Early Ontogeny of Face Grooming in Mice

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A U-shaped function of behavioral growth characterizes the early ontogeny of face grooming in mice. In the first few postnatal days (0–100 hr), mice groom their face by using temporally isolated strokes, or bouts of strokes, which vary in amplitude and symmetry. Later on (100–200 hr), bouts disappear, asymmetry is eliminated, and the amplitude of strokes is gradually restricted; the infants engage in stereotyped, double-handed, temporally isolated strokes. Finally (200–300 hr), bouts reappear, including both short and long, symmetrical and asymmetrical, strokes. These changes, are accompanied by unidirectional changes such as an increasing participation of the trunk, the neck, and the head in grooming, which lead to the flexible organization of face grooming seen in adults. Instead of describing development in terms of emerging unitary "acts," we have recorded from high-speed films three simultaneous aspects of movement: the movements of the separate limb and body segments, the resultant paths which are traced by the forepaws, and the paths of contact which are traced on the face. This method of description discloses (a) reversible changes, and (b) a change in the relative stability of each of these aspects of face grooming, in the course of early ontogeny.

Face grooming is a phylogenetically ancient, cyclical behavior, found in a variety of marsupial and placental species. In adult rodents, it is a highly structured behavior, performed in a variety of behavioral contexts including transitions between locomotion and quiescence, following eating and drinking, and in stressful situations, (Fentress, 1972, Fentress & Stilwell, 1973). The control of grooming in these contexts reflects a subtle and often changing balance between endogenous and exogenous states (Fentress, 1972; 1976).

During the first two weeks of life, grooming behavior changes day by day; therefore, it is impossible to establish fixed categories of behavior during this period. Instead, we have focused on specific aspects of movement, and recorded their change in the course of these days. The aspects which were recorded were movements of the segments of the forelegs, the neck, and the head, paths traced by the forepaws (both in the air and on the face), and paths of contact on the face. A description in terms of these aspects is only partly redundant because the forepaw paths involve face contact during only part

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of the stroke cycle, and this part may vary in different strokes. Also, identical paths may be produced by a variety of movements of the foreleg segments, the neck, and the head.

In adults, all these aspects of face grooming show functional unity, and are therefore difficult to distinguish. In ontogeny, these aspects can be examined in partial isolation because of their differential rate of development, and because of the lack of tight coupling between them.

The continuous follow-up of specific aspects of movement in the course of ontogeny can be instructive in uncovering developmental trends. Different aspects of behavior may change progressively in the same direction, or else undergo temporary reversal in trend. For instance, by following the aspect of support of the body in young macaques, Hines (1942) demonstrated a transient excessive development of leg extension and unarching of torso followed by a subsequent regression of these aspects to a level seen in adult macaques. Similarly; Golani, Bronchti, Moualem, & Teitelbaum (1981), have shown an opposite trend of temporary disappearance with subsequent re-emergence of forward walking in neonate laboratory rats (*Rattus rattus*) and common badgers (*Meles meles*) placed outside their nests. In human infants, stepping (when supported), and imitation of facial expressions, are seen postnatally, then disappear for several months, and then reappear gradually (Bower, 1979). In the present study we describe both progressive and reversible changes along several aspects of face grooming in mice.

Another issue, which is only touched upon in the present study, involves the relative stability of the various aspects of face grooming. When confronted with naturally or artificially induced perturbations, a mouse actively maintains some aspects of grooming, and modifies, or gives up the management of other aspects. By analyzing face grooming under such perturbations, it is possible to establish behavioral priorities in ontogeny.

Method

Samples of face-grooming behavior of 6 individually marked neonate DBA2J-wild hybrid mice were filmed daily from Day 0 postnatally to Day 14. These hybrids were chosen because they groom readily during early ontogeny, and as adults exhibit grooming behavior similar to that described previously (Fentress & Stillwell, 1973).

Before filming, the shoulder, elbow, and wrist joints of the infants were marked with small india ink dots, to demarcate the foreleg segments. Face-grooming behavior was obtained by holding each infant mouse in an upright position, thereby freeing its forelegs. When grooming did not occur spontaneously, pressing the tail or hindquarters facilitated the occurrence of the behavior when the animal was held in the appropriate posture. Using this procedure, it was possible to induce grooming from postnatal Day 0.

Once to several times daily, each mouse was placed in a mirror chamber which had two perpendicular walls and a 45° tilted floor. The mice were inserted into the mirror chamber through a hole in the floor cut to fit the size of their torso, and their hindquarters were held upright, between thumb and forefinger of experimenter, belly and chest above floor level. This procedure provided four simultaneous views of the grooming mouse (Fig. 1).

A high-speed Locam camera and a set of 6 strobe lights synchronized with it, were mounted on the same shaft as the mirror chamber. Strobe lights were used to obtain high-quality sharp images without overheating the young mice during filming. Films were taken at a speed of 100 fps, totaling 1200 m.

To describe the morphology of face grooming during development, the behavior was notated using the conceptual framework of the Eshkol-Wachman Movement Notation (Eshkol & Wachman, 1958). This method is designed to express the relations and changes

