

Motor competition in the prenatal ontogeny of species-typical behaviour

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Abstract. Facial wiping, an action pattern antecedent to grooming behaviour in adult rodents, can be elicited during the prenatal period by infusion of a lemon solution into the mouth of the fetal rat, *Rattus norvegicus*. In altricial species such as the rat, the wiping response to chemosensory infusion temporarily disappears during early postnatal development. The expression of facial wiping may be constrained by features of the postnatal environment, or may be suppressed through competition with incompatible motor responses. To test these alternative hypotheses, a comparative study of altricial and precocial rodent fetuses was conducted. Fetuses of two altricial species, Norway rats and Mongolian gerbils, *Meriones unguiculatus*, expressed the wiping response during the last 1–2 days of gestation. In contrast, fetal cotton rats, *Sigmodon hispidus*, and spiny mice, *Acomys cahirinus*, exhibited accelerated emergence followed by prenatal disappearance of the wiping response, which is consistent with a motor competition hypothesis. The age at which the wiping response disappeared coincided with the emergence of contact righting and quadrupedal locomotor behaviour, which appear to interfere with the expression of facial wiping.

The development of motor behaviour often is portrayed as a process involving the initial expression of a simple or rudimentary behaviour pattern that undergoes steady, monotonic improvement in coordination and organization with advancing age. However, many examples of behaviour patterns that exhibit temporal discontinuity or transient retrogressive change in their development are now recognized. For instance, human neonates exhibit stepping movements when the body is supported externally and the feet are placed in contact with a substrate. The stepping reflex can be elicited for about 2 months after birth. In older infants, stepping is not expressed until 10–12 months of age, when bipedal walking appears. The temporal discontinuity between the disappearance of neonatal stepping and the emergence of walking has been interpreted as evidence that the two motor patterns are developmentally unrelated (McGraw 1940). More recent kinematic and electromyographic analyses of stepping by newborns, spontaneous

kicking by older infants, and walking by toddlers have revealed an underlying continuity in all three expressions of motor behaviour (Thelen & Fisher 1982). Experimental evidence suggests that infants 3–10 months old fail to exhibit stepping because leg mass increases faster than muscular strength in the legs during early growth; gravitational load appears to constrain the continuous expression of the walking step cycle (Thelen et al. 1984).

A second case of reversible changes in motor development involves the response of fetal and neonatal rats, *Rattus norvegicus*, to certain forms of chemosensory stimulation. A solution prepared from lemon extract infused directly into the mouth of the fetus consistently elicits a distinctive response. One aspect of the response is an increase in overall motor activity that quickly rises to a peak and dissipates more slowly; the entire time-course of the response is about 1 min (Smotherman & Robinson 1987). A principal component of the behaviour expressed during the peak of fetal activity is facial wiping, a stereotyped action pattern that involves placement of one or both forepaws along the side of the head, generally just behind the eyes, and sweeping the limb(s) in a rostral direction

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in contact with the face. Facial wiping is similar to the overhead limb strokes that occur during face grooming in young mice (Golani & Fentress 1985) or chemically evoked aversion responses (Grill & Norgren 1978; Johanson & Shapiro 1986) in pre-weaning and adult rats, suggesting that prenatal facial wiping is developmentally related to mature grooming behaviour.

The expression of the wiping response, like the stepping reflex of human neonates, is discontinuous during postnatal development. Although facial wiping is rarely expressed by fetuses in the absence of explicit stimulation, the wiping response is reliably elicited in fetal rats by chemosensory or somatosensory stimuli on days 20 and 21 of gestation. It also can be observed in newborn rats, but during the 3 days subsequent to birth rat pups become much less likely to exhibit wiping in response to lemon infusion. Experimental manipulation of features of the postnatal environment can help to promote the expression of the wiping response. For instance, suspension of the pup's body in a buoyant fluid, which decreases the effects of gravity on the neonatal motor system and frees the forelimbs from involvement in postural support, significantly increases the incidence of facial wiping on postpartum day 1, but is less effective on day 3 (Smotherman & Robinson 1989). Facial wiping does not re-emerge as a consistent element of the rat's behavioural response to chemosensory stimulation until near the end of the second postnatal week (Johanson & Shapiro 1986; Robinson & Smotherman, in press), when pups begin to exhibit the ability to balance on the rear legs.

Two hypotheses may be advanced to account for the neonatal disappearance of the wiping response. The first hypothesis maintains that unique contextual features of the postnatal environment constrain the expression of facial wiping, in much the same way that stepping is constrained in human infants. For instance, the neonatal rat experiences greater mass loading on the limbs because it is no longer surrounded by a supportive fluid medium. At the same time, the newborn is perpetually in contact with a hard substrate that has no clear counterpart in utero. The effects of gravity and a hard substrate thus may limit the expression of motor behaviour.

