetrically by both paws over the entire face, often reaching above the ear. Phase IV consists of a postural shift in which the rat turns and lowers its head, and then begins a bout of torso or flank licking. The first three phases typically are completed within 3-5 s; the fourth phase may persist for more than 30 s. The chain is regarded as 'syntactically complete' after Phases I, II, and III are emitted and Phase IV has been initiated (Berridge *et al.*, 1987; Berridge & Fentress, 1988).

This highly stereotyped pattern is emitted with only minor variation by rodents from diverse species and suborders: mice, deer mice, hamsters, and gerbils (*Myomorpha* suborder), ground squirrels (*Sciuromorpha* suborder), and guinea pigs (*Caviomorpha* suborder). Each species has its own 'signature', an idiosyncratic way of forming constituent actions that can be seen when grooming movements are transcribed by a choreographic analysis, but all species follow the same syntactic schema for arranging the serial order of actions within the chain (Berridge, 1990). Approximately 80% to 90% of chains begun by normal adult rats are completed syntactically through Phase IV. For normal adult guinea pigs syntactic completion rises to 100% (*e.g.* Berridge, 1990; Berridge & Whishaw, 1992).

Ontogeny of rodent grooming

Several studies have described aspects of the development of grooming behavior in infant rats and mice (Bolles & Woods, 1964; Golani & Fentress, 1985; Fentress, 1992; Coscia & Fentress, 1993; Berridge, 1994). Even before birth, grooming-like movements, such as forelimb wiping strokes along the face, can be elicited from the late-stage rat fetus (20-21 days of gestation) by chemical and tactile stimuli (Smotherman & Robinson, 1989; Robinson & Smotherman, 1991; Smotherman, pers. comm.). Spontaneous bouts of face grooming by rat or mouse pups may occur as early as the day of birth (postnatal Day 1), especially if artificial postural support is given (Bolles & Woods, 1964; Richmond & Sachs, 1978; Golani & Fentress,

1985; Sachs, 1988; Fentress, 1992). Forelimb strokes over face are the first to appear, followed by paw and forelimb licking, and then body scratching, by the end of the first week, and last by tail licking by the third week (Richmond & Sachs, 1978).

The ontogeny of individual facial stroke components was studied in exquisite detail for mice by Golani & Fentress (1985). By propping up the newborn mice pups with postural support, substantial grooming could be elicited each day after birth, and the development of stroke trajectories was exposed to view. They showed that during the first four days after birth stroke trajectories were poorly controlled, often overshooting their target or missing the face entirely. Trajectories became much more controlled, bilaterally synchronous, and simple during Days 4-8. Finally, after Day 9, trajectories remained controlled but became diversified, as successive strokes began to be connected into integrated sequential bouts (Golani & Fentress, 1985).

The ontogeny of grooming *syntax* in Weaver mice has been described briefly by Coscia & Fentress (1993). They showed that the serial coordination of syntactic grooming chains by normal heterozygous mice of this strain, as reflected in the successful performance of the complete pattern, appeared rapidly between the 14th and 15th day after birth. Although the pattern was completed successfully in less than 20% of instances during the two-day period of Day 13-14, more than 60% were completed successfully during Day 15-16. By contrast homozygous mutant Weaver littermates, which have substantial neurological defects of the nigrostriatal system and cerebellum, never exceeded 20% completion rates (Coscia & Fentress, 1993). The development of syntactic grooming chains in outbred rats and guinea pigs was briefly compared in a preliminary description by Berridge (1994). Similar to the results for normal mice described by Coscia & Fentress (1993), syntactic coordination of grooming sequences by rats began to appear near the end of the second week, but required at least several days to achieve sequential competence. Grooming sequences by guinea pigs, by contrast, appeared to follow adult-like syntactic patterns in the first few days after birth.

The purpose of the present study was to provide a more detailed description of the comparative development of grooming syntax in rat and guinea pig pups. Our goal was to map the day-by-day changes in sequential coordi-

nation for both species. We wished to ascertain whether 'syntactic' patterns of serial order appear at the same time as the constituent movements versus whether syntax develops as a level of behavioral organization independent of simple movements. It seemed advantageous to compare species that develop postnatally at different rates. Rats are relatively altricial rodents: newborns are naked and helpless, with poor postural or motor control. Guinea pigs are highly precocial: newborn guinea pigs appear adult-like, with hair, eyes open, and good motor control, able to eat solid food and to walk about on their day of birth (Fig. 2). The gestation period of guinea pigs (65 days) is nearly three times longer than that of rats (22 days).



Fig. 2. A newborn guinea pig pup and a newborn rat pup, both within a few hours of birth. The physical maturity of the precocial guinea pig contrasts strongly with the naked and blind altricial rat. From: Berridge (1994).

Methods

Experimental subjects & behavioral testing

Seven guinea pig pups were born in our laboratory to three mothers (1-3 pups per litter) obtained pregnant from Charles River suppliers. Eighty-four Sprague-Dawley rat pups were born to nine mothers (6-18 pups per litter) mated in our colony at the University of Michigan. No litters were culled. All were raised on a 14/10 light/dark cycle. Each litter lived with its mother in a plastic tub family cage. The floor of the cages had a soft bedding of wood shavings, and tissue paper was provided to the mother for nest building. Food and water (rat chow for rats; guinea pig chow supplemented with fresh vegetables for guinea pigs) were freely available.

For behavioral testing of guinea pigs, an individual guinea pig pup was removed from the home cage, placed in a transparent observation chamber for a 30-min videorecording trial. It was moistened with a light water mist to elicit grooming. Videotaped grooming records of 5 adult guinea pigs from a previous study (Berridge, 1990) were used for comparison of infants to adults. For behavioral testing of rat pups, a pup was removed from the nest for a 10-min videotaping session or else was videotaped in its home cage. Each pup was tested daily, beginning on the day of birth and continuing for three to four weeks. Grooming behavior was elicited from pups by placing one to several drops of water on the nose or face.

For both species, pups that were able to stand by themselves (all guinea pig pups, and rat pups after postnatal Day 8) were simply placed on a transparent floor of the test chamber. Because grooming strokes were most visible when viewed from a ventral position, a mirror was placed beneath the transparent floor to angle the image of the pup's face, forepaws, and ventral body into the videocamera. This gave a clear view of the animals' paw and facial movements, so that licking movements and the trajectory of the paws under the face could be viewed by the videocamera. In some instances, a second videocamera was placed above the chamber to gain a dorsal view of the head.

For rat pups younger than Day 7, which lacked sufficient postural control or muscle tone to support themselves in the test chamber, two methods were used to observe grooming. First, pups were videotaped within their home litter. As Golani & Fentress (1985) reported for mice, occasionally a pup that found itself propped up on a pile of littermates would engage in a bout of grooming, especially if sprinkled with a drop of water. Second, grooming was induced from individual pups outside the litter by providing artificial postural support. Several methods of artificial support were tried: the Golani & Fentress (1985) method of inserting the upper half of a pup through a snug hole in cardboard that supported it like a life-preserver; floating the pup in a warmed saline bath; lifting the upper body with support threads glued to the head and dorsal torso; propping the pup up on siblings or on a heating pad; or grasping the pup gently by the abdomen and torso and simply holding it upright between the experimenter's fingers. This handheld procedure proved to be the most effective for eliciting grooming from young rat pups, while at the same time not eliciting disruptive 'escape' behavior (a bout of wide sweeps or flails with both forepaws). Most data from rat pups prior to Day 7 were obtained from handheld pups.

