The Ontogeny of Sibling Recognition in Rodents: Superfamily Muroidea

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A brief review of the relevant literature indicates that familiarization is the primary (and possibly sole) proximate mechanism mediating the development of sibling recognition in muroid rodents. Littermates that are raised together are discriminated from unfamiliar agemates. Previously unencountered kin may be recognized through their resemblance to familiar relatives (a process of indirect familiarization). A recent experiment with spiny mice reveals that phenotypic similarity among full siblings can be discerned by other conspecifics, even those that are not their kin. Olfactory signatures involved in social recognition are the product of a complex interaction between genotypic and environmental components.

INTRODUCTION

Prior to weaning, young rodents routinely maintain close physical proximity to their mother and littermates. Aside from nursing, the most conspicuous manifestations of maternal behavior include grooming, retrieving, and huddling with offspring. Simultaneous feeding by littermates ensures that they will be brought into direct contact with one another. Even in the absence of the mother, pups commonly remain clumped together—in the nest, as for altricial Norway rats (Alberts, 1978) and Syrian hamsters (Schoenfeld and Leonard, 1985), or elsewhere, for relatively precocial species such as spiny mice (Porter and Wyrick, 1979). As a function of such social exposure, pups become familiar with specific family members or their characteristic phenotypes (signatures). Experimental

studies indicate that learned familiarization with conspecific signatures (possibly including one's own) is the most important mechanism mediating the development of sibling recognition in the several species of muroid rodents investigated to date (e.g., Blaustein *et al.*, 1987). As elaborated below, siblings (as well as other classes of close kin) may be recognized through either a direct or an indirect process of familiarization, and recognizable phenotypic signatures arise from several sources.

DIRECT FAMILIARIZATION

Familiarization through direct association is perhaps the most obvious means by which animals develop the ability to recognize particular conspecifics. Individuals with which an animal has had sufficient interactions will subsequently be discriminated from those not previously encountered. Such interactions need not involve actual physical contact, providing that the animals have access to one another's salient phenotypic signatures (e.g., Porter *et al.*, 1984). To the extent that social encounters are restricted to close relatives, at least during certain stages of the organism's life history, social familiarity will be correlated with kinship. Thus, for species in which females care exclusively for their own offspring, familiar littermates would also be biological siblings—either full or half-siblings, depending upon the likelihood of multiple paternity within a single litter.

To assess the role of direct familiarization independent of genetic relatedness in the development of discriminative social interactions (the most common index of recognition), investigators have reared rodent pups with unrelated foster females and littermates. This experimental manipulation allows for the subsequent testing of various combinations of animals differing in prior exposure to one another and genetic relatedness. With reciprocal cross-fostering, for example, a portion of the pups from two litters is exchanged shortly after birth. In this manner, unrelated pups are raised together as littermates, while full siblings are separated and have no further association until testing.

Studies employing differing variations of the pup-fostering manipulation document the marked influence of rearing association on the development of social recognition. Albino rat pups evince differential responsiveness to unrelated (foster) littermates compared to unfamiliar unrelated agemates (Hepper, 1983). When tested after weaning, familiar siblings huddle more frequently than do siblings that had been separated within 24 h after birth (Wills *et al.*, 1983). In spiny mice (*Acomys cahirinus*), weanlings huddle discriminatively with unrelated foster littermates rather than with unfamiliar siblings or nonkin (Porter *et al.*, 1981). Similar

results have been reported for *Mus musculus*—social investigation among siblings is inversely correlated with the length of prior exposure (Kareem, 1983; see also Kareem and Barnard, 1982)—and *Peromyscus leucopus*—when tested in a choice apparatus, both siblings and nonsiblings that had been reared together were preferred over siblings reared apart (Halpin and Hoffman, 1987; cf. Grau, 1982).