A second hypothesis is derived from the observation that newborn rats exhibit a variety of motor responses immediately after infusion. At different points in development the response of the fetus and

neonate may not be unitary, but rather consist of multiple patterns of behaviour that are simultaneously or sequentially activated. Because different behavioural patterns may involve limb movements that cannot physically be expressed at the same time, different motor responses in effect compete for expression. The consequence of such motor competition may be the disruption of behavioural patterns, such as facial wiping, that require coordination of multiple body parts and occur only in close temporal association with the moment of stimulus presentation. The appearance of conflict between incompatible behavioural processes is a concept with a long tradition in ethology (Tinbergen 1951; Hinde 1970), but the potential importance of motor competition as a determinant of pattern in behavioural development has received scant attention (cf. Kruijt 1964; Groothuis 1989).

An environmental constraint hypothesis and a motor competition hypothesis both yield predictions that are consistent with observed patterns of expression of facial wiping by fetal and neonatal rats. A critical test of these two hypotheses should dissociate the effects of potentially incompatible behavioural responses from the neonatal transition to a postnatal environment. This ideal is difficult to achieve in studies of *R. norvegicus*, which, like most other murid rodents, give birth to altricial offspring. However, examination of closely related rodents that bear precocial offspring can serve to separate the developmental timing of behavioural maturity and birth. Precocial development has independently evolved in two lineages within the family Muridae, once in the murine genus *Acomys* (the spiny mice of the Middle East and North Africa), and once in the cricetine genus *Sigmodon* (the cotton rats of North and South America). The offspring of these rodents are well furred, have eyes that open within 24 h, and exhibit relatively adult-like motor abilities (such as walking) soon after birth.

The action patterns employed in grooming or comfort behaviour are highly conserved during evolution. Virtually all mammals with non-specialized limb anatomy employ the forelimbs in grooming movements that are directed toward the head and face (Eisenberg 1981), and overhead face washing strokes are expressed by Myomorph, Hystricomorph and Sciuromorph rodents (Berridge 1990). Therefore, if facial wiping is ontogenetically related to adult grooming behaviour, then it should be present in the repertoire

of other fetal rodents. Moreover, prenatal facial wiping should exhibit a developmental time course that is accelerated relative to the timing of birth in precocial species. Differences in the ontogenetic timing of this action pattern in altricial and precocial species thus provide a means for testing critically the environmental constraint and competing response hypotheses. If the expression of facial wiping is constrained solely by features of the postnatal environment, then precocial fetuses should exhibit a continuous distribution of facial wiping from its earliest emergence during gestation through term. If, on the other hand, facial wiping is suppressed due to competition with other behavioural patterns, then the prenatal expression of facial wiping in precocial fetuses should disappear before birth coincident with the appearance of incompatible motor responses.

METHODS

Subjects

Subjects were fetuses produced in timed matings of four species of murid rodents. Two species, representing the murine and cricetine branches of the family Muridae, give birth to altricial offspring: Norway rats (the progeny of Sprague-Dawley females bred to Long-Evans males; gestation length = 21 days) and Mongolian gerbils, *Meriones unguiculatus* (gestation length = 24 days). The other two species, from the same subfamilies, give birth to precocial offspring: spiny mice, *Acomys cahirinus* (gestation length = 38 days), and cotton rats, *Sigmodon hispidus* (gestation length = 27 days). Gestational ages of fetal subjects were determined by different means for different species (vaginal smear, detection of copulatory plug, date of birth of previous litter) and were confirmed by comparing the body mass of each subject to tables of fetal growth constructed for each species from pregnancies of known duration. At all times, adult and fetal subjects were maintained and treated in accordance with guidelines established by the National Institutes of Health and the Animal Behavior Society.

Preparation of Fetuses

To permit direct observation of fetal behaviour, the pregnant female was placed under brief ether anaesthesia and a small volume of ethanol (30–

100 μ l) was injected into the spinal canal between the first and second lumbar vertebrae, producing complete blockade of the spinal cord in the upper lumbar–lower thoracic region. The prepared female was placed in a holding device and immersed to chest depth in a buffered physiological saline solution maintained at 37.5°C. This preparation has the effect of eliminating sensation in the lower half of the body of the pregnant female, permitting direct access to fetuses without the use of general maternal anaesthesia, which suppresses fetal activity. This general experimental procedure has been employed extensively in previous research on fetal rats (Smotherman & Robinson 1986; 1991).

The uterus was externalized through a low midline incision in the abdomen. A single fetus was selected as an experimental subject for this study and was externalized into the saline bath through a small incision in the uterus. (The data in this report were collected as part of a larger study of fetal development (Robinson 1989). To minimize the number of pregnant females needed, other fetuses within each pregnancy were used as subjects in different experiments.) Special care was exercised to maintain unimpaired blood circulation within the umbilical cord and intact placental–uterine attachment. All subject fetuses remained healthy throughout the period of observation. A minimum sample size of five fetuses, each from different pregnancies, was tested in each species at each gestational age.