Grooming analysis: Criteria for syntactic chain initiation

The videotaped records were scored frame-by-frame using a modification of the choreographic notation system developed originally to depict adult rat grooming sequences (Fig. 1; Berridge & Fentress, 1986). For normal adult rats, syntactic chains are initiated by a complete Phase I (a bout of 5 to 9 'ellipse strokes', rapid bilateral strokes that trace a tight elliptical trajectory around the nose at a rate faster than 6 Hz), followed immediately by a Phase II stroke (unilateral or asymmetrical paw stroke along the vibrissae) or a Phase III stroke (bilateral and symmetrical forelimb strokes at the level of the eye or ear). For adult guinea pigs, syntactic grooming chains are similar, except that a) their Phase I ellipse cycles are slower (3 Hz) and contain a pause between strokes, b) they often skip Phase II, and c) their Phase III large-amplitude strokes are unilateral, performed with only one forelimb (Berridge, 1990). But since immature neuromotor systems might produce distorted movements even to a perfect generating signal, a 'relaxed' criterion was used here for both species to recognize the initiation of infant syntactic chains. This relaxed initiation criterion was similar to that used for adult decerebrate rats that have postural and movement control deficits (Berridge, 1989a). By this criterion, Phase I was considered to be two or more ellipses with no interruption. Phase II consisted of one or more unilateral facial strokes which succeeded in making facial contact. Phase III was considered to be any large amplitude stroke that directly followed Phases I or II. A syntactic chain was thus judged to have been *initiated* either when three or more Phase I ellipses occurred in series, or when components from three adjacent phases of the chain were seen contiguously: for example, two ellipses (Phase I) followed by two unilateral strokes (Phase II) and a bilateral stroke (Phase III); or two unilateral strokes (Phase II) followed by a bilateral stroke (Phase III) and an attempted body lick (Phase IV).

Criterion for syntactic chain completion

Syntactic grooming chains are typically completed by a 'perfect' Phase IV for both adult rats and guinea pigs: turning, lowering the head, and initiating a bout of body licking directed towards the side torso. Normal adult rats complete 85% or more of the syntactic chains they begin. Normal adult guinea pigs complete 100% of their chains syntactically. However, certain brain lesions such as decortication or striatal damage can produce Phase IV 'imperfections' in rats, perhaps due in part to a disturbance of the postural control needed to maintain balance during the turn and head duck involved in body licking (Berridge & Whishaw, 1992). With the possibility in mind that physical or neural immaturity might also introduce Phase IV imperfections into an otherwise syntactic sequential pattern, several degrees of Phase IV 'perfection' were recognized in this study. 'Perfect completion' was scored when the tongue made actual contact with the flank. 'Attempted completion' was scored when the pup lowered its head and turned at least partly toward its flank, emitting licks that appeared directed toward the torso, but failed to make actual tongue contact with its body. 'Imperfect completion' was scored when the pup substituted a different target for Phase IV licking, after emitting Phases I, II, and III in order, such as its forelimbs, the floor or wall, or another littermate. 'Incomplete' chains were those which, once initiated, never progressed fully to any form of Phase IV, but instead continued back into sequentially flexible grooming, or simply halted, or were actively interrupted by an event (*e.g.* falling over or the active obstruction of a movement by an external object).

Results

Infant guinea pig grooming

Newborn guinea pig pups had excellent physical development (Fig. 2) and moderately good postural control, rarely losing balance even during complex behavior. Guinea pig pups groomed spontaneously on the day of birth. Newborn guinea pigs were remarkably adult-like in their grooming patterns. On Day 1 guinea pig pups engaged in 54 ± 16 s of grooming per 30 min observation trial, which did not differ from adults (43 ± 14 s/trial: $F(1, 11) = 1.27$, NS). On subsequent days of development, guinea pig pups continued to devote an adult-like proportion of their time to grooming.

Serial organization of grooming: Normative chain syntax of adults for comparison

For adult rodents of all species examined so far, the initiation of a syntactic grooming chain is marked by the occurrence of distinctive Phase I ellipse strokes centered around the nose (Berridge, 1990). Ellipse strokes are faster, tighter in trajectory, more stereotyped and more repetitive than other small strokes performed around the mouth and nose. These are often preceded by other strokes (called 'circles' by Fentress, 1972), which are more fluid in form, typically centered more posteriorly at the mouth, and interspersed with paw licks. As Phase I begins, the center of the strokes shifts anteriorly, the paws begin to move in tighter synchrony and in a more symmetrical and stereotyped trajectory, and the stroke cycle speed increases. For adult guinea pigs, the stroke cycle advances to approximately 3 Hz: a stroke duration just over 200 ms followed by a pause of about 100 ms. For rats, the cycle advances to approximately 6 Hz: a continuous series of strokes of 150 ms duration without pause (Berridge, 1990). This particular configuration rarely occurs outside the context of a syntactic chain (unlike the components of other Phases, which occur often in other grooming). During Phase I adults emit a series of at least five consecutive ellipse. Phase II for guinea pigs comprises small-amplitude strokes over the vibrissae performed with one or both paws, and Phase III large strokes over the ear and eye with a single paw (the reverse of rat Phases II and III). Approximately 50% of adult guinea pig syntactic chains skip Phase II and

progress directly from Phase I to III. However, all adult syntactic chains contain a series of at least three Phase III strokes, and 100% of guinea pig chains are completed by perfect Phase IV body licking, which for guinea pigs is invariably directed at the side of the torso ipsilateral to the paw which made the Phase III strokes (Berridge, 1990).

Chain initiation by infant guinea pigs

Competence in serial coordination, as reflected by performance of syntactic grooming chains, can be assessed most simply in two ways: 1) the propensity to *initiate* syntactic chain patterns during a grooming bout, and 2) the ability to *complete* a chain pattern syntactically, from Phases I to IV, once begun. For the purpose of identifying syntactic chains in infants, a repetition of at least three consecutive ellipse strokes, faster than 3.3 Hz, followed immediately by a Phase II or Phase III overhand stroke was considered here to constitute the *initiation* of a chain. On Day 1, newborn guinea pigs initiated syntactic chains during grooming at a rate of 1.2 ± 0.4 chains initiated per minute of grooming. This was equivalent to adult initiation rates of 1.3 ± 0.4 (ANOVA $F(1, 11) = 0.02$, NS). Similarly, the *serial organization* of Phases I, II, and III typically corresponded to the adult syntactic pattern even on Day 2, although in some instances abnormalities could be detected in the *form* of Phase I ellipses and in the organization of Phase structure within the chain (see below). Infant guinea pigs initiated syntactic chains at frequencies equivalent to adults' on every day throughout their first three weeks after birth.

