

Behavioral Development in Three Hamster Species

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The preweaning behavioral development was compared in 3 hamster species: the golden (*Mesocricetus auratus*), Chinese (*Cricetulus griseus*), and Djungarian (*Phodopus sungorus*). Differences in the age of appearance of action patterns could not be summarized by simply ranking species on either precocity or developmental speed, nor were they eliminated by measuring age from conception. Problems in the interpretation of species differences in the age of appearance of action patterns are discussed.

The 16-day gestation period of the hamster genus *Mesocricetus* is the shortest known in eutherian mammals. The terms of the 6 other genera of hamsters (subfamily *Cricetinae* of the family *Cricetidae*) range from 17 to 22 days (Flint, 1966). Such differences in term might represent species differences in over-all developmental speed. For example, *Peromyscus* species which live in more productive habitats have shorter pregnancies, more rapid postnatal (PN) development, and breed sooner than species inhabiting semi-desert environs (Douglas, 1969). Alternatively, differences in term might represent differences in the developmental stage at birth. *Acomys*, for example, after a long gestation for a murid, is unusually precocious at birth (Dieterlen, 1963).

In the present study, 3 hamster species, the golden (*M. auratus*), the Djungarian (*Phodopus sungorus*), and the Chinese (*Cricetulus griseus*), with gestation periods of 16, 18, and 20 days respectively, were observed. If the variability is in over-all developmental speed, the golden should exhibit developmental landmarks at the earliest PN age, and comparisons of postconception (PC) age should exaggerate any differences. If the variability is in maturity at birth, the golden should be retarded postnatally, and comparisons of PC ages should abolish differences. These may be called the "speed" and "birth stage" hypotheses, respectively.

Richards (1966) has invoked the latter to explain the fact that newborn golden pups are suboptimal stimuli for maternal retrieval, and further hypothesized a recent evolution of shortened gestation. Okon (1971) endorsed the birth stage hypothesis as an explanation of retarded ultrasound production in goldens as compared to rats. Neither author compared the golden hamster with related species of longer gestation.

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Behavioral development has been described for the golden (Dieterlen, 1959), and Chinese (Stolba & Kummer, 1972) hamsters, as well as for the European (*Cricetus cricetus*; Eibl-Eibesfeldt, 1953), and migratory (*Cricetulus migratorius*; Sviridenko, 1969) hamsters. Unfortunately, detailed comparisons of such reports are fruitless for 2 reasons. First, the conditions of stimulation of pups are not specified, although minor handling such as that involved in weighing pups can dramatically influence developmental speed (see review by Daly, 1973). Second, the distributional data necessary for statistical comparisons are not presented, nor are observational regimes specified. Without these details, we can have little confidence in apparent species differences.

Methods

Subjects

The subjects were 10 litters of golden hamsters descended from stock obtained from the Department of Zoology, University of Toronto, Canada; 8 litters of Djungarian hamsters bred from stock from the Medical Research Council laboratory, Carshalton, Surrey, England; and 5 litters of Chinese hamsters bred from stock from the Medical Faculty of Edinburgh University, Scotland.

Maintenance

The mothers were housed individually. (Matings were conducted in separate cages during pairings of less than 3 hr duration.) The home cages were metal, or plastic and metal, standard laboratory cages of different floor areas: 650 to 850 sq cm for Djungarians and Chinese, and 1700 sq cm for the larger goldens. The floors were covered with wood shavings and sawdust, and shredded paper towels were added as nest paper. This material was changed about halfway through pregnancy, and again when the pups were 20 days old. Before Day 20, pups were not touched or moved.

One Djungarian and 5 golden litters were reared in burrow boxes: wood and Plexiglas boxes with about 950 sq cm of floor surface, part of which gave access to a deep earth-filled chamber between 2 sheets of Plexiglas 5 cm apart. Here the hamsters could burrow and yet be observed. In the goldens, the same mothers (or, in one case, a pair of littermate sisters) reared 1 litter each in cage and burrow box, affording matched pairs for comparisons between the 2 rearing environments.

Food, commercial rodent chow supplemented daily with greens and skim milk powder plus occasional root vegetables and seeds, was added daily to the cage 3-5 min prior to the end of an observation session. Water was available *ad libitum*. A reversed light cycle prevailed, with lights on at 2130 hours and off at 0930 hours.

Observation

The pups were observed during one 15-min session daily from Day 1 (Day 0 = Day of Birth) to Day 25, with the mother removed. The observer listed those action patterns (AP's) which occurred during the session, and wrote brief topographical descriptions of those AP's undergoing developmental change in form.

For statistical comparisons, litters were treated as units, and the basic datum was the age in days at which each litter was 1st observed to have performed each AP.