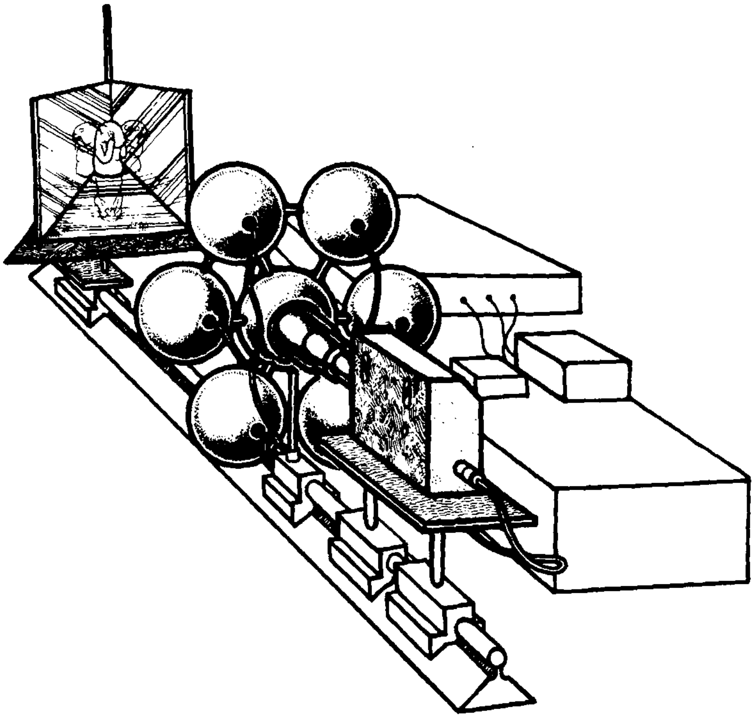

Fig. 1. Filming apparatus.

of relation between the parts of the body, and information which can be derived from these. In the present study, the segments of each of the forelegs, and the neck and the head, are imagined as straight lines (axes), and the body is treated as a system of articulated axes. The movements of a single axis of constant length, free to move about one fixed end, are enclosed by a sphere. Every limb segment in the body can be regarded as such an axis. The curves traced on the surface of the sphere by a moving axis are circles or parts of circles of various sizes and orientations. The stationary axis around which the circle (or its part) is traced is called the axis of movement. A type of movement is determined by the angular relation between the stationary axis (the axis of movement) and the moving axis (the axis of the limb segment). This angle establishes the shape of the path of movement. When the angle between the stationary and the moving axis is 90 degrees, the surface which results from the movement is a plane. When the angle is less than 90 degrees, the surface which results is a cone. When the two axes coincide, the movement becomes a rotatory movement. The positions and movements of each segment of the body are related to a sphere centered upon the joint about which the segment moves. Every segment has its own individual sphere. Movement of a foreleg is the sum of the movements of the separate segments. The positions and movements of the neck and the head, and of the upper arms are described in relation to the chest; those of the forearms in relation to the upper arms; and those of the forepaws in relation to the forearms. In addition to the description of the movements of the segments in relation to one another, the paths traced by the forepaws in space, as well as the paths of contact on the face were drawn directly from the films.

Initially, we employed a high degree of resolution in our descriptions. Then, the degree of resolution was broadened systematically to the point where it was possible to extract statements that applied to all cases of grooming for each animal. To avoid premature pooling of the data, and subsequent loss of structure, the development of grooming in one animal was recorded and analyzed in particular detail (filmed at 19, 39, 40, 57, 62, 82, 86, 87, 106, 107, 108, 131, 153, 175, 205, 223, 253, 278, 300 hr; for a total of more than 200 grooming strokes). These data were then compared to another 350 strokes obtained during the ontogeny of the other 5 mice. Grooming in the nest was also filmed and videotaped to ascertain that it occurred in a natural setting during the developmental period being examined.

Results

Grooming behavior in 2-week-old mice involves preparatory postural adjustments which are then joined by movements of the head and the neck, the upper and lower arms, and the paws. Each grooming stroke is composed of a phase where the forepaws are raised along the face, followed by a phase where they are lowered. In raising, the forepaws pass through the mystacial vibrissae, but do not make direct contact with the face; it is only during part or all of the lowering phase that paw-to-face contact is maintained. During the first two weeks of life, grooming consists of variable number of strokes, ranging from 1 to more than 10 in sequence. These strokes may involve one or both forelimbs, simultaneously, or in succession.

In face grooming, simultaneous and successive spherical movements of the upper arms, forearms, and paws, are transformed into curved paths which are traced by the paws in the air. When these movements are in turn joined by the spherical movements of the head and neck, paths of contact are traced on the face by the forepaws. To understand the control of face grooming and its development, it is necessary to take into account the movements of the limb segments, and their transformation into forepaw paths, which during part of their excursion produce paths of contact on the face. In what follows, we describe briefly the limb segment movements, and then proceed to the other two aspects.

Movements

Arm Movements

Isolated and complete individual grooming cycles start and end with the upper arms dropped, and the forearms slightly flexed so that the forepaws are held below chest level with the back of the paws facing upward. Raising a forepaw toward the face is accomplished through raising of the upper arm in relation to the chest in the sagittal plane, and raising (flexion) of the forearm in relation to the upper arm. As soon as the forepaw reaches the proximity of the chin or earlier, an outward rotation of the upper arm around its longitudinal axis (carrying the forearm laterally, away from the midsagittal plane) is added to the upper arm plane movement. This rotation, sometimes accompanied by upper arm abduction, carries the forearm horizontally sideways, which, when combined with the raising of the forearm, results in a curved path of the forepaw laterad, thereby avoiding direct contact with the face during raising. Toward the end of raising, the forearm supinates, so that the inside of the paw is turned to oppose the side of the face. If the paw is flexed, it aligns with the forearm in midposition. The supination of the forearm continues into the first part of the lowering phase.

Lowering includes an adduction and a rotation of the upper arm that carry the forearm and paw toward the face until paw contact is established. Simultaneously, the forearm is lowered (extension) on the upper arm; when this movement is accompanied by antagonistic raising of the upper arm, the forepaw is transported rostrad along the face. A pronation of the forearm shifts and restricts at this stage the forepaw's contact with the face to the thumb. After the release of paw-to-face contact at snout tip or at the mouth, the forearm continues to extend, carrying the forepaw to chest level. Sometimes, the forearm is carried along further down by an agonistic lowering movement of the upper arm.