The subject fetus was fitted with an intra-oral cannula, which consisted of a 2–3 cm length of PE-10 polyethylene tubing. Installation of the cannula was accomplished using procedures developed for application to neonatal rats (Hall & Rosenblatt 1977; Kehoe & Blass 1985) and subsequently adapted for use with rat fetuses (Smotherman & Robinson 1991). Rat fetuses with an intra-oral cannula do not differ behaviourally from unmanipulated fetuses. To deliver the infusion, the free end of the cannula was connected to a longer piece of PE-50 tubing, which in turn was attached to a micrometer syringe containing the chemosensory test solution. This system permits precise infusion ($\pm 1 \mu$ l) of a test solution to a fetus without otherwise interrupting ongoing activity. The test solution employed in the present study was prepared as a well mixed 1:3 dilution of pure lemon extract (Schilling) in isotonic saline, which is the same test stimulus as used in previous studies of chemosensory responsiveness and prenatal facial wiping in fetal and neonatal rats.

Each subject was tested in a 2-min observation session. A 20- μ l infusion of the lemon solution was delivered in a 1–2 s pulse at the end of the first minute of the session. Subjects were observed continuously during the session, and each instance of fetal movement was noted and entered into a micro-computer serving as a real-time event recorder, preserving information about the frequency and timing of fetal motor activity. In addition, the entire observation session was recorded on videotape (VHS format, 33.35 mm/s) for later analysis.

Activity Analysis

The sum of all instances in which the fetus moved was used as a measure of overall fetal activity. To measure the fetal response to lemon infusion, the motor activity of fetuses during the observation session was broken into a series of 5-s intervals for analysis. A baseline activity score (designated 'pre-infusion') was calculated from the total number of fetal movements during the 55 s (11 intervals) before infusion and expressed as a mean rate per 5-s interval. To measure the fetal response to lemon infusion, activity of fetuses during the 60-s period following infusion was divided into 12 intervals. Activity was also tabulated for the 5-s window in which the infusion occurred. For each age tested, fetal activity across these 14 scores was analysed in a one-way repeated measures ANOVA. Where a significant main effect of 5-s intervals was evident ($\alpha = 0.05$), a planned comparison using a one-tailed Dunnett *t*-test (Roscoe 1975) was conducted to determine whether the post-infusion interval exhibiting the highest rate of fetal movement was significantly greater than the pre-infusion baseline. A fetal activity response to lemon infusion was judged to be present only if this planned comparison was significant. To assess age-related changes in the magnitude of fetal response to lemon infusion, activity scores for the six 5-s intervals immediately following infusion were summed for each age. This combined 30-s activity score was compared across ages in a one-way ANOVA.

Videotape Analysis

Videotapes of each observation session were reviewed at reduced speed and frame-by-frame to determine whether facial wiping occurred in response to lemon infusion. An instance of wiping was scored if one or both forelegs made contact

with the face while moving in a rostral direction. All wiping strokes expressed after infusion were considered part of a single bout of wiping and the time between the first and last strokes was the duration of the wiping bout. Videotapes were further examined for evidence of organized fetal responses other than facial wiping. The expression of two patterns of motor behaviour in particular, contact righting and quadrupedal locomotion, was examined explicitly.

The righting reflex is a fundamental behaviour pattern of terrestrial vertebrates that involves actively returning the body to a prone posture after displacement. Contact righting is the form of this behaviour that occurs when the body is in contact with a solid substrate (as distinct from air-righting, which is governed by a vestibular sense). The development of contact righting has long been appreciated to have its origin in the prenatal period (Windle & Fish 1932), particularly in precocial species (Carmichael 1934; Robinson & Smotherman, *in press*). A principal component of the contact righting response of neonatal rodents is ventriflextion or torsion of the body trunk around its long axis (Altman & Sudarshan 1975). To quantify righting behaviour in response to infusion, the incidence of both trunk torsion and successful attainment of a prone body position during the post-infusion interval were determined. A positive trunk torsion response was scored if the fetus's shoulders and hips were rotated at least 45° relative to one another in the 60-s interval following infusion. Similarly, a positive prone position was scored if the fetus attained a position within 45° of prone for at least 1-s during the 60-s post-infusion interval.

Another pattern of behaviour that is exhibited to varying degrees by neonatal mammals is quadrupedal locomotion. Mature walking locomotion involves coordination of stepping movements by all four limbs in a characteristic pattern of foot contact (Halbertsma 1983). In young animals, particularly in altricial species, inter-limb coordination is first apparent within a girdle: cyclic movements of contralateral limbs are alternated, with each limb about 50% out of phase with the other limb. Alternated stepping movements by limbs in the pectoral or pelvic girdles previously have been described for 20-day-old rat fetuses (Bekoff & Lau 1980) and are spontaneously produced by many neonatal mammals, even when removed from contact with a substrate (so-called air-stepping) (Bradley & Smith 1988). A positive locomotor

response was scored in the present study if the fetus exhibited activity of all four limbs while in a prone position, with the contralateral limbs moving in an alternated, stepping pattern.