Syntax efficacy: Rates of syntactic completion by infant guinea pigs

On postnatal Day 1 for guinea pig pups, 63% of Day 1 syntactic chains were completed perfectly without any flaw whatsoever (compared to 100% for adult guinea pigs). 'Perfect completion' implies that each individual component of the chain is emitted in perfect form, as well syntactically arranged in proper Phase. During the first two days of postnatal life, however, guinea pig pups showed a slight degree of postural instability, as they switched from facial grooming to body grooming. This requires leaving a stable sitting posture, to make an extreme lateral swing of the head, in order to begin body licking, displacing the center of gravity. Occasionally a guinea pig pup younger than Day 3 lost its balance as it did this,

sometimes toppling onto its side in mid swing. Often it would begin to emit tongue protrusions appropriate to body licking even as it began to fall. In the context of syntactic grooming chains, such instances were considered 'attempts' to initiate Phase IV. These attempted completions constituted 24% of initiated syntactic chains on Day 1. Finally, a still more degraded form of syntactic completion is replacement of Phase IV body licking with licking of the forelimbs or other body part. Phase IV replacement occurs occasionally in adult rodents after some forms of brain damage (Berridge & Whishaw, 1992) though virtually never in normal adult guinea pigs. This is the 'least perfect' form of syntactic completion possible. For Day 1 guinea pig pups, 'replacement' completion constituted 13% of initiated chains. When instances of 'perfect', 'attempted', and 'replacement' Phase IV completion were combined together, 100% of syntactic chains begun by Phase I were completed syntactically by guinea pig pups even on the day of birth. In no case did a pup simply fail to complete the syntactic pattern (either by halting grooming or by returning to sequentially flexible grooming strokes without progressing to Phase IV) once it had begun a series of Phase I ellipses.

On Day 2, 100% of syntactic chains begun by Phase I were completed syntactically through the remaining phases, ending either in a perfect or attempted Phase IV (divided equally between perfect and attempted). From Day 3 onward, 100% of syntactic chains were completed perfectly through Phase IV (Fig. 3). The loss of balance and accompanying falls, which had occasionally disrupted transitions from face to body grooming on Days 1 and 2, were no longer seen.

Microstructure of guinea pig syntactic chains during the first postnatal week

Deviations from the syntactic pattern could nonetheless be detected throughout the first postnatal week even though infant guinea pigs completed chain patterns syntactically from Phase I to Phase IV (Fig. 3). These deviations were chiefly of two types: nonsyntactic addition of extraneous actions to the pattern, and failure to use both paws to make Phase I ellipse strokes. Insertion of an unexpected component occurred on 25% of Day 1 syntactic chains, 30% of Day 5 chains, 14% of Day 7 chains, and disappeared by Day 15. The extraneous component was usually either paw licking, typi-

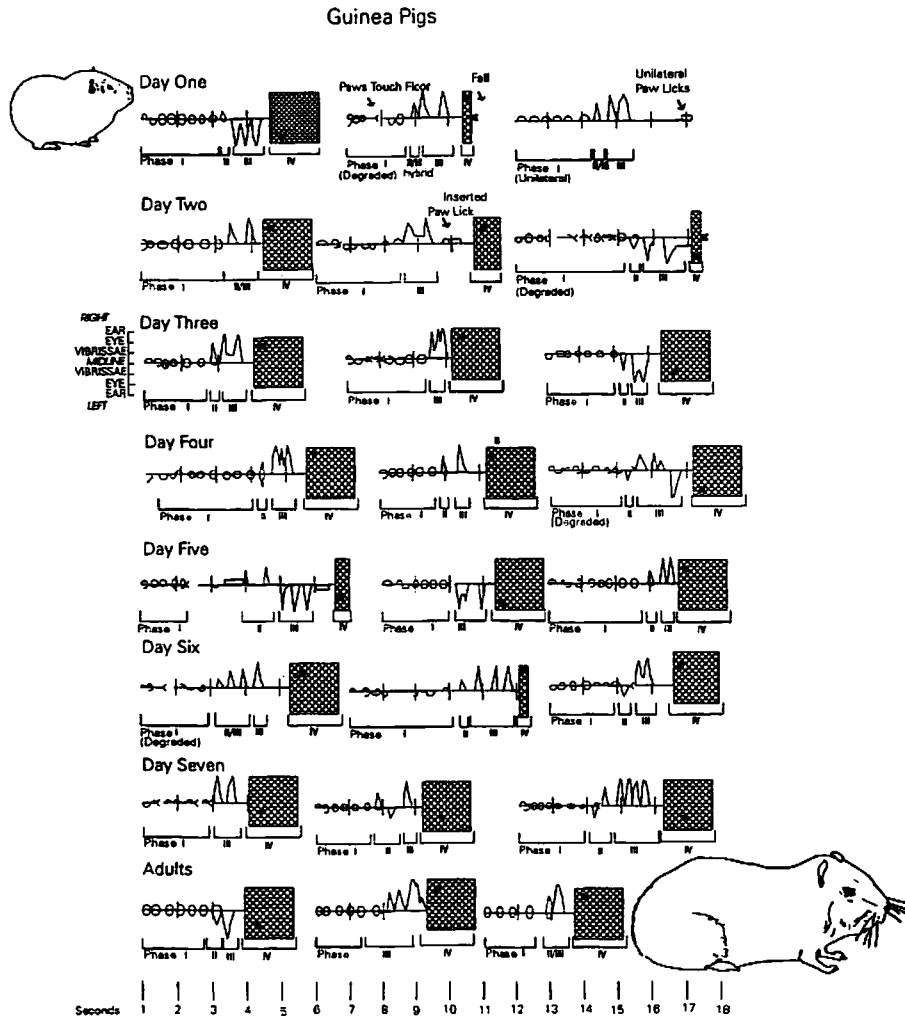


Fig. 3. Syntactic grooming chains of guinea pig pups. Three representative chains are shown from each day for pups and three chains for adults. Special symbols for infant actions are labeled.

cally as a transition between Phases III and IV, or a momentary placement of both paws on the floor (less than 1 s duration), typically during Phase I, after which the syntactic pattern was resumed (Fig. 3).

The *timing* of Phase I elliptical cycles was similar to adults' even on Day 1. Just as for adults, ellipse cycles emitted by pups on the day of birth contained a stroke that lasted approximately 240 ms (238 ± 4 ms), separated from contiguous strokes by a roughly 80 ms pause (75 ± 4 ms), for a total cycle duration of about 320 ms. During the first days of postnatal life, an unusual *form* of *unilateral* Phase I ellipse stroke was sometimes seen (performed with only one paw rather than simultaneously with both paws). Adult guinea pigs always use both paws simultaneously to trace a symmetrical bilateral trajectory around their nose (Berridge, 1990). Aside from its unilateral form, the timing and other features of these unusual Phase I strokes appeared similar to a normal bilateral ellipse. Approximately 50% of syntactic chains emitted on Days 1 and 2 had a Phase I that comprised only unilateral ellipses. After Day 2, Phase I bouts composed entirely of unilateral ellipse strokes were never seen. However, guinea pig pups continued to incorporate occasional unilateral ellipse strokes, especially at the onset of Phase I, into more than 50% of chains until Day 12, and at least 10% of chains until Day 20.

The *number* of Phase I ellipse strokes, Phases II and III strokes, and the *duration* of syntactic grooming chains, from the onset of the first Phase I ellipse stroke to the onset of Phase IV body licking (or its attempt), was similar across all infant ages and adults (Fig. 3; ANOVA $F(14, 492) < 1.0$, NS). The average latency required to reach Phase IV was 4.3 ± 0.6 s.

Infant rats

Spontaneous grooming

Infant rat pups younger than Day 7 never groomed spontaneously in the test chamber. However, grooming-like forelimb strokes could be elicited from Day 1 pups by propping them upright so that their forelimbs were free, as described by Golani & Fentress (1985) for mice, and by sprinkling them with water. Elicited grooming of posturally-supported newborns consisted primarily of series of 1 to 3 quick, bilateral, large-amplitude strokes over or immediately above the surface of the face (Fig. 4). These bouts were typically interspersed with flailing motions in which the forelimbs were waved at some distance from the face. Approximately 30% to 50% of all strokes emitted on Day 1 failed to make contact with the face (instead passing above its surface), a pattern that remained unchanged up to Day 7.