While occasionally some of the above described movements are absent, most are present in a complete grooming cycle. However, in many cycles during early ontogeny there are both exaggerations and reductions in the amplitude of the movements; plane movements and rotations of the same limb segment are often performed in succession rather than at the same time; and rotations of the upper arm and plane movements of the lower arm may be inappropriately synchronized, resulting in a ''staircase'' path of the paw (since the elbow joint is a hinge, conical movements of the forearm must involve a simultaneous plane movement of the forearm and a rotation of the upper arm).

In the first 100 hours or so postnatally, a mouse may engage in grooming movements with a single forelimb only, and when the two forelimbs are involved, the raising and lowering phases of the strokes on both sides may not be simultaneous. As show in Table 1, during the first 100 hours, single- or double-handed grooming cycles are performed either individually or in immediate succession, forming bouts of up to 10 strokes (ratio of isolated strokes to bouts approximately 1:1). Following this, nearly all (ratio greater than 10:1) grooming over the next 100 hours is comprised of individually isolated strokes, while still later, uninterrupted bouts containing many strokes begin to reappear, leading to the nearly universal occurrence of protracted grooming sequences seen in older mice.

Head and Neck Movements

The head and the neck play a substantial role in the kinematics of grooming. From the first postnatal day on, at the initiation of a grooming cycle, the head aligns in the midline, the lower jaw forming a right angle with the neck and the chest. The head moves into these coordinates from a variety of initial positions, either before or during the onset of each grooming cycle, so that it arrives there at the initiation of the downstroke. Thus, the hands do not ''search'' for the head, since it is always in the appropriate midline position during the downstroke. Through Day 7 or so, (the first two developmental periods summarized in Table 1), the head stays arrested in the midline until the paws cease contact with the face. Upon release of contact, the head moves up and rotates sideways, out of this position. Movement in and out of this midline position demarcates

TABLE 1 Frequency Distribution of Isolated Grooming Strokes and Uninterrupted Bouts of Grooming Strokes, Shown for Three Phases of Development[a]

	Number of Isolated Strokes	Number of Uninterrupted Bouts[b]	Total Number of Individual Strokes
Phase 1 (0–100 hr)	19	24	123
Phase 2 (100–200 hr)	244	21	307
Phase 3 (200–325 hr)	31	24	141
Total	294	69	571

[a] Since data are pooled for each phase, the gradual reduction and disappearance of bouts toward the end of the second phase is not represented in the table.

[b] Each bout is comprised of a variable number of strokes.

and defines individual cycles, and occurs at the start and end of successive strokes. During the first few hundred hours, when grooming strokes of the forelegs are not yet fully formed, this head position distinguishes grooming from other forms of foreleg raising, such as struggling to escape.

Once paw-to-face contact is established, contact paths can theoretically be generated by movements of the hands alone, movements of the neck and the head in relation to the stationary paws, or movements of both the hands and the head and neck, on the chest. In the first 200 hr or so, the head is arrested during the downstroke, and the hands trace the contact paths on the face alone. Beyond 200 hr, head movements play an increasing role in the production of contact paths: at first, the head is lowered only during the performance of long paths that start at or above eye level. It is lowered before the establishment of contact, to a 45° angle with the chest, and then raised in the course of the foreleg's downstroke. The head movements are not ''necessary'' at this developmental stage for the actual production of long contact paths, since the paws are themselves raised above the point of subsequent contact with the face during the performance of such strokes. Instead of moving up and then rotating sideways out of midline position at the end of a downstroke, the head movements become restricted to the midsagittal plane. Furthermore, whereas at first the head moves up only during the downstrokes of long, individual, isolated, strokes, or during the downstroke of the last grooming stroke in a bout, later it is raised during the tracing of shorter paths, and within bouts. The same applies to head lowering, so that gradually most strokes also involve head lowering during paw raising. The involvement of head movements in the production of contact paths is even more pronounced during grooming in the nest: the more the hands are constrained by being used for support, the greater are the movements of the head. When the paws are fixed, as when a mouse leans on its paws on a sibling in the nest, contact paths may be exclusively produced by the movements of the head, the neck, and even the torso, in relation to the stationary paws (e.g. see Fig. 8). The recruitment of the torso is presumably part of a kinematic synergy that serves to maintain the mouse in balance on its hindlegs as the hands are repeatedly brought toward the center of gravity in raising and away from it in lowering.

Forepaw Paths

During the first developmental period, up to 100–125 hr postnatally, forepaw paths often miss the face completely on one (see Figs. 3B,D, and 4F) or both sides of the face (Fig. 2A). This phenomenon is never observed again after Day 5. Another common phenomenon during the first developmental period is that at the end of the upward path, the paw is displaced excessively both upward and sideways, and then descends for a relatively long distance before establishing paw-to-face contact. This applies for both spatially long (Fig. 2B), and short (Fig. 2C, D) paths of contact. It is as though the forepaw overshoots both up and sideways before descending toward the face. Such overshooting was also observed during the second developmental period, 100–200 hr postnatally (see Fig. 5A); however, the vertical upward component diminishes considerably during this period, involving both shorter paw and contact paths. In other words, the shortening of contact paths during this period is due to a shortening of the forepaw paths, and not to a delay in the establishment of contact in the course of the downstroke. By 200 hr postnatally, all forms of overshooting disappear.