RESULTS

Fetal Activity after Infusion

The results of the repeated-measures ANOVAs and planned comparisons for the four murid rodents are summarized in Table I. Fetuses exhibited an increase in overall motor activity after infusion. The pattern of change in activity was consistent with previous reports: activity quickly increased during the first 5–15 s after infusion, then decreased over the next 20–30 s, eventually returning to pre-infusion levels (Fig. 1). Planned comparisons of fetal activity before infusion and at the peak of activity indicated significant behavioural responses occurred at all five ages (Fig. 2). The amount of fetal movement after infusion also varied with age ($F_{4,34} = 3.7$, $P = 0.014$); fetuses on days 17 and 21 were less active after infusion than fetuses on days 18–20.

Owing to their small size, *M. unguiculatus* fetuses were tested only on days 21–24 of gestation. Except on day 24, lemon infusion elicited little or no fetal response (Table I and Fig. 2). At this age, the characteristic spike in activity immediately after infusion followed by a gradual decline in fetal activity was apparent (Fig. 1). Although the number of movements expressed after infusion looked to be greater on day 24, fetal activity did not vary significantly with fetal age.

Acomys cahirinus fetuses expressed responsiveness to lemon infusion at a relatively early age. At all ages tested, fetal activity increased sharply after infusion (Table I and Fig. 2). The rate of fetal movement began to rise during the interval of infusion and reached a peak only 5 s after infusion. By the third post-infusion interval (15 s), fetal activity returned to near baseline levels (Fig. 1). Comparison of 30-s activity scores at different ages revealed no significant change in the magnitude of fetal response during gestation.

Sigmodon hispidus fetuses expressed responsiveness to lemon infusion at a relatively early age. The slight increase in activity on day 18 was not significant, but at all subsequent ages fetal activity increased sharply after infusion (Table I and Fig. 2). The temporal pattern of activity change was

very similar to that described for *A. cahirinus*: the rate of fetal movement was noticeably elevated during the interval of infusion, increased to a peak within 5 s, and diminished to near-baseline levels only 15–20 s after infusion (Fig. 1). Examination of 30-s activity scores indicated that the total number of fetal movements also varied as a function of age ($F_{9,59} = 3.9$, $P < 0.001$). Post-hoc comparison of means revealed that activity after infusion was significantly reduced on days 18–19 relative to later ages.

Facial Wiping

Facial wiping in response to lemon infusion exhibited very regular patterns of expression in all four species. In *R. norvegicus*, facial wiping was not observed on days 17–19, but was performed by 18 of 20 fetuses tested on the last 2 days of gestation (Fig. 3). The apparent difference in the ages of fetuses showing expression of facial wiping was confirmed by a chi-squared test of independence ($\chi^2 = 32.7$, $df = 4$, $P < 0.001$). This finding corresponds precisely to previous descriptions of the developmental emergence of this action pattern among rat fetuses tested under comparable conditions.

The occurrence of facial wiping was very consistent across individuals. Wiping typically appeared in a flurry of multiple strokes during the phase of elevated fetal activity. Comparison by *t*-test indicated that the number of strokes performed during the bout of wiping did not differ between days 20 and 21; a mean (\pm SE) of 6.5 ± 0.8 strokes occurred during the wiping bout. The mean latency between infusion and the first facial wipe, measured to the nearest 1-s from videotape records, was 5.6 ± 0.7 s on day 20 and 7.4 ± 1.3 s on day 21. The difference in mean latency to wipe was not different between these two ages.

In *M. unguiculatus*, facial wiping was not observed until day 24, when about half of the subjects exhibited wipes in response to lemon infusion (Fig. 3). To permit statistical comparison, days 21–23 were collapsed together, creating a 2×2 matrix. This comparison revealed a significant difference between ages ($\chi^2 = 10.5$, $df = 1$, $P = 0.001$). On day 24, a mean of 1.8 ± 0.2 strokes occurred in the wiping bout. The latency between infusion and the first facial wipe was 8.6 ± 4.0 s.