Inbreeding avoidance by siblings also appears to be an outgrowth of prepubertal association and familiarization in several species of Muroidea. Regardless of genetic relatedness (siblings or nonsiblings), pairs of gray-tailed voles (*Microtus canicaudus*) raised together produced fewer litters than did unfamiliar pairs (Boyd and Blaustein, 1985). While unrelated prairie voles (*M. ochrogaster*) raised as littermates avoid breeding, siblings separated from shortly after birth through weaning subsequently display no evidence of incest avoidance (Gavish *et al.*, 1984). Similarly, fewer litters were born to *Peromyscus eremicus* nonsiblings reared together rather than apart (Dewsbury, 1982), and delayed reproduction was observed in Mongolian gerbils (Agren, 1984) and *P. maniculatus* (Hill, 1974) for both siblings and nonsiblings paired before puberty.

INDIRECT FAMILIARIZATION

Although rearing association is a major factor contributing to the development of discriminative interactions among littermates, not all accounts of sibling recognition can be explained in this way. *Mus* and *Rattus* biological littermates separated shortly after birth nonetheless interact differently than unfamiliar nonkin when reunited as juveniles or adults (e.g., Hepper, 1983, 1987; Kareem, 1983). Behavioral indicants of recognition have also been reported for unfamiliar *Mus* and *Peromyscus* siblings that were born in successive litters and therefore had no opportunity to associate directly with one another, either prenatally or postnatally, before testing (Grau, 1982; Kareem and Barnard, 1986; Winn and Vestal, 1986).

Nepotistic interactions in the absence of prior association do not necessarily eliminate a possible role of familiarization in the recognition process. Rather, familiarity with particular kin may enable individuals to discriminate between previously unencountered relatives and nonkin, a process commonly labeled signature—or phenotype—matching (Beecher, 1982; Holmes and Sherman, 1983). Animals that associate and thereby become acquainted with their mother or littermates, for example, may discern a resemblance between those individuals and novel relatives (assuming a correlation between genetic relatedness and phenotypic similarity). An organism's own self-perceived phenotype could also serve as

a standard against which to assess others. This would allow for mutual recognition by unfamiliar kin that have had no contact with other relatives in common, such as paternal half-siblings reared apart (e.g., Kareem and Barnard, 1982). Unfamiliar kin would thus be discriminated to the extent that their signatures approximate those of already familiar conspecifics including oneself; in the terminology of learning theorists, some degree of stimulus generalization would be evident (e.g., Bateson, 1980; Holmes and Sherman, 1983; Halpin and Hoffman, 1987). The more similar the phenotypic signature of a novel animal is to those of known relatives, the greater the likelihood that it will be responded to in a discriminative manner (i.e., the greater the generalization). Recognition of kin in this manner is the result of *indirect* familiarization since there would have been no prior direct contact between the individuals involved.

    In discussions of the ontogenetic mechanisms of kin recognition, phenotype matching is often presented as distinctly different from recognition through association and familiarization (e.g., Blaustein *et al.*, 1987; Holmes and Sherman, 1983; Porter, 1987). Nevertheless, it seems more parsimonious to consider direct familiarization and phenotype matching (what I have termed indirect familiarization) as variations of the same basic ontogenetic mechanism (e.g., Waldman, 1987). In both instances, kin recognition is mediated by learned familiarization with salient phenotypic signatures. Therefore, the underlying basis for recognition is the same, regardless of whether or not the particular relatives in question have been previously encountered. There is additional ambiguity associated with the term phenotype matching. Ultimately, all proposed kin recognition mechanisms are arguably dependent upon some type of assessment or matching of phenotypes (see recent discussion by Waldman, 1987). Thus, in the case of direct familiarization, an animal retains a memory trace or template of the signature of an individual with which it has associated. Subsequent recognition requires a correspondence between that template and the current phenotype of the "familiar" animal.

    In theory, the ontogeny of kin recognition could be entirely independent of any learned familiarization—direct or indirect. That is, both the phenotypic signature and the ability to decode or recognize that signature could be determined by (hypothetical) recognition alleles. At present, there appear to be no experimental manipulations to enable one to distinguish clearly the possible mediation of kin recognition through recognition alleles versus generalization from an individual's own familiar phenotype (self-matching). Unambiguous support for the recognition allele hypothesis would require evidence of kin discrimination by animals that have been deprived of any access to their own phenotype plus those of all other kin (e.g., Blaustein, 1983). Although the possible existence

of recognition alleles should not be entirely discounted, all known reports of sibling recognition in muroid rodents are consistent with the single ontogenetic mechanism of familiarization—at least when broadly defined to include direct association and indirect familiarization (*viz.*, learned familiarization and generalization to similar phenotypes).