In another group of strokes, one or both paws ascend until reaching the level of the tip of the snout, then proceed almost horizontally sideways and away from the face, and only then are displaced horizontally toward the tip of the snout: in this group, the

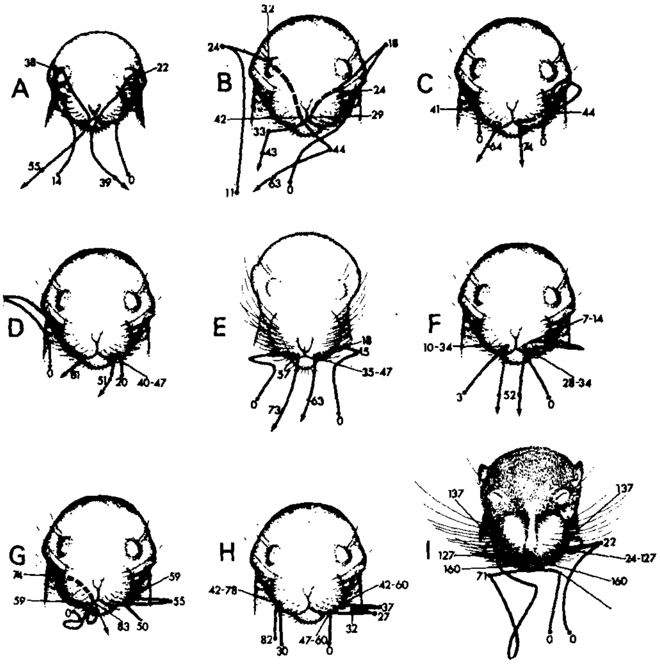

Fig. 2. Frontal views of forepaw paths (uninterrupted lines), and paths of contact (interrupted lines) in specific examples of face grooming, drawn from films taken at 100 fps. Numerals indicate successive frame numbers along the paths. Pairs of numbers refer to the duration of cessation of movement.

overshooting occurs only in the horizontal dimension (Fig. 2E). Such strokes are observed quite often until Day 6 or so (150 hr).

In still another group of strokes the paws are raised toward the snout, and then—instead of ascending along the face without touching it—establish contact with the tip of the snout, bounce sideways, proceed back toward the face, and either re-establish contact with the tip (Fig. 2F,G left paw path) or repeat the sideways movement before making contact with the face (Fig. 2H). These strokes disappear by 200 hr.

Finally, strokes which presumably involve application of excessive paw-to-face pressure during the downstroke are observed until 200 hr. This is indicated by the form of forepaw paths immediately after releasing contact with the snout. Instead of being lowered straight downward (e.g., Fig. 2E,F,H), the paws proceed diagonally sideways to the contralateral side of the body (Fig. 2B), sometimes getting stuck under the chin.

From 200 hr on, ascending paths proceed toward and then along the face, almost touching it. During the third developmental period (beyond 200 hr), the end part of the ascending path may involve contact as well (see Fig. 6E).

Contact Paths

First Developmental Period (Up to 100 hr)

As illustrated in Figures 3 and 4, during the first 100 hr postnatally, contact paths along the face are of a large spatiotemporal variety. They may be restricted to point locations at different facial placements (Fig. 3 A-E), that are maintained momentarily, or for extended periods of time (e.g., 3 B,C,D and 3 A, respectively). The contact paths

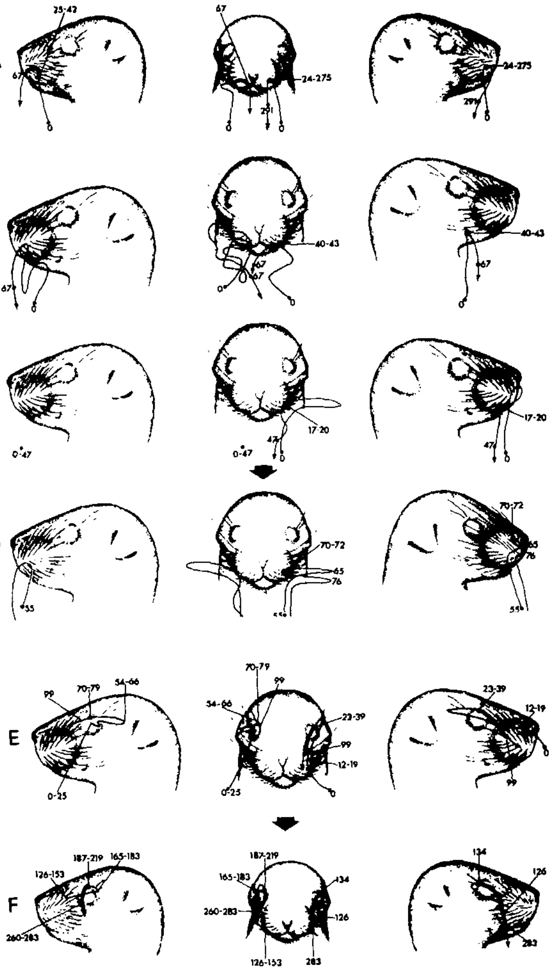

Fig. 3. Frontal and side views of forepaw paths (thin lines), and paths of contact (heavy lines) in specific examples of face grooming performed during the first 100 hr postnatally. Since these drawings were made directly from films taken at the mirror chamber, the left column reflects the right side of the face and the right column reflects the left side of the face. Heavy arrows between rows C and D, E and F indicate that the illustrations were taken from successive strokes in the same bout.

extend from either above or just below the eye to the tip of the snout (Fig. 4). They may also be restricted to relatively short paths at various topographical positions on the face, and have a variety of durations (Fig. 3 A, E, F; Fig. 4 A, B). In all instances, contact is established only during the downstroke and proceeds in a rostral direction. Unlike the contact paths observed later on, contact may be released in the middle of the face without proceeding all the way down to the snout tip (Fig. 3 E,F). During many cycles, contact of one or both paws may not be established at all (Fig. 3 B,D). Sometimes the contact paths on both sides of the face are spatially symmetrical (Fig. 4D), at other times they are alternatingly symmetrical in the sense that over successive strokes a line is traced on one side, and a short path, or no contact at all on the other side; this is followed by the reverse pattern, and so on (Fig. 4 E,F), and at still other times no relation at all between the traces on the two sides can be seen. Whereas sometimes almost identical contact paths are traced during successive cycles, at other times no such consistency can be