Facial wiping also was elicited by lemon infusion in *A. cahirinus*, but at a relatively earlier age (Fig. 3). Wiping was not expressed on day 26 or on days

Table 1. Results of one-way repeated-measures ANOVAs, presenting sample size, *F*-ratio, degrees of freedom and level of significance for each analysis, of fetal motor activity after lemon infusion

<i>R. norvegicus</i>											
Day	17	18	19	20	21	22	23	24	25	26	27
<i>N</i>	5	5	9	11	9	5	5	9	5	7	7
<i>F</i>	3.5	4.5	4.5	6.4	2.8						
<i>df</i>	13,52	13,52	13,104	13,130	13,104						
<i>P</i>	<0.001	<0.001	<0.001	<0.001	<0.001						
Peak response†	**	**	**	**	**				**	**	**
<i>M. unguiculatus</i>											
Day	21	22	23	24							
<i>N</i>	5	5	5	9							
<i>F</i>	0.7	0.7	0.5	2.1							
<i>df</i>	13,52	13,52	13,52	13,104							
<i>P</i>	>0.10	>0.10	>0.10	0.022							
Peak response†	NS	NS	NS	*							
<i>A. cahirinus</i>											
Day	26	28	30	32	34	37					
<i>N</i>	7	5	8	5	5	6					
<i>F</i>	12.6	9.0	7.2	5.9	12.8	3.3					
<i>df</i>	13,52	13,91	13,52	13,52	13,65	13,78					
<i>P</i>	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001					
Peak response†	**	**	**	**	**	**			**	**	**
<i>S. hispidus</i>											
Day	18	19	20	21	22	23	24	25	26	27	
<i>N</i>	5	6	11	13	5	5	5	5	7	7	
<i>F</i>	1.7	2.3	5.5	10.8	5.7	4.3	2.4	4.4	9.4	3.6	
<i>df</i>	13,52	13,65	13,130	13,156	13,52	13,52	13,52	13,52	13,78	13,78	
<i>P</i>	>0.05	0.016	<0.001	<0.001	<0.001	<0.001	0.014	<0.001	<0.001	<0.001	
Peak response†	NS	*	**	**	**	**	**	**	**	**	

†Results of the planned comparisons of the peak response employing the Dunnett-*t* statistic are presented as NS (not significant), **P* < 0.05 or ***P* < 0.01.

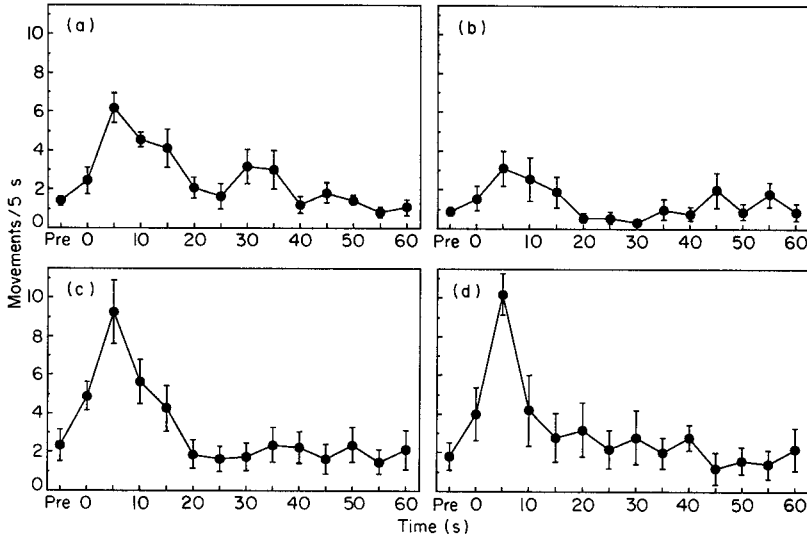


Figure 1. Temporal changes in overall fetal activity during the 60-s period after lemon infusion. A typical graph, depicting the fetal response at a single age, is presented for each of the four murid species: (a) *R. norvegicus*, day 20; (b) *M. unguiculatus*, day 24; (c) *A. cahirinus*, day 30; (d) *S. hispidus*, day 22. The four graphs are grouped to reflect differences in development (altricial a, b; precocial c, d) and taxonomic lineage (murine a, c; cricetine b, d). Points represent the mean \pm SE number of fetal movements per 5-s interval.