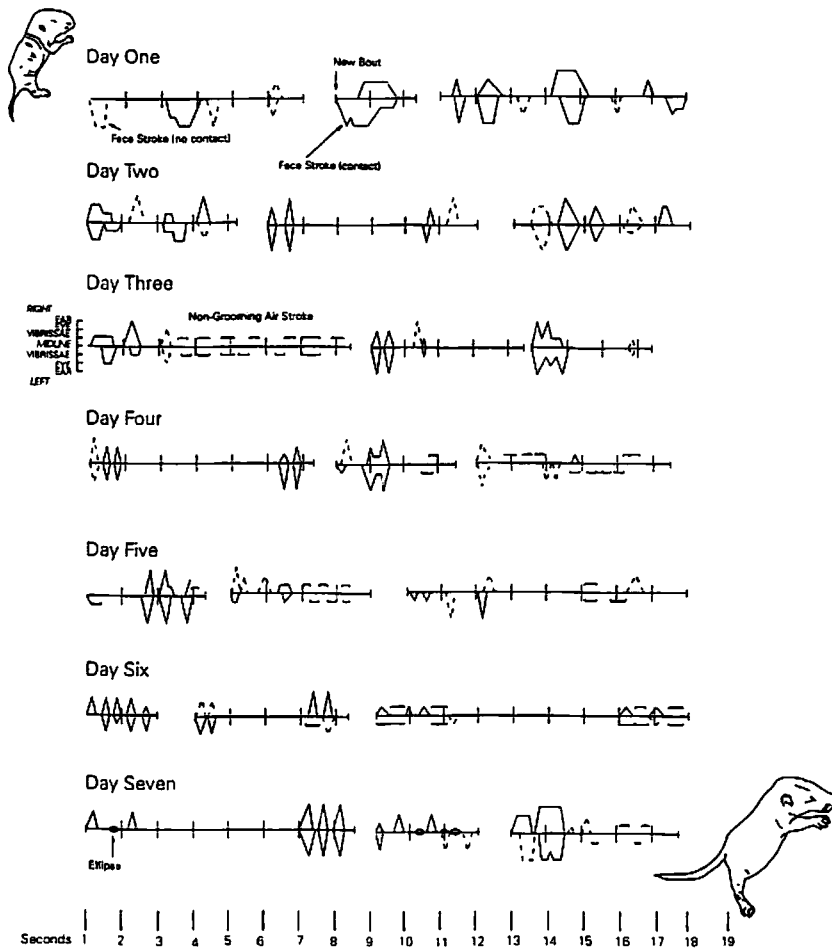


Fig. 4. Best syntactic grooming chains of rat pups. Choreographic representations of the 'most syntactic' sequences emitted each day by developing rat pups. Note the dramatic improvement in syntactic organization that begins around Day 11.

The average duration of grooming bouts was 3 s on Day 1, but dropped to only 1 s by Day 3 (ANOVA $F(6, 325) = 8.9$; $p < 0.01$), before rising gradually again several days later. Coincident with this fall and rise in grooming duration was a temporary narrowing of stroke path trajectories over the face, followed by a gradual expansion after Day 3, similar to that described for mice by Golani & Fentress (1985).

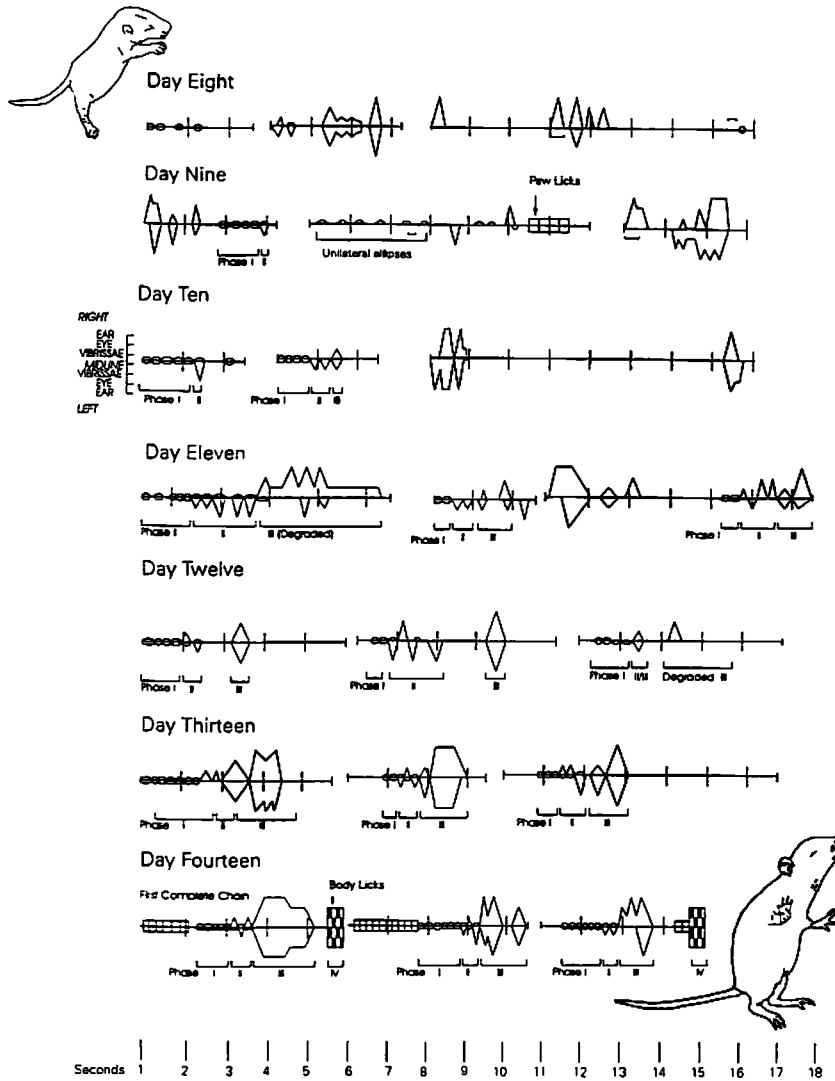


Fig. 4. (Continued).

Spontaneous grooming within the home cage, in the absence of water, began to be seen between Days 8 and 10, particularly if the litter were disturbed (for example, by the mother's removal or replacement).