Data from the daily sessions were the only ones used in dating the 1st appearance of AP's, although pups were also observed with their mothers. In addition, observations of single and paired adults in cages, burrow boxes, and larger enclosures were used to describe adult repertoires.

Results

Gestation Periods and Litter Sizes

Gestation periods (see Table 1) could usually be determined within a few hours; they were measured from the 1st ejaculation to the delivery of the 1st pup. Some pups, especially among goldens, were killed by the mother within the first 3 postnatal days, but all who survived to Day 3 survived to weaning except 2 Djungarians who died on Day 6.

Repertoires

Most AP's were virtually identical in form in the 3 species. The few substantial differences are summarized in Table 2. Species differences mostly involved AP's which appeared relatively late (as is generally true in development, see Waddington, 1966, p.6).

Burrow vs. Cage Rearing in Goldens

The manipulation of the preweaning environment of goldens was without apparent effect on the emergence of AP's. Of 24 tested, only 1 AP appeared significantly ($p < .05$) earlier in 1 environment, as would be expected by chance. However, the manipulation had a number of effects on the frequency and situational control of post-weaning behavior in home cages and in a variety of test situations (see Daly, 1971).

Species Comparison of Age of Appearance of AP's

Species comparisons (see Table 3) manifest no simple pattern. The order in which species manifested AP's varied with the AP considered. In PN comparisons, all 6 possible orderings of the 3 species occurred for one or another AP, whereas in PC comparisons, the Chinese was last on all but 4 AP's and never first. The birth stage hypothesis predicted

TABLE 1. Gestation Periods and Litter Sizes.

	Gestation Period (days)			Litter Size (weaned)		
	Mean	S.D.	Range	Mean	S.D.	Range
Golden	16.0	.3	15.6-16.8	7.4	2.1	4-12
Djungarian	18.1	.4	17.5-18.5	3.5	1.3	1-5
Chinese	20.1	.1	20.0-20.2	4.4	1.9	2-7

TABLE 2. Differences in Behavioral Repertoires.

	Golden	Djungarian	Chinese
Sexual behavior	Prolonged rigid lordosis No intermount pursuit No lock Repeated thrusting only as male tires	Brief lordosis Slow intermount pursuit Brief post-ejaculatory lock. Repeated thrusting only as male tires	Brief lordosis Rapid intermount pursuit Brief post-ejaculatory lock 1-3 thrusts per mount
Striking	No such AP	“Strike” from upright posture by simultaneous forepaw snatching movement, usually with chirping vocalization. Unreceptive females strike at males. Both sexes strike at strange objects.	No such AP
Lateral scent-marking	Rub flank against vertical surface while stepping forward mincingly	Roll on side or back, rubbing flank on substrate. (Like sand-bathing of desert rodents. Related <i>P. roborovskii</i> is the only hamster psammophile [Flint, 1966].)	No clear scent-mark AP Flank rub like golden's is occasional in pups. Wall contact frequent in locomotion
Self-covering	No such AP	Long unilateral forepaw strokes down and away from body while on side efficiently bury exposed pup. Only about Days 8-14.	No such AP

that PC differences would be smaller than PN, whereas the speed hypothesis predicted that PC differences would be greater. The latter hypothesis is better supported: 23 of 28 PC comparisons were significant compared to 13 PN, and the PC value of the Kruskal-Wallis H statistic (inversely related to the degree of overlap between species) exceeds the PN value for most AP's. However, exceptions did occur, the most notable of which were for body grooming and self-righting. Therefore, neither "speed" nor "birth stage" affords a single dimension adequate to describe all species differences.

Discussion

Is the Golden Hamster "born early"?

Immediately after birth, the golden is decidedly more limited in its movements than the other species: the amplitude of limb movements is relatively small; the extremities never touch the body except under application of an external force; and an inept locomotory "swimming" on the back, peculiar to new-born goldens, is evident. The golden indeed appeared to be born in a less mature state. However, "early birth" is an oversimplification. Species differences were not minimized by PC comparisons as the birth stage hypothesis predicts. In fact, species could not be ranked satisfactorily on either birth stage or speed.

That such rankings are simplistic becomes particularly clear when we compare more distantly related species, such as Norway rats and golden hamsters (members of different families of the superfamily *Glirres*). Rats are more advanced at birth on some characters (e.g., brown fat deposition, Smalley & Smalley, 1967), but less advanced on others (e.g., development of heart rate controls, Adolph, 1971). Conspicuous behavioral contrasts are that rats groom much earlier but eat much later than hamsters (compare data in Table 3 with Bolles & Woods, 1964).