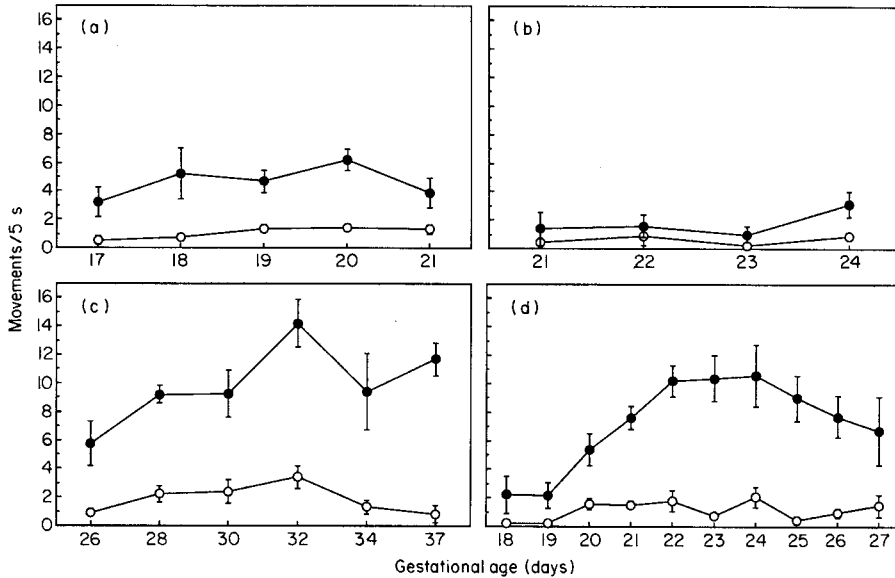


Figure 2. Fetal motor activity during the pre-infusion baseline period (○) and the peak of fetal response to lemon infusion (●) for four murid species: (a) *R. norvegicus*; (b) *M. unguiculatus*; (c) *A. cahirinus*; (d) *S. hispidus*. The graph for each species summarizes changes in fetal responsiveness to infusion across a range of gestational ages. Points represent mean \pm SE activity.

32–37, but occurred in response to lemon infusion on days 28 and 30. To analyse this pattern, samples from adjacent ages were collapsed together, creating

three age groups: 26+28, 30+32, 34+37. Even when the two ages for which wiping was apparent were split in this fashion, significant age-related

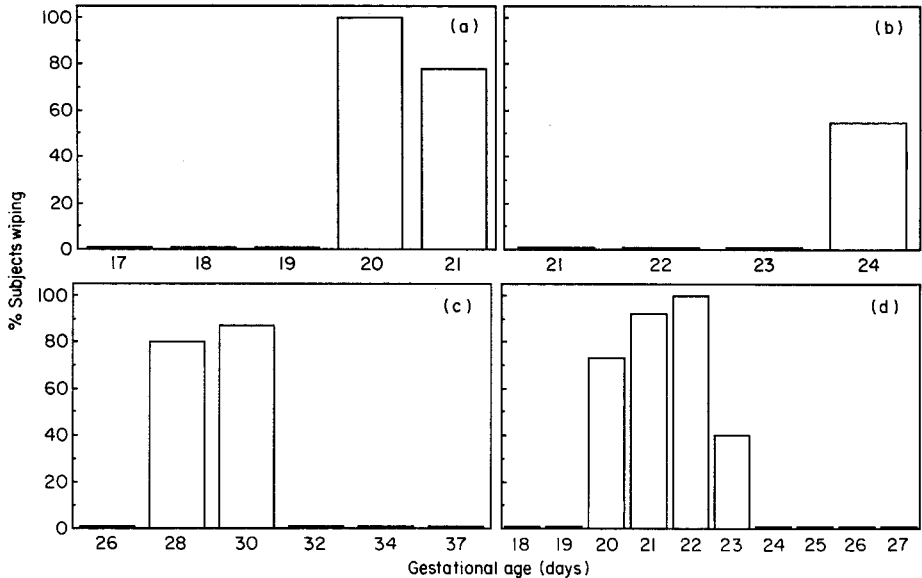


Figure 3. Percentage of fetal subjects that exhibited facial wiping in response to lemon infusion at different gestational ages in four murid species: (a) *R. norvegicus*; (b) *M. unguiculatus*; (c) *A. cahirinus*; (d) *S. hispidus*.

change in the expression of the wiping response was evident ($\chi^2 = 8.2$, $df = 2$, $P = 0.017$). It was particularly notable that facial wiping was not expressed after day 30. An overall average of 4.2 ± 1.0 strokes occurred in the bout of wiping, which did not vary between days 28 and 30. The delay between infusion and the first facial wipe also did not differ significantly as a function of fetal age. On day 28, wiping latency was 8.3 ± 4.0 s; on day 30 it was 11.7 ± 2.3 s.

The pattern of developmental expression of facial wiping was virtually identical in *S. hispidus* (Fig. 3). Wiping was not expressed on days 18–19 or on days 24–27, but was exhibited by the majority of fetuses tested on days 20–23. To compare the incidence of facial wiping at different ages, adjacent ages with sample sizes less than 10 were collapsed together, yielding the following age groups: 18 + 19, 20, 21, 22 + 23, 24 + 25, 26 + 27. The expression of wiping varied significantly among these six age groups ($\chi^2 = 47.1$, $df = 5$, $P < 0.001$). As in *A. cahirinus*, facial wiping was expressed by *S. hispidus* fetuses only during a narrow window relatively early in gestation. The number of strokes performed during the bout of facial wiping (2.4 ± 0.3 strokes) did not vary with fetal age. However, variation was apparent in the latency between infusion and the first facial wipe (in s): 4.3 ± 1.9 (day 20), 13.5 ± 2.2 (day 21), 17.0 ± 3.8 (day 22), 3.0 ± 0.0

(day 23). Excluding day 23 from analysis (owing to small sample size), a one-way ANOVA indicated that wiping latency was significantly less on day 20 than on subsequent days ($F_{2,22} = 5.9$, $P < 0.01$).