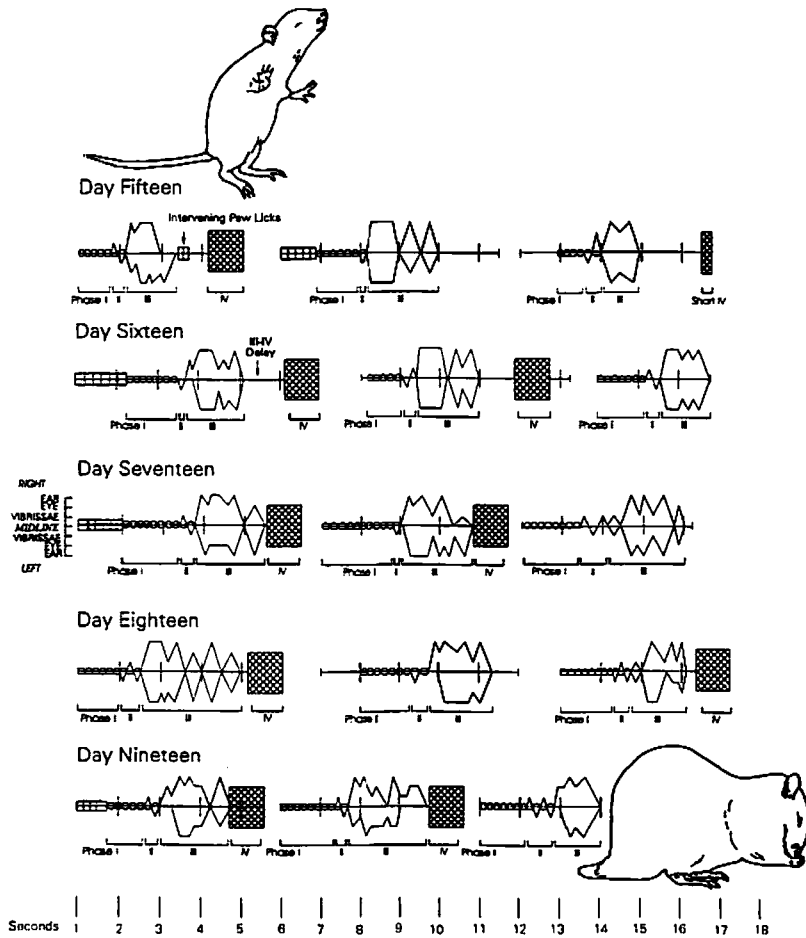


Fig. 4. (Continued).

Development of ellipse strokes in infant rats

Although large amplitude stroke-like motions over the face could be elicited on Day 1, the first ellipse-like strokes were not observed until Day 7 (Fig. 4). Compared to other strokes, early ellipses were relatively rapid and tightly controlled motions which traced a symmetrical trajectory around the nose. When they first appeared on Day 7, they typically occurred as a single isolated event. By Day 9, however, they began to be grouped into bouts similar to an adult Phase I, and to be followed by other Phases of

syntactic chains. From Days 9-11, when postural support was still shaky, the movements showed more variability than adult ellipses. Occasionally, only one paw would participate, while the other paw supported the animal above the floor. Adult ellipse strokes, by contrast, are always bilateral. Ellipses increased in speed from under 4 Hz before Day 12 to roughly adult-like 6 Hz on Day 19 (ANOVA $F(8, 116) = 9.0$; $p < 0.001$). The number of ellipses linked together within a bout also increased during this time from 3 to 6-8 (ANOVA $F(8, 116) = 11.3$; $p < 0.001$). As early as Day 15 in our sample, ellipse speed was found to be correlated with syntactic completion of the chain, as has previously been reported for adults (Berridge, 1990; Berridge & Whishaw, 1992). Ellipses emitted during Phase I were faster if the chain was eventually completed syntactically than if the chain failed to be completed to Phase IV (6.17 ± 0.16 Hz for complete chains *vs* 4.5 ± 0.12 Hz for incomplete chains (Day 15; $F(1, 116) = 29.252$; $p < 0.0001$). Up to Day 14, infant rats initiated 0.4 or fewer chains per minute of grooming. Initiation rates rose to 1.2 per minute by Day 15 and to adult-like rates of 1.6 chains per minute by Day 18.

Development of Phases II & III in infant rats

Days 10 and 11 were the first on which Phases II and III strokes sequentially followed Phase I ellipses. These early versions of syntactic organization consisted of only one or two medium or small strokes immediately after Phase I (Fig. 4). After Day 10, the bilateral strokes of Phase III became more adult-like: larger in trajectory amplitude, and combined in longer bouts so as to triple in duration by Day 17 (ANOVA $F(8, 110) = 2.7$; $p < 0.01$). Interestingly, the Phase III strokes of Days 10 and 11 were actually *smaller* than equivalent grooming strokes emitted *outside* the syntactic chains. For example, when sprayed with a mist of water, these 10-Day-old infants would emit multiple large strokes in order to clean themselves, but on that same day would make only small strokes for Phase III. Approximately 50% of chains initiated on Days 10 or 11 were carried through Phases II and III. The incidence of completion through at least Phase III rose gradually from Day 10 to Day 17, when adult-like 100% completion through Phase III was attained.

Phase IV

Body licking was first observed on Day 14, and first appeared within the context of a syntactic chain (*i.e.* it immediately followed Phases I, II, and III). Body licking was not observed in non-chain grooming until the next day, Day 15. These first bouts of body licks were often quite short, lasting fewer than 5 licks. These bouts grew in length over subsequent days to reach adult-lick durations by Day 17.

Full Phase IV completion by infant rats

During Days 10-13, no chains were completed *perfectly* by Phase IV body licking. However, approximately 10% of chains initiated on these days were completed by *attempted* Phase IV body licking (partial head turn and lick), and an additional 10% were completed by forepaw lick *substitution* (Fig. 5). The first chain of a grooming bout was less likely to be completed syntactically than the second or third chain of the same bout, as has been reported previously for adult rats (Berridge, 1990; Berridge & Whishaw, 1992). Perfect syntactic completion by Phase IV body lick was first observed on Day 14. On that day, approximately 5% of initiated chains were completed perfectly. By any completion criteria, success rose gradually during the second and third week of postnatal life (Fig. 4). By the 'perfect' Phase IV criterion, adult-like completion rates (above 80% of chains initiated) were attained on Day 19. Even after Day 20, a small proportion of chains (approximately 10%) continued to end in attempted turns or substituted forelimb licking.

Causes of syntactic failure during Days 13-19

Deviation from the syntactic pattern before Phase III usually occurred when the pup began the chain from an improper posture (*e.g.* positioned against an obstruction or not in a balanced crouch on the hindquarters), and occasionally was accompanied by falls. For chains that were completed at least through several strokes of Phase III, but that failed to progress to Phase IV, 35% were terminated by falls, 22% ended Phase III in a position from which a turn was not readily possible (*e.g.* lying flat), and 12% were blocked. Approximately one-third of failures were not accompanied by any visible cause of interruption.