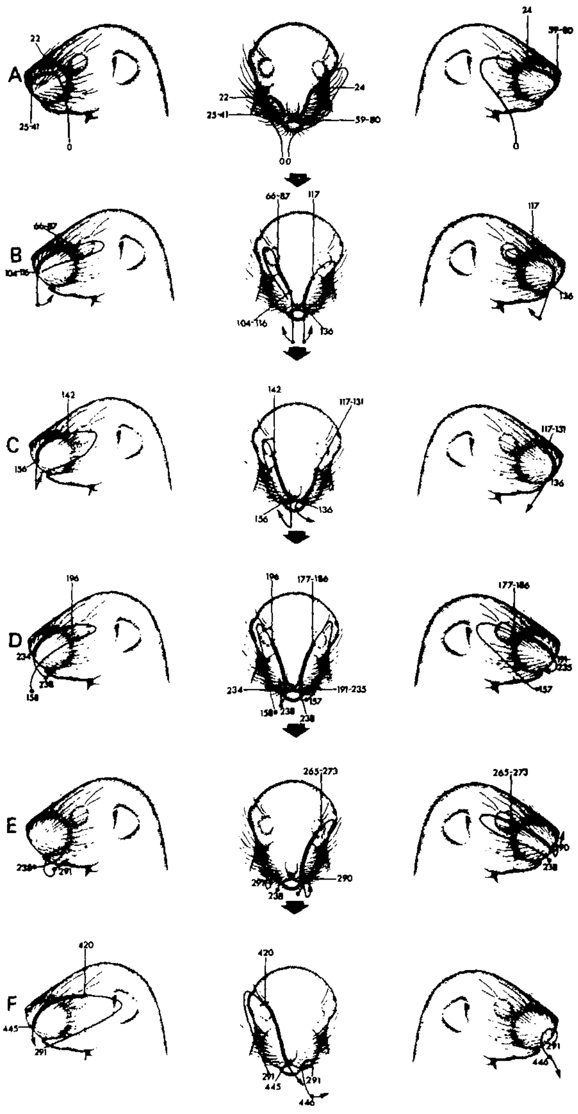

Fig. 4. An uninterrupted bout of face grooming in an 82-hr-old (Phase 1) mouse. Explanation as in Fig. 3.

detected. Successive strokes within the same bout can thus be very similar to each other, and as a group contrast with groups of successive strokes in other bouts that also show within-bout similarity. It is as though the mice have short-term motor habits. This period is characterized by the occurrence of relatively uncoordinated strokes, by the performance of long paths of contact that start above the eye level, and by the occurrence of bouts of several strokes in sequence.

Second Developmental Period (Up to 200 hr)

From 100 to 200 hr, there is a gradual restriction in the variety of forms of contact paths, until by 200 hr, they become quite stereotyped. As is illustrated in Figure

5, by 200 hr (at the end of this developmental period), there are almost no grooming strokes which miss the face; point "paths" disappear; contact is now never released before the paws reach the tip of the snout or mouth; and contact paths which involve extreme spatial or temporal asymmetry on both sides of the face, also disappear. Concurrently, long contact paths which start above eye level, disappear, and there is a progressive restriction of contact paths to the facial area of the mystacial vibrisae; alternatingly symmetrical contact paths which involve an alternation between long paths on the two sides of the face during successive strokes (Fig. 4 E,F) disappear as well; and the mouse no longer performs long bouts of successive grooming strokes. Contact paths include exclusively short-line paths that start just below eye level or lower, and end at the tip of the snout, on the upper lip. Paw-to-face contact is almost always established on both sides of the face relatively symmetrically and simultaneously; the downward movements proceed either simultaneously or in immediate succession; and both paths proceed in a relatively straight line toward the tip of the snout where contact is released (Fig. 5).

Two concurrent trends are manifested during the second developmental period: the two paws always reach the face, contact paths on both sides of the face are temporally connected, and these paths are carried to completion. On the one hand, there is an improvement in motor control. On the other hand, there is a progressive restriction of patterns and elimination of bouts. These two trends result in isolated, short, double-handed, simultaneous, and topographically restricted contact paths.

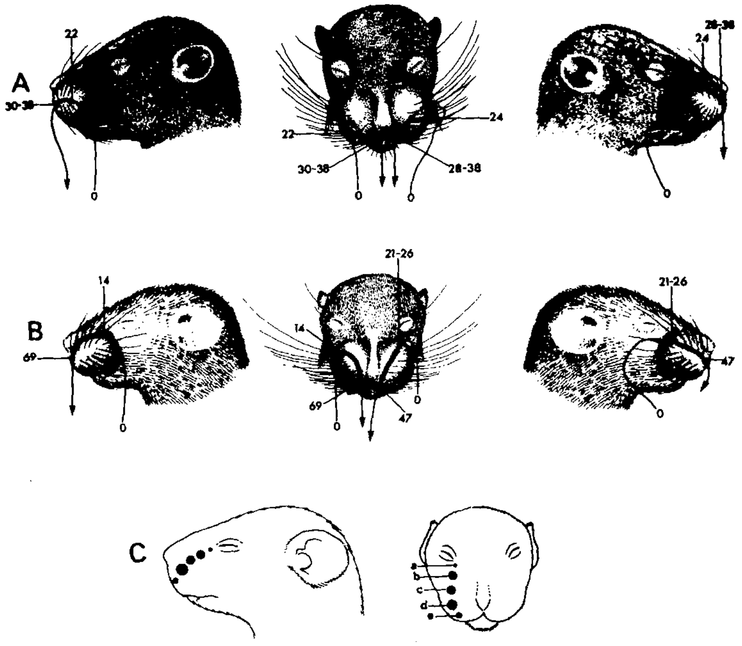

Fig. 5. A and B illustrate two specific examples of face grooming during Phase 2 (100–200 hr). Because of the relative uniformity of the form of isolated strokes, C summarizes the initial topographical location of contact on the face during downstrokes. The diameter of each filled circle represents the percentage of paths of contact ($N = 307$) initiated on this region of the face: a = less than 10%, b = 20%, c = 20%, d = 35%, e = 15%. Since data are pooled for the whole period, the progressive restriction of contact paths in the course of this period is not represented.