Other Responses to Infusion

Organized responses other than facial wiping were absent in both *R. norvegicus* and *M. unguiculatus*. Among *R. norvegicus* fetuses, only one subject (out of 39) exhibited trunk torsion, and none attained a prone position or exhibited a locomotor response during the post-infusion interval. In *M. unguiculatus*, none of the subjects exhibited any of these responses.

Examination of videotape records provided evidence for righting and locomotor responses to lemon infusion in *A. cahirinus*, especially in older fetuses. Trunk torsion was performed by 8 of 20 fetuses (40%) on days 26–30, which was significantly less than the 12 of 16 fetuses (75%) that exhibited torsion on days 32–37 ($\chi^2 = 4.4$, $df = 1$, $P = 0.036$). The incidence of prone positions after infusion showed a similar trend, with 0 of 20 fetuses (0%) on days 26–30 compared to 11 of 16 fetuses (69%) on days 32–37 ($\chi^2 = 19.8$, $df = 1$, $P < 0.001$; Fig. 4). When expressed, prone positions seemed to be maintained longer on day 37 than at earlier ages. To test this idea, the duration of the prone position was obtained from videotape

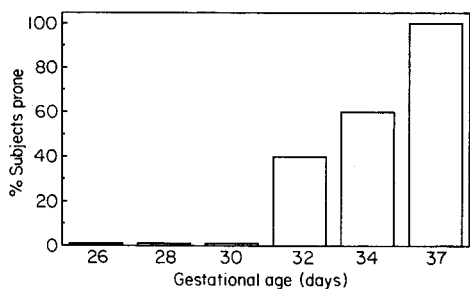


Figure 4. Percentage of fetal subjects that attained a prone position during the 60-s period following lemon infusion in *A. cahirinus*.

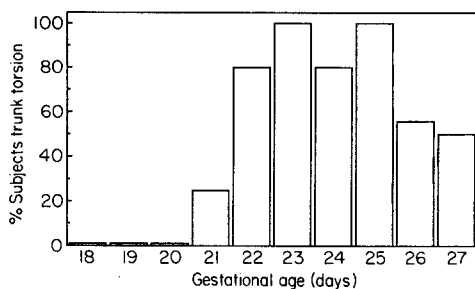


Figure 5. Percentage of fetal subjects that exhibited trunk torsion, a component of righting behaviour, in response to lemon infusion in *S. hispidus*.

records; duration scores were measured from the moment that the fetus attained a prone posture until the fetus moved into a lateral or supine position, or until the end of the 60-s post-infusion interval. (Thus, scores of continuous prone positions were truncated at 60 s.) Among *A. cahirinus* fetuses, the apparent trend in prone duration was not significant (prone duration on days 32–34 = 19.4 ± 9.5 s; day 37 = 47.3 ± 8.5 s; $t_9 = 2.19$, $P = 0.056$). A locomotor response to infusion was observed on day 37, but not at earlier ages (day 37 versus earlier: $\chi^2 = 29.9$, $df = 1$, $P < 0.001$).

Observation of *S. hispidus* fetuses originally suggested the existence of other organized responses to infusion, and not surprisingly, the occurrence of trunk torsion, prone position and locomotor activity in this species was confirmed. Trunk torsion was absent earlier than day 21 and increased sharply in frequency between days 21 and 22 (Fig. 5). With adjacent ages collapsed for analysis (in the same way as in the wiping analysis), the incidence of trunk torsion exhibited significant variation with age ($\chi^2 = 37.1$, $df = 5$, $P < 0.001$).

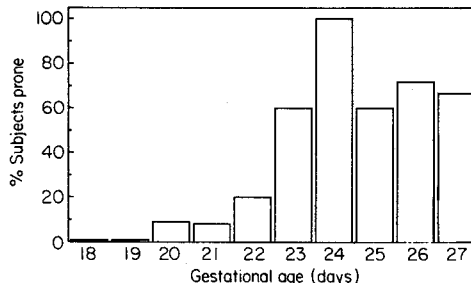


Figure 6. Percentage of fetal subjects that attained a prone position during the 60-s period following lemon infusion in *S. hispidus*.