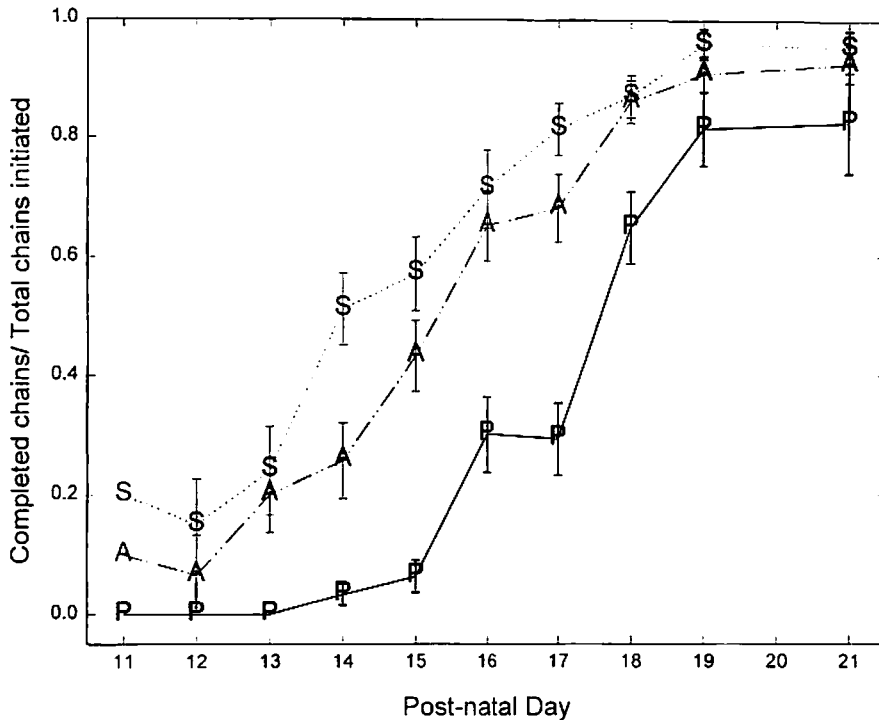


Fig. 5. Syntactic completion rates for rat pups. The percentage of initiated syntactic grooming chains that were completed syntactically to Phase IV on each day, according to three criteria of Phase IV perfection. 'P' denotes completion by 'perfect' Phase IV body licking. 'A' includes also 'attempts' to body lick, in which the pup turned as if to begin body licking before falling over. 'S' includes also 'substitution' of paw licking as the Phase IV component.

Degraded forms of syntactically complete chains

Among chains that were completed syntactically during Days 13-15, two additional types of syntax *degradation* were commonly observed (Fig. 6). The first type were phase *omissions*, in which a single Phase was skipped. Examples were omissions such as Phase II → III → IV (skipped Phase I); Phase I → III → IV (skipped Phase II); or Phase I → II → IV (skipped Phase III). Omission of Phases I or III is almost never seen in normal adult rats, but has been observed to occur during 'brainstem grooming' emitted by decerebrate rats (Berridge, 1989). The second form of degradation was *hybridization* of two adjacent Phases that are normally distinct into

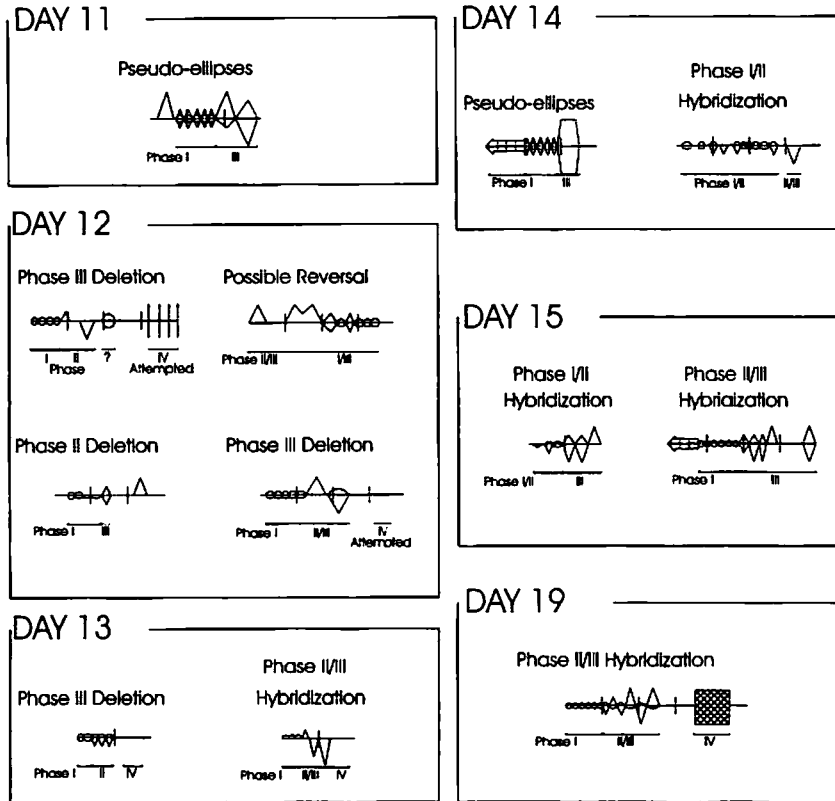


Fig. 6. Examples of degraded syntax by rat pups. Choreographed instances of syntactic-like patterns, but with significant distortion, emitted by rat pups. These distortions of syntax are not typically seen in adult grooming.

a blended intermediate form that shared features with both. For example, hybridization of Phase I (series of small-amplitude bilateral ellipses) and Phase II (a medium amplitude unilateral stroke) resulted in a Phase I/II hybrid: a larger than usual ellipse trajectory traced by a single paw. Similarly, Phase II (medium amplitude unilateral stroke) & Phase III (large-amplitude bilateral strokes) were often hybridized into a Phase II/III series of unusually large unilateral strokes. Hybridization of chain phases and syntactic omissions were observed in the grooming of rat pups on every day between Days 11 and 15.

Discussion

Two issues are of special interest for this study. The first issue concerns the similarities and differences between rats and guinea pigs. To what extent does the sequential fine structure of grooming reflect the precocial versus altricial features of guinea pig and rat development?

The second issue concerns the nature of action syntax, and the relation of sequential organization to simpler features of action. Is action syntax merely a secondary feature that emerges out of the elemental properties of action components? Or does action syntax represent a distinct 'entity' on its own, a level of behavioral organization that is separate from the lower level of action components, with its own syntactic control processes and neural substrates?

Grooming syntax of infant guinea pig

Our data indicate that the physical maturity of newborn guinea pigs is matched by a well-developed behavioral grooming repertoire and action syntax. There is no component of adult guinea pig grooming that cannot also be found in the grooming of a guinea pig pup on the first day of postnatal life. Forelimb strokes over the face, of every form, both large and small, single paw or bilateral, were all seen on Day 1. Paw licks, limb licks, and body licks of adults cannot be distinguished from corresponding forms shown by a guinea pig pup on Day 1. Action components, in other words, appear virtually adult-like on the first day of postnatal life.

Grooming syntax also appears strikingly adult-like in newborn guinea pigs. All four phases of syntactic grooming chains can be seen in proper order. If a relaxed criteria for syntactic completion is used, which allows aborted attempts to begin Phase IV body licks to qualify as successful Phase IV performance, then guinea pig pups attain 100% completion rates on Day 1. Even by a strict criteria of 'perfect' completion, Day 1 pups completed 64% of chains syntactically on Day 1 and reached 100% by Day 3.

However, syntactic chains by newborn guinea pigs show some early minor distortions of Phase I (unilateral ellipses) and Phase IV (largely due to postural deficits). More specifically related to sequential organization, they occasionally allow extraneous events to invade a proportion of chains. First, guinea pig pups younger than Day 15 occasionally allowed their paws

to drop away from their face while performing Phase I ellipses, and sometimes actually planted both paws momentarily on the floor in the middle of a series of ellipses. Typically the pup carried on with the chain after this momentary interruption, completing Phase I and the remaining Phases. Also, pups occasionally allowed paw licks to intervene as a transition action between Phase III strokes and perfect Phase IV body licking. These instances do not reflect syntax failure as such, since such chains still coordinated all four phases in syntactic order in spite of the incursion of strange elements. However, they show a weakening of the syntactic pattern. Such 'leakage' of extraneous actions into the syntactic pattern occurred in one out of four chains on Day 1, and still in more than 10% at the end of the first week.