Third Developmental Period (200–325 hr)

After 1–2 days of repeated and almost exclusive performance of relatively stereotyped contact paths at the end of the second developmental period, a new developmental trend appears: while the infants continue to perform the above-described stereotyped contact paths, some paths begin to extend at one or both ends. Instead of releasing contact at the tip of the snout, on the upper lip, the paths extend downward toward the mouth and then continue backward along the lips, to the corners of the mouth where they are released (Fig. 6A). At first, the mouth is closed, and then, it may occasionally open minimally as contact passes along the lips. Ultimately, several days later, as the mouth opens, the tongue may come out, presumably wetting the paws. Extension of contact also occurs at the proximal end of the paths which gradually become longer and

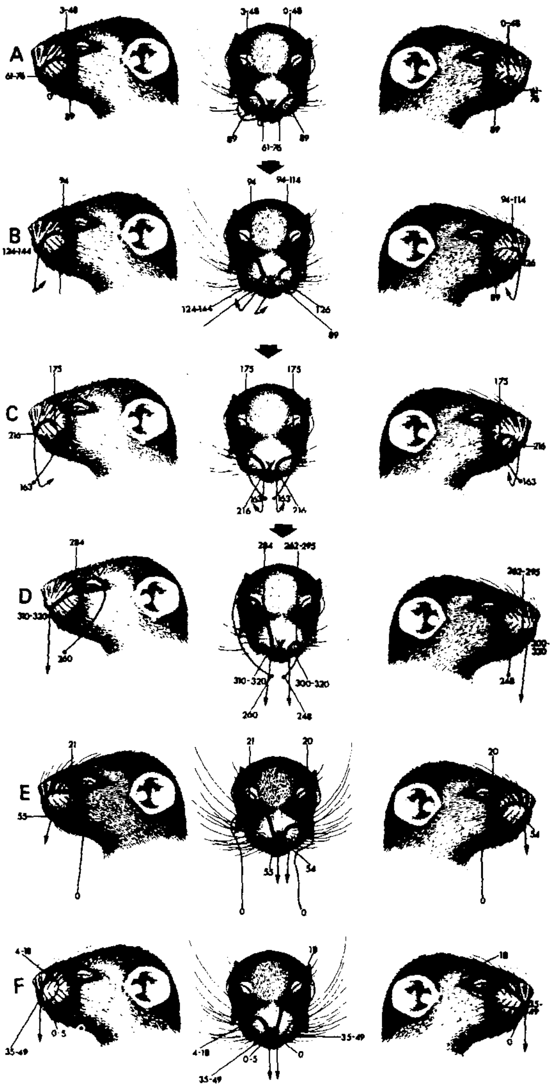

Fig. 6. Representative forepaw and contact paths performed during Phase 3 (200–325 hr). Explanation as in Fig. 3.

curve downward (Fig. 6C,E). The relative number of these extended paths increases over time, ultimately comprising the majority of contact paths. By approximately 275 hr, after an absence of almost a week, the long contact paths which start on the forehead, above eye level, reappear (Fig. 6F). These long paths, are similar in form to the "overhands" previously classified for adults. However, here they occur in isolation, without the progressive build up, and outside of the syntactic context in which they are regularly performed in adults (Fentress, 1972).

The bilateral spatiotemporal symmetry which characterized the majority of strokes performed during the second developmental period, is also observed during the third period, (Fig. 6C), but other topographic forms occasionally observed during the first developmental period reappear as well (Fig. 6F). Similarly, whereas simultaneity in contact path production is preserved, spatial assymmetry reappears not only during the production of long paths (Fig. 6F), but also during the tracing of shorter paths, as one paw traces a "minimal," and the other a much longer path (Fig. 6D). This form of bilateral coordination, which also involves alternation in path length in successive strokes, was classified in adult grooming as "singlestrokes" (Fentress & Stilwell, 1973). When two identical extended and semicircular contact paths (Fig. 6C), are traced simultaneously on both sides of the snout, the so-called "parallels" (Fentress & Stilwell, 1973), can be classified unambiguously for the first time.

Although isolated double-handed strokes are still performed frequently during the third developmental period, bouts of up to 7 or 9 successive strokes, shown only during the first developmental period, reappear as well. These now include "parallels," "singlestrokes," and "overhands"; at first without any apparent sequential order. The characteristic adult alternation of the long contact paths from one side of the face to the other during successive strokes, is not seen yet, and the infants repeatedly trace the long path on the same side.

In general, there is an increasing tendency with age to establish paw-to-face contact on both sides of the face simultaneously. When contact is established on one side of the face at a higher topographical position, the lower paw may often stay in the same position until the contact path on the other side reaches a symmetrical position. At this time both paws proceed downward symmetrically and simultaneously. With age, there is a growing tendency for both paths to reach the frontal aspect of the upper lip within a few film frames (Fig. 6 A–F). If they do not, as often happens during early ontogeny, the paw that reaches the tip first does not release contact, and "waits" for the other paw to reach the symmetrical position, at which time they may either both release contact, or pause for some time in contact (Fig. 5A), and then either release it or, during the third period, proceed to the mouth (Fig. 6A). The frontal aspect of the upper lip serves as a nodal point to which all paths converge, and from which contact is either released or propagated to the mouth.

The Relative Stability of the Three Aspects of Grooming

Naturally occurring and artificially induced perturbations of grooming provide an opportunity to assess the relative stability of the various kinematic aspects of this behavior.