The attainment of prone position during the post-infusion interval was observed in a single *S. hispidus* fetus on days 20, 21 and 22, but occurred consistently after day 23 (Fig. 6). Age-related changes in prone position also were significant ($\chi^2 = 28.9$, $df = 5$, $P < 0.001$). Although some younger fetuses successfully righted themselves, they seemed less capable of maintaining a prone position. To analyse the duration of prone posture, data from fetuses younger than 24 days were collapsed into a single category ($N = 6$) and compared with two groups of older fetuses. The one-way ANOVA confirmed that the duration of prone position was less on days 20–23 (14.5 ± 2.5 s) than on days 24–25 (56.1 ± 1.6 s) or days 26–27 (56.4 ± 2.6 s) ($F_{2,20} = 93.7$, $P < 0.001$). This finding suggested that dynamic postural maintenance, as distinct from the active righting response itself, emerged about day 24.

The incidence of a quadrupedal locomotor response to infusion also varied with gestational age in *S. hispidus*. A locomotor response was not observed before day 24, but occurred in about half of the subjects observed on each of the subsequent days. Comparing the incidence of quadrupedal locomotion during the post-infusion interval before day 24 versus on or after day 24 revealed a significant deviation from independence ($\chi^2 = 22.5$, $df = 1$, $P < 0.001$).

DISCUSSION

All four species observed in this study exhibited a general increase in activity and expressed facial wiping in response to lemon infusion. Emergence of the wiping response was relatively abrupt. At the earliest age that facial wiping was observed in each species, the majority of individual fetuses expressed

the wiping response. These findings represent a replication of results previously reported for *R. norvegicus* and confirmation of the general prediction that facial wiping is a conservative pattern of fetal behaviour that should be expressed across rodent taxa.

An environmental constraint hypothesis, as formulated above, presumes that the developmental disappearance of a motor pattern is a passive consequence of the changing physical relationship between the young animal and its environment. An alternative hypothesis views the disappearance as the result of active choice (in the cybernetic sense) among competing behavioural options. One choice of response to chemosensory stimulation is facial wiping, which involves movement of the forelimbs through a trajectory oriented with respect to the head. Another option is postural maintenance, which in young animals with poorly developed motor abilities requires use of all four limbs to maintain a prone position with respect to a substrate (Altman & Sudarshan 1975). Forelimbs employed in postural maintenance are not available for facial wiping, and vice versa, suggesting that a hierarchy of behavioural priorities is reflected in the underlying control system (Fentress 1984).

It is evident in precocial species that the fetal response to lemon infusion is not unitary. At different ages, one or more patterns of behaviour, including facial wiping, righting, and locomotion, are evoked by infusion. This finding is consistent with studies of postnatal responses to chemosensory stimuli in altricial species (e.g. Johanson & Shapiro 1986; Smotherman & Robinson 1989), including trigeminal-mediated contact righting (Troiani et al. 1981). The facial wiping response disappears at just the time that trunk torsion and successful righting to a prone position develop (days 23–24 in *S. hispidus*; days 30–32 in *A. cahirinus*). Prenatal disappearance of the wiping response would not be predicted by a passive environmental constraint mechanism, which presumably would operate only in a terrestrial (i.e. postnatal) environment. But prenatal disappearance is consistent with the hypothesis of competition among incompatible and simultaneously activated behavioural processes.

The exceptions to this hypothesis may well prove the rule: on days 21–23 some *S. hispidus* fetuses exhibited both righting and facial wiping behaviour. Closer scrutiny of the expression of these responses by individual fetuses provides further confirmation of the behavioural competition

model. Prior to day 24, *S. hispidus* fetuses were relatively unable to maintain a prone position after righting themselves: the average duration of prone position was 14.5 s. The latency between infusion and wiping, which was longer on days 21–23 (when righting behaviour was elicited by infusion) than on day 20 (and also longer than exhibited by *R. norvegicus* or *M. unguiculatus* fetuses), was virtually equal in length to the duration of prone position: 13.0 s. Examination of videotapes indicated that when both patterns of behaviour were expressed by the same subject, facial wiping always occurred after righting. In fact, wiping occurred soon after the fetus reverted from a prone to a lateral or supine position. Only one day later (day 24), the average length of prone position after infusion was in excess of 56 s, a time that was longer than the duration of elevated fetal activity after infusion. Presumably, the control command to perform facial wiping was no longer present when the prone position was finally abandoned.

Although behavioural organization is recognizable in the responses of fetuses to intra-oral infusion, conflict among different patterns of behaviour that are simultaneously activated is also evident. One of the hallmarks of adult behaviour is that simultaneous activation of physically incompatible patterns of movement rarely occurs. The occasional expression of ambivalent, blended, uncoordinated or contextually-inappropriate patterns of behaviour under specific conditions of stimulation was of great interest to the early students of animal motivation, who erected categories such as 'redirected' and 'displacement' activities to account for unusual forms of behavioural conflict (Hinde 1970). Nevertheless, by far the most common response of mature animals to simultaneous presentation of conflicting stimuli is expression of one response and complete inhibition of the other. If the fetal response to lemon infusion serves as a general indicator, then the ability of fetuses to inhibit all but one response is poorly developed in altricial species and does not develop in precocial species until late in gestation.

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