King (1961) noted, "Gross differences in the over-all rate of development are often quite apparent, but perhaps they are less significant than differential rates or heterauxesis." The adaptive significance of heterauxesis can sometimes be surmised: for example, a specific acceleration of the development of eating in the specialized leaf-eating gerbil *Psammomys obesus* is explicable as a maternal time-budgeting adaptation (Daly, 1975). Differences among hamsters are not yet so neatly explicable, but some suggestions are possible. The Djungarian inhabits the most extreme northern climates (Flint, 1966), and is a relatively shallow burrower (at least in the laboratory). Thus, danger of exposure to cold may account for the unique AP of self-covering, and danger of dampness for the relatively rapid postnatal development of grooming. The significance of *Mesocricetus*' short gestation remains obscure. Richards (1966) suggested it might be a rapid-reproduction adaptation to more extreme semi-desert than the steppes inhabited by most hamsters. This seems unlikely. Of the several hamsters discussed by Flint (1966), *Tscherkia triton* has the shortest gestation and inhabits the most productive habitat. Likewise, in *Peromyscus*, developmental speed is positively related to productivity (e.g., Douglas, 1969). Moreover, the 16-day gestation is shared by other *Mesocricetus* species (M. Murphy, personal communication). Information on the ecology and habitat of the golden hamster and its congeners is obviously needed.

TABLE 3. Age of 1st Appearance of AP's, Based on I Score per Litter.

Species Order (PN) Behavior	Golden (n = 10)			Djungarian (n = 8)			Chinese (n = 5)			PN		p	
	PN	PC	Mdn	PN	PC	Mdn	PN	PC	Mdn	H	H		
	Mdn ^b	Min ^c	(1)	Mdn	Min	(-)	Mdn	Min	(-)	p ^d	p		
G-C-D ^a Yawning	2	(1)	18	7	(2)	25	4	(1)	24	7.9	*	16.0	***
Stretching	18.5	(16)	34.5	-	(-)	-	-	(15)	-	11.5	**	14.4	***
G-D-C Eating sitting up	11.5	(11)	27.5	12	(9)	30	12	(11)	32	0.6		7.9	*
Independent defecation	11	(8)	27	16	(9)	34	17	(13)	37	4.0		9.5	**
Chewing nest material	13.5	(11)	29.5	15	(12)	33	16	(13)	36	1.6		6.3	*
Mature nest-building	18	(17)	34	-	(-)	-	-	(-)	-	19.0	***	19.0	***
D-G-C Rearing on hind legs	17	(15)	33	14	(12)	32	18	(12)	38	3.2		4.9	
Climbing	19	(14)	35	17	(15)	35	20	(19)	40	4.2		8.4	*
Mouthing food	8.5	(5)	24.5	8	(7)	26	9	(8)	29	3.1		11.3	**
Independent urination	14	(11)	30	13	(11)	31	17	(13)	37	4.0		9.5	**
Lateral scent-marking	21	(16)	37	18	(16)	36	-	(21)	-	11.4	**	8.0	*

D-C-G Nest exit	11.5	(9)	27.5	10	(8)	28	11	(10)	31	8.5	*	11.2	**
Eye-opening	15	(15)	31	12	(11)	30	13	(13)	33	19.0	***	16.2	***
Snout grooming	10.5	(8)	26.5	7	(5)	25	9	(8)	29	7.1	*	7.2	*
Overhead grooming	13	(12)	29	9	(7)	27	13	(11)	33	11.6	**	13.5	**
Contactless scratching	8.5	(7)	24.5	5	(4)	23	6	(5)	26	17.8	***	11.6	**
Scratching with contact	12	(6)	28	5.5	(5)	23.5	6	(6)	26	12.5	**	7.7	*
Scratching with foot-licks	13	(12)	29	12.5	(9)	30.5	13	(11)	33	1.4		9.5	**
Eating (except feces)	10	(8)	26	8	(8)	26	9	(8)	29	3.1		11.3	**
Forepaw digging	15	(12)	31	10	(9)	28	13	(12)	33	15.3	***	15.1	***
C-G-D Carrying food to nest	14	(12)	30	16	(13)	34	14	(12)	34	5.7		15.2	***
Quadrupedal saltation	19	(17)	35	-	(20)	-	17	(17)	37	5.0		6.1	*
Swatting playfights	14	(13)	30	16	(12)	34	14	(13)	34	3.0		14.5	***
Full playfights	16	(15)	32	17	(15)	35	15	(14)	35	3.7		16.5	***
C-D-G Self-righting	5	(4)	21	4	(2)	22	2	(2)	22	7.9	*	5.9	
Body grooming	15	(13)	31	12.5	(11)	30.5	11	(10)	31	12.6	**	0.6	
Shaking	19	(14)	35	17	(13)	35	15	(14)	35	3.8		0.3	
Complete digging	19.5	(16)	35.5	17.5	(13)	35.5	16	(14)	36	5.9		0.7	

^aG-C-D = Golden (earliest)-Chinese-Djungarian (latest)