Infant rat grooming syntax

By contrast, altricial rat pups did not even begin to show syntactic like features of grooming during the first postnatal week, and only gradually progressed toward good syntax during the second and third weeks. This pattern of gradual syntax emergence is similar to that reported for infant Weaver mice by Coscia & Fentress (1993). Stroke patterns resembling Phases I, II, III appeared almost together beginning on Day 9 or 10. The earliest phases were often distinctly abnormal in movement constituents compared to their adult versions. The development of the syntax of the chain, in this sense, preceded the development of the constituent elements. Pups often first showed body licking within the context of syntactic chains, as Phase IV, beginning on Day 14. They typically began to emit body licking in other grooming contexts within one day later. The attempts at syntactic completion became increasingly successful over Days 14 to 19.

If paw lick substitutions are accepted as an imperfect form of Phase IV completion, then approximately 20% of chains began to be completed syntactically as early as Day 11 (Fig. 5). Paw licks as an action began to appear in grooming outside of syntactic chains on Day 9 (Fig. 4), but were not incorporated into syntactic chains until 2 days later. On Days 11 and 12, paw lick substitutions were the primary means of 'completing' Phase IV. Beginning on Day 13, rat pups began to make visible attempts to engage in body licking at the transition to Phase IV, turning their head and ducking toward their flank before losing balance and toppling over. From Day 14

to Day 17, such aborted 'attempts' to engage in body licking were the primary means of Phase IV completion (rising from approximately 20% to approximately 50% of initiated chains), although an additional 10% to 20% of chains continued to be completed instead by paw lick replacement. Perfect Phase IV completion by successful body licking jumped from less than 10% on Day 15 to 25% on Day 16, and then rapidly climbed again to achieve 80% rates, which is within the range for normal adult rats, over Days 17 and 18.

The shift from 'attempted' to actual Phase IV body licking between Days 13 and 18 is no doubt due in large part to postural maturation. The first few attempts to move from Phase III strokes to body licking simply fail, and the pup falls over. Gradually over several days the ratio of successes to attempts rises. But it is of interest to note that the gradual increase in Phase IV completion from Day 12 to 17 also involves a gradual strengthening of the syntax rule, quite apart from postural competence. Even if one allows aborted attempts or paw lick replacement to qualify as Phase IV, syntactic completion still rose only gradually from 20% on Day 12 to 80% on Day 16. Pups are well able to make paw licks on Day 12, and in principle could complete every syntactic chain with that action before becoming proficient at the transition to body licks. But they do not complete even half of their chains by paw lick substitution until Day 14. This gradual increase in completion rates between Days 12 and 17, which occurred even by relaxed criteria that require movements the pup can easily make, must be due to some factor separable from mere movement competence. The gradual rise in syntactic completion may be viewed as a strengthening of the tendency to follow a syntactic rule. This aspect of grooming syntax matures in rats during the second and third week.

Syntax as an autonomous process

These observations bear on the second general issue raised above, namely, the relation of action syntax to simpler movements in development. Do action syntax and movement competence both reflect the same level of maturational organization? Such could be the case if patterns of sequential coordination were simply a passive emergent property of elemental movements. It could also result even if action syntax were more than the sum of the elements, as long as sequential combinations were endogenously gen-

erated by the *same* neural generating system that generated the elements themselves: a single grooming control system. Alternatively, does action syntax represent a level of behavioral organization that is fundamentally different from the component movements themselves? If action elements and syntax were truly distinct levels of organization they might appear with a different time course of development, and have different underlying control systems.

Our results are most consistent with the second alternative of independent levels of organization. Guinea pig and rat pups present dramatically different relations between movement competence and syntactic development. But both guinea pig and rat species have aspects of grooming development in which sequential organization shows a degree of independence from constituent elements.

Newborn guinea pigs are highly competent both at performing grooming movements and at coordinating sequences into syntactic grooming chains. But there is a sense in which their syntactic patterns must still mature after birth, even after movements appear adult-like. The few movement component abnormalities shown by newborn guinea pigs, such as unilateral ellipses and loss of balance, disappeared by the third day of postnatal life. Their coordination of syntactic grooming chains, however, while sufficiently efficacious to reach full Phase IV completion by body licking, failed to exclude extraneous pauses or paw licks. Similar failure to exclude extraneous actions occurs in syntactic grooming chains performed by adult decerebrate rats after midbrain transection (Berridge, 1989a). Although invasion by extraneous movements indicates a weakening of the sequential pattern, it also shows that syntax is produced as an entity (rather than emerging from chained reflexes), since the pattern is re-imposed after 'unexpected' intrusions. Instead the syntactic pattern appears imposed from above upon the elements — with sufficient strength to continue on even if a minor interruption disrupts the ordinary flow of action.

The pattern of development for infant rats illustrates even more clearly the independence of syntactic sequences from elemental properties of component movements. The phase structure of syntactic grooming began to be seen on Day 11, at a time when component grooming actions themselves were often poorly formed. Syntactic coordination of phases appeared during the second week even when the movements composing each phase

were grossly distorted. Such instances of syntactic imposition in the face of degraded components were most apparent on Days 12 and 13, though they extended on either side of this period (Fig. 6). Syntactic coordination of Phases I, II, III, and attempted Phase IV can occur even if ellipses are inappropriately formed or even missing, if an entire Phase II or Phase III is dropped, if the movements from two adjacent Phases are partially interleaved either sequentially or hybridized in form, and even perhaps if the order among Phases is reversed (see Day 12, Fig. 6). The persistence of the pattern when the 'raw materials' of component movements are so poor is again reminiscent of similar syntactic persistence despite movement deformations in the grooming of adult decerebrate rats (Berridge, 1989a). Both infant and decerebrate grooming sequences indicate that syntax patterns have an organization of their own which is asserted even when motor elements are disorganized either by neural transection of movement control systems or by the immaturity of a developing nervous system.

Comparative development of neural substrates

Guinea pigs are born with nearly adult-like rates of microtubule assembly (Lennon *et al.*, 1980). Rat pups, by contrast, do not reach adult levels of microtubule assembly until 25 days after birth (Lennon *et al.*, 1980). Relative neoteny of brain development thus sets the stage for differences between species in behavioral competence.

The neostriatum is the single most crucial forebrain structure for the implementation of adult grooming syntax (Berridge & Fentress, 1986, 1987, 1988; Berridge, 1989b; Berridge & Whishaw, 1992; Aldridge *et al.*, 1993; Cromwell & Berridge, in press). Maturation of neostriatal circuits has been suggested to mediate the ontogeny of grooming syntax (Fentress, 1992; Berridge, 1994). Our results show that behavioral syntax develops in close correlation with the reported timeframe of neostriatal maturation.

For guinea pigs, neuronal density in the neostriatum is adult-like at birth, and activity levels of neostriatal enzymes that synthesize neurotransmitters are close to adult asymptotes (Karlaria & Prince, 1988). In rats, by contrast, 50% of neostriatal neurons develop after birth, and neostriatal enzymes related to monoamine synthesis triple in activity between Days 10 and 20 (Fentress *et al.*, 1981; Karlaria & Prince, 1988).