Occasionally, after 150 hr or so postnatally, the newly developed fingernails of the mouse's forepaw may get stuck to the face during a downstroke. At such times, the other, free hand which has descended all the way down to chest level, is raised again up to and beyond the symmetrical topographical location on the face. When it reaches the symmetrical vertical coordinate, the stuck foreleg joins it in raising, thereby getting disentangled (e.g., see Fig. 2I). In such observations, the forepaw paths of the two hands are mutually constrained. To mimic these observations experimentally, the wrist on one forepaw of an adult mouse was tied to a string which was then pulled in the course of a bout of two-handed downstrokes. In the illustrated example (Fig. 7), the pulled forearm continued to perform two circular paths in the air, in front of the mouse's snout while the other, free forearm, immediatey released paw-to-face contact, and performed simultaneous circular paths in the air, in parallel to the constrained hand. This indicates that the paw paths are not only mutually constrained, but also more stable than the contact paths. In other words, in the examined context, the mouse gave up the management of paw-to-face contact for the sake of maintaining the symmetry of the two forepaw paths.

In another filmed observation, a naturally occurring perturbation indicated the priority of contact paths over the specific movements of the limb segments. In this case, a 325-hr-old infant leaned on a sibling with its abducted left elbow, while tracing in sequence three simultaneous and symmetrical contact paths on both sides of its face (Fig.

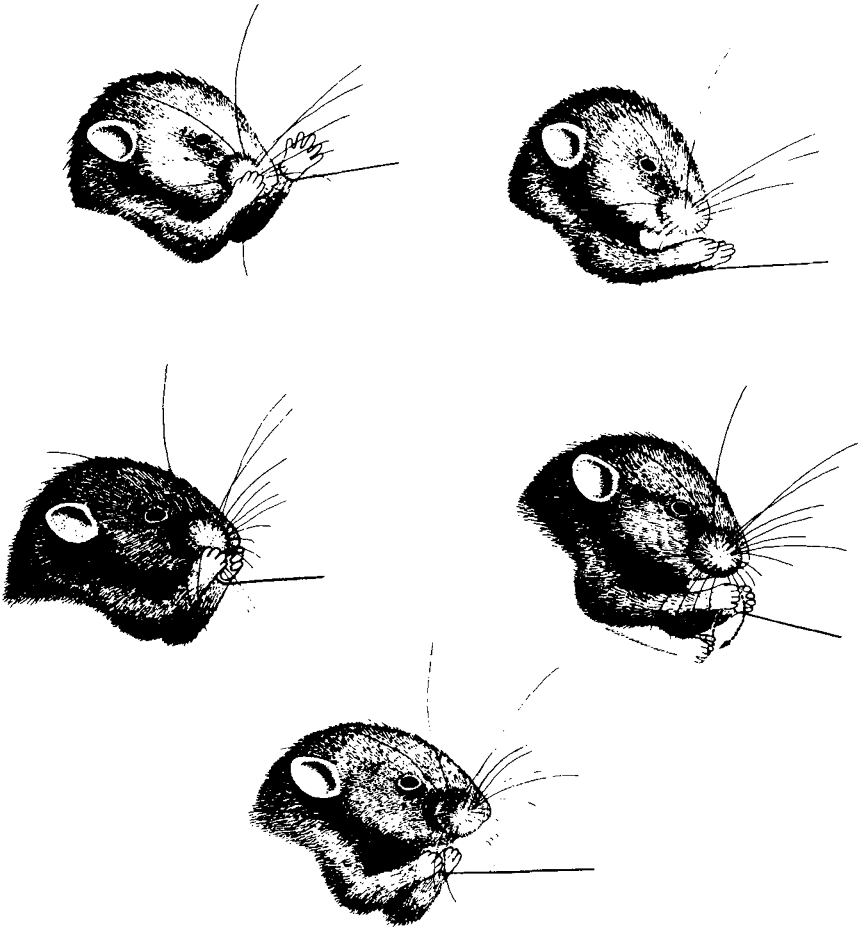

Fig. 7. Experimental perturbation of face grooming in a young mouse. During the course of a grooming cycle, the left arm was gently pulled away from the face with a thread. The direction of two successive circular paths which were traced by each of the forepaws in the air is indicated by the interrupted arrows. The extreme lower and upper positions of the forearms during these cycles are illustrated. Illustrations were made from a film taken at 24fps. The order of occurrence is from bottom left, clockwise, to bottom center.

8). On its free right side, the contact paths were produced using the common strategy of movements of the upper arm on the chest, and the forearm on the upper arm. On its left, the elbow was anchored and used for support, hence the forearm and paw were stationary. In grooming, a kinetic chain was formed between the anchored elbow and the hindlegs. To produce the contact paths on the face, the torso moved on the hindlegs, and the upper arm moved on the stationary elbow. These movements carried the head toward, up, and away from the stationary paw, three times in sequence. Thus, two different strategies of movement were simultaneously involved on both sides in the production of symmetrical paths. In still other observations made in the nest, when a mouse leaned on a sibling on both paws (thus making the paws stationary) it produced symmetrical contact paths on the face by moving the torso, the upper arms, and the head—transporting the face in relation to the stationary paws. As before, the movements of the segments of the body were modified to maintain the form of contact paths.