^bMdn = Median age

^cMin = Minimum (earliest) age

* $p < .05$

** $p < .01$

*** $p < .001$

Problems in Interpretating Species Differences

Many ethologists (e.g., Dieterlen, 1959; Eibl-Eibesfeldt, 1953) have constructed developmental chronologies presenting a single minimum age for each AP. Such ages must be suspect without specification of observation schedules, nor can species be compared without distributional data. Unfortunately, even statistically reliable species differences may be difficult to interpret. For example, Djungarians first exhibited yawning significantly later than goldens ($p < .005$ by Mann-Whitney U -test). However, Djungarians yawned in only 6 of 200 sessions, whereas goldens yawned in 89 of 250. In this case, the species may differ only in performance rate and not at all in maturation schedule. Here, the traditional minimum age measure seems more meaningful than an average. Unlike yawning, most AP's in Table 3 were seen virtually every day after the 1st occurrence. Nevertheless, any significant differences in age of appearance might reflect, at least in part, differences in performance rate (which may itself change over days in species-typical fashion) rather than differences in maturation age. Nor need a difference be one of *motor* maturation, but instead may involve the development of sufficient motivation, or the removal of inhibition which has kept maturational progress covert (see Oppenheim, 1974, p. 142). Some activities of solitary hamsters, such as complete nest-building and hoarding, are evidently inhibited while pups are maintained socially and may be exhibited within an hour of isolation. A period of isolation may also facilitate the expression of mature agonistic and sexual behavior, neither of which were observed in this study. For all of these reasons, the behavioral record may only indirectly reflect a covert maturational chronology.

Notes

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References

- Adolph, E. F. (1971). Ontogeny of heart-rate controls in hamster, rat, and guinea pig. *Am. J. Physiol.*, *220*: 1896-1902.
- Bolles, R. C., and Woods, P. J. (1964). The ontogeny of behaviour in the albino rat. *Anim. Behav.*, *12*: 427-441.
- Daly, M. (1971). Behavioural development, early experience, and maternal behaviour in golden hamsters (*Mesocricetus auratus*). Unpublished doctoral thesis, University of Toronto, Toronto, Canada.
- Daly, M. (1973). Early stimulation of rodents: a critical review of present interpretations. *Br. J. Psychol.*, *64*: 435-460.
- Daly, M. (1975). Early use of solid food by a leaf-eating gerbil, *Psammomys obesus*. *J. Mammal.*, *56*: 509-511.

- Dieterlen, F. (1959). Das Verhalten des syrischen Goldhamsters (*Mesocricetus auratus* Waterhouse). *Z. Tierpsychol.*, 16: 47-103.
- Dieterlen, F. (1963). Vergleichende Untersuchungen zur Ontogenese von Stachelmaus (*Acomys*) und Wanderratte (*Rattus norvegicus*). *Z. Säugetierkunde*, 28: 193-227.
- Douglas, C. L. (1969). Comparative ecology of pinyon mice and deer mice in Mesa Verde National Park, Colorado. *University of Kansas Publication, Museum of Natural History*, 18: 421-504.
- Eibl-Eibesfeldt, I. (1953). Zur Ethologie des Hamsters (*Cricetus cricetus* L.). *Z. Tierpsychol.*, 10: 204-254.
- Flint, W. E. (1966). *Die Zwerghamster der Paläarktischen Fauna*. Wittenberg: Ziemsen Verlag.
- King, J. A. (1961). Development and behavioral evolution in *Peromyscus*. In W. F. Blair (Ed.), *Vertebrate Speciation*. Austin: University of Texas Press. Pp. 122-147.
- Okon, E. E. (1971). The temperature relations of vocalizations in infant golden hamsters and Wistar rats. *J. Zool.*, 164: 227-237.
- Oppenheim, R. W. (1974). The ontogeny of behavior in the chick embryo. In D. S. Lehrman, R. A. Hinde, and E. Shaw (Eds.), *Advances in the Study of Behavior*, Vol. 5. London: Academic. Pp. 133-172.
- Richards, M. P. M. (1966). Maternal behaviour in virgin female golden hamsters (*Mesocricetus auratus* Waterhouse): the role of the age of the test pup. *Anim. Behav.*, 14: 303-309.
- Smalley, R. L., and Smalley, K. N. (1967). Brown and white fats: development in the hamster. *Science*, 157: 1449-1451.
- Stolba, A., and Kummer, H. (1972). Zur Verhaltensontogenese des chinesischen Zwerghamsters, *Cricetulus griseus* (Milne-Edwards, 1867). *Rev. Suisse Zool.*, 79: 89-101.
- Sviridenko, P. A. (1969). Rost i razvitie chomyatchka serogo (*Cricetulus migratorius* Pall.). *Vestn. Zool.*, 3: 45-49.
- Waddington, C. H. (1966). *Principles of Development and Differentiation*. London: MacMillan.