Neuroanatomical developments in the neostriatum are correlated strikingly with the behavioral maturation of grooming syntax. For example, an increase in matrix to patch ratios (between Days 7 and 20; Lanca *et al.*, 1986), and in establishment of functional projections from tegmentum to the neostriatum (between Days 7 and 14; Iniguez *et al.*, 1990) occurs between Days 7 and 20, coincident with the emergence of grooming syntax. Neurochemically, dopamine and its receptors are present at birth (Andersen & Gazzara, 1993; Schambra *et al.*, 1994), but receptors double over the next two weeks (Murrin & Zeeng, 1990; Rao *et al.*, 1991), and neurotransmitter levels rise more than 30 times in the weeks after birth (Altar *et al.*, 1987; Kalsbeek *et al.*, 1989). The ratio of DOPAC metabolite to dopamine, which provides a measure of the rate of dopamine use within the brain, also rises by 25% in the week after Day 8 (Herregodts *et al.*, 1990). The firing rate of dopamine neurons also increases between Days 5 and 13 (Tepper *et al.*, 1990).

Behavioral grooming syntax matures most dramatically in the third post-natal week, when completion rates reach adult levels. Dramatic maturation of the rat neostriatum continues during this time. For example, dopamine autoreceptors on nigrostriatal neurons become more sensitive after Day 14 to cumulative inhibition by intravenous apomorphine (Wang & Pitts, 1995). Conversely, at Day 21, but not at Day 14, amphetamine can induce adult-like neural sensitization of dopamine neurons (Tsuchida *et al.*, 1994). What emerges is a picture of the striatum 'wiring up' and 'coming on line' coincident with the emergence of syntactic order in behavioral sequences.

Speed: Developmental constancy of allometry in movement timing

The timing of grooming movements made by adult rodents has a striking feature. Movement speed of fast stereotyped strokes, such as Phase I ellipses, is inversely related to body mass (Berridge, 1990). The duration of ellipse cycles performed by adult guinea pigs, ground squirrels, rats, hamsters, gerbils, and mice is directly proportional to the average body weight of the species (Fig. 7). Heavier rodents emit longer ellipse cycles. Cycle duration for each species follows an allometric equation (of the type $y = a \times x^b$, where y is cycle duration, x is body mass, and a and b are constants calculated from the data):

$$[\text{Duration in ms}] = 17.4 \times ([\text{average adult body weight in grams}]^{0.4})$$

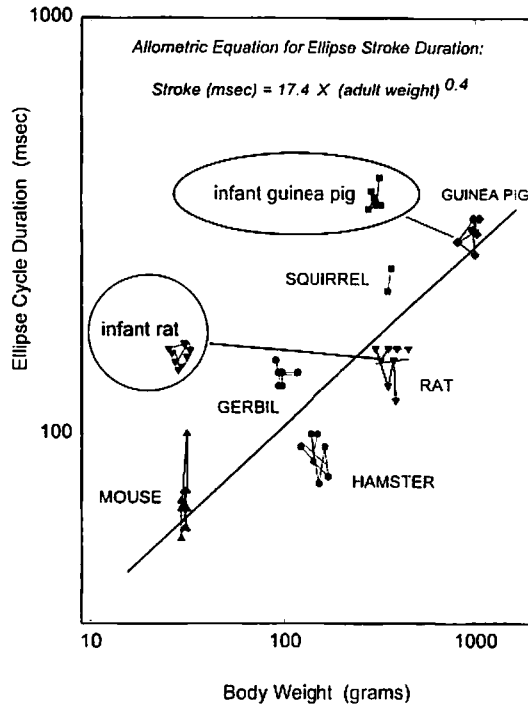


Fig. 7. Allometric programming of action duration. Infant guinea pigs and rats are compared to the adults of six species. Data for adults are from Berridge (1990). Duration of ellipse stroke cycles (Phase I) is represented by the vertical axis, and body weight by the horizontal axis. Cycle duration is essentially constant across development. The infant data points were chosen at a time when infant guinea pigs are roughly the size of a 300 g adult rat (Day 18), and when infant rats are roughly the size of a 30 g adult mouse (Day 15). Infant rats and guinea pigs conform in advance to the allometric relationship appropriate to adults of their species, rather than to their own size-equivalent match, indicating that allometry is programmed into the neural circuitry that generates action timing. Modified from Berridge (1994).

Although it would in principle be possible for allometric control of movement duration to arise passively from the physics of movement, since longer limbs have greater mass and inertia, this is not the source of the allometry (Berridge, 1990, 1994). The movement durations observed in this developmental study show conclusively that the timing of ellipse cycles is not controlled passively by physical body weight. Instead, ellipse duration is relatively constant within a species, even across different ages. Thus the

allometric relationship between eventual body size and movement duration must be programmed into the neural timing circuit that controls stroke speed, and this circuit must operate at roughly the same speed throughout life regardless of developmental changes in body mass.

Both guinea pig and rat pups showed ellipse cycle durations appropriate to their future adult body weights, even though their actual weight was considerably less than adult conspecifics (Fig. 7). For example, the ellipse cycles of guinea pig pups on Day 18 (when they weigh approximately as much as a 300 g adult rat) did not differ from those of adult guinea pigs, but are slower than those of adult rats. Ellipse cycles of rat pups on Day 19 (when they weigh approximately as much as a 30 g adult mouse), are equal in duration to those of 300 g adult rats, and slower than those of adult mice (Fig. 7; mouse data from Berridge, 1990). In other words, the movement timing of a 'mouse-sized' infant rat is more similar to an adult rat than to an adult mouse, and that of a 'rat-sized' infant guinea pig more similar to an adult guinea pig than to an adult rat. Species-typical timing parameters, appropriate to average adult body mass, thus appear to be programmed from the beginning of postnatal life into the neural circuits that control these action patterns.

Evolution of action syntax

Action syntax patterns are shared across rodent species that have evolved separately for over 50 million years. Variations in the pattern are so closely tied to genotype that phylogenetic relationships among species can be traced from them (Berridge, 1990). This suggests that syntactic rules for ordering action appeared early in mammalian evolution. Our results, and those of Coscia & Fentress (1993), show that syntactic patterns also emerge early within ontogenetic development. Why does action syntax appear so early in development?

There is no clear functional role served by syntactic grooming chains that could not also be accomplished by other means available to young rodents (Hall & Oppenheim, 1987). Syntactic chains are by no means the only way available to rodents to distribute grooming over different body targets, and both adults and infants make use of alternative sequences. Unless there is an additional hidden function provided specifically by the syntactic pattern of grooming studied here, which is not provided by other

grooming sequences, it is difficult to conclude that fitness pressures have existed specifically to foster the evolution of syntactic grooming chains.

Alternatively, a broader view of the evolution of action syntax may help to understand the existence of serial patterns in grooming. Perhaps specific grooming sequences have emerged early in evolution and ontogeny, not because they fulfill specific functions, but because syntax has been selected as a *general* property of brain systems that generate action. This was essentially the hypothesis put forth by Karl Lashley (1961) in his original concept of action syntax. By this view, syntax has been built into action production as an ineluctable property. Serial coordination of action is crucial for success in many life tasks. That is why neural systems of action have evolved to be syntactic. Serial coordination is imposed on other action too, even if unnecessary, because syntax is now programmed as a mandatory feature into mechanisms of action production.

The hypothesis that grooming syntax exists because brains have evolved to be 'syntactic generating machines' does not explain why any particular sequential pattern is produced in the order it is. But the hypothesis provides some insight into why rodent pups behave syntactically even before they may have perfected constituent movements. Syntactic patterns emerge early in life because syntax is a fundamental feature of neural systems that generate behavior.

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