Discussion

Our observations on face grooming in infant mice reveal two kinds of changes in early development. One kind is monotonical, and the other involves changes which undergo a temporary reversal in trend. The monotonical changes include the gradual disappearance of strokes which miss the face, the elimination of discontinuous and incomplete forepaw and contact paths, and the abolishment of overshooting of the paws

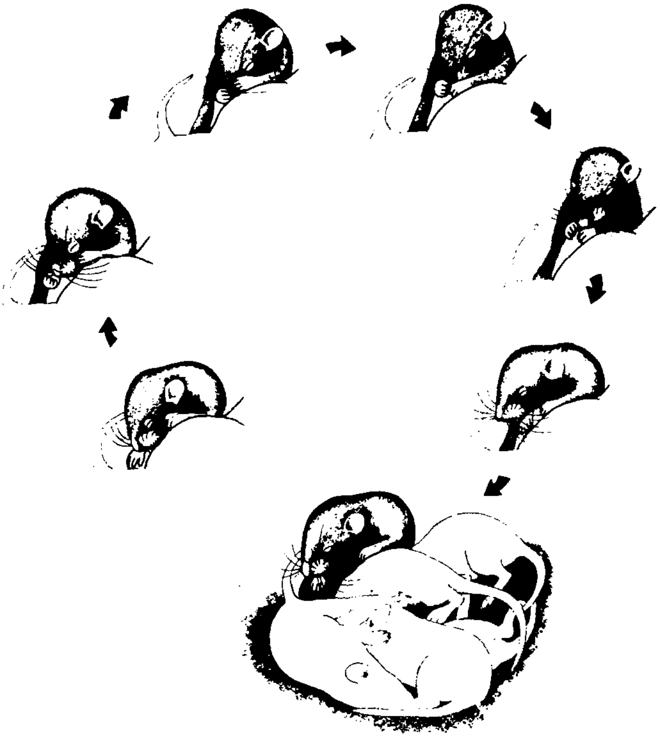

Fig. 8. One out of three successive grooming strokes of a 325-hr-old mouse leaning with its left forearm on a sibling in the nest. Order of occurrence is clockwise, ending with an illustration of the whole litter. The mouse overcomes the constraint imposed upon it by rearing and carrying the head toward the fixed left forepaw, thereby producing symmetrical paths of contact on both sides of the face.

sideways and upward in relation to the face. In time, contact paths are traced during each and every downstroke; once contact is established it is never released before the paw reaches the tip of the snout or the mouth; the paws move smoothly upward along the face without touching it, and downward on the face without halting or getting stuck; upper arm rotations and forearm plane movements become combined in raising; smoothly curved paw paths turn into contact paths without first moving away from the face; and the grooming strokes on both sides of the body start and end at about the same time.

The changes which undergo a reversal in trend include the gradual restriction and subsequent extension of forepaw and of contact paths; the disappearance and subsequent re-emergence of simultaneous asymmetric paths, and the disappearance with subsequent re-emergence of bouts of strokes.

The occurrence of reversible changes during development forces us away from the view that development consists exclusively of a gradual improvement in performance (Oppenheim, 1981; Strauss & Stavy, 1981). The appearance of U-shaped functions of behavioral growth is quite common. Repetitive processes which involve acquisition, loss, and subsequent reacquisition of sensorimotor skills in human infants have been described by Bower (1979; 1981). To cite but one example, reflexive stepping (Thomas & Autgarden, 1966) shows a clear U-shaped function of behavioral growth. Similarly, both laboratory rat (*Rattus norvegicus*) and common badger (*Meles meles*) infants, walk forward when placed outside their nest during the first few days postnatally, then forward walking disappears for a period of 2 days in the rat and 7 weeks in the badger, to re-emerge gradually, day by day, in the third developmental period (Golani et al., 1981). Depending on which aspects of behavior are measured, nonmonotonical behavioral functions may take the form of an inverted U. For instance, the amount of extension of the legs in walking, and the amount of erectness of the torso in sitting in infant rhesus monkeys, first reaches in ontogeny an exaggerated peak, and only then returns to the level observed in the adult (Hines, 1942). Finally, the appearance of U-shaped functions of behavioral growth in the course of speech development has been described by Kent (1976), and Menn (1981).

Upon juxtaposing the three complementary representations of face grooming in neonate mice, we have found that postnatal development of grooming in the mirror chamber situation may be divided roughly into three phases. Initially (first 100 hr), the kinematic articulations of the forelegs are rich and loosely structured while the articulations of the axial body segments are limited, involving only a few head and neck movements; forepaw and contact paths are diverse, but the congruence between these paths is poor. As in the human neonate walking response (Forssberg & Wallberg, 1981; Thelen, 1983), grooming is elicited only when the infant is supported. During the second phase (second 100 hr), the size, symmetry, and number of strokes becomes restricted and relatively stereotyped, while the timing and coordination of the limb-segment movements improves. The kinematic contribution of the head and the neck is still small, involving only movements of the head in and out of the midline position at the start and end of individual strokes. Subsequently (200–350 hr), the initial variety reappears, involving bouts of extended simultaneous forepaw and contact paths which are coupled smoothly, producing two basic types of symmetry. The involvement of the head, neck, and sometimes the torso increases progressively as the head joins the paws by moving in the opposite direction, first during the initiation and termination of strokes within bouts, and then during the stroke itself, so as to contribute to the tracing of contact paths on the face. Ultimately, with the establishment of support, the torso also joins in moving. At this stage it is the interplay between the torso, neck, head, and forelimbs that produces the contact paths. The system has now become fully interconnected and failure in the movement of one or several segments of the forelegs is immediately compensated by movement of other parts of the body.

By describing the development of face grooming in terms of three simultaneous aspects of movement rather than as a sequence of unitary acts, and by using natural and experimental perturbations, one is led to ask about priorities of control in the sense suggested by Powers (1973). What are the aspects of movement that have priority at different developmental ages in particular situations? How is it, for example, that circular contact paths on the face gain priority over a specific allocation of movements to the individual limb and body segments in one situation (Fig. 8), while such paths of contact are sacrificed for the sake of the production of circular and symmetrical forepaw paths in the air in another situation (Fig. 7)? Such examples indicate that it should be possible to study experimentally the change in priorities in the course of development. A specification of these priorities is a prerequisite for any future theory of the control of face grooming by the central nervous system.

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