BASIS OF RECOGNIZABLE SIGNATURES

The preeminence of olfactory cues for rodent social recognition is well established (e.g., Halpin, 1986). Individual animals can be discriminated through their urine (Yamaguchi *et al.*, 1981), saliva (Block *et al.*, 1981), and various other glandular secretions (e.g., Halpin, 1986; Johnson, 1983), as well as the chemical mixture deposited onto their bedding material (D'Udine and Partridge, 1981; Gilder and Slater, 1978). Discriminative social interactions are reduced or entirely eliminated among animals suffering experimentally induced anosmia (e.g., Halpin, 1986; Porter *et al.*, 1986). The remainder of this paper focuses upon the interacting genetic and individually acquired environmental components of the complex odor signatures that mediate sibling recognition.

Environmentally Mediated Component

Throughout their lifetime, rodents ingest or are otherwise exposed to substances that can alter their odor profiles. The question of interest in the present context is, Are such individually acquired (environmentally mediated) cues of any biological significance? In particular, do they contribute to kin recognition or other forms of social discrimination?

Suckling rodent pups are annointed with various chemical secretions emanating from their mother (e.g., urine, saliva, milk, and other glandular products). These "maternal labels" in turn provide a means by which mothers can discriminate their own offspring (Leon, 1983; Wallace *et al.*, 1973). *Acomys cahirinus* pups that are labeled by the same lactating female are also able to discriminate one another using that common marker. Littermate siblings that were separated and housed in individual cages beginning on day 4 postpartum subsequently recognized one another, providing that they had suckled from the same lactating female during alternating 12-h intervals (Porter *et al.*, 1981, 1984). When control siblings suckled from different females, no evidence of discriminative interactions was observed. Even unrelated, unfamiliar, pups that had previously shared a mother in common interacted differently than did unfamiliar unrelated animals nursed by different females. Thus, direct contact with the same lactating female appears to be sufficient for the development of

agemate recognition. In the natural world, discrimination of other pups bearing the same maternal label would be functionally equivalent to sibling recognition since young labeled by the same mother would almost invariably be littermate siblings.

Drastic changes in diet will result in relatively rapid alterations in the chemical composition of urine, feces, and other metabolic by-products. Few empirical studies have addressed the extent to which mammalian social interactions vary according to dietary-dependent chemical cues. Rat and *Acomys* pups are attracted preferentially to chemical signals (maternal pheromone) produced by lactating females fed the same diet as the pups' mother (Leon, 1975; Porter and Doane, 1977). Recently parturient spiny mice were shown more readily to retrieve unfamiliar 1-day-old pups born of same-diet females than pups of novel-diet females (Doane and Porter, 1978). Spiny mouse weanlings are also sensitive to dietary-dependent olfactory cues produced by agemates. When tested with soiled bedding material, both male and female weanlings orient preferentially to the odor of agemates fed the same diet as themselves (and their mother) over that of animals fed a different diet (Porter and Doane, 1979). Dietary familiarity therefore appears to influence the attractiveness of weanling chemical cues as well as the specificity of early mother–infant interactions.

Given the eclectic opportunistic feeding habits of omnivorous rodents, the diet consumed by one mother–offspring group in the wild probably will not be exactly identical to that of another conspecific family unit. The dietary component of individual odor phenotypes should therefore be more similar among littermate siblings than for unrelated agemates, at least until dispersal from the natal home area.

The metabolic activity of microorganisms is a final, but not well-understood, environmental component of olfactory phenotypes. Various chemical secretions and excretions often have little odor until metabolized by microbes distributed throughout the body surface (e.g., Albone, 1984). Gorman (1976) has hypothesized that animals living together may share common species and strains of symbiotic microflora that give rise to similar odors among group members. This is an intriguing possibility that will be difficult to assess because of problems in identifying and classifying relevant microorganisms (Albone, 1984). In addition, populations of microorganisms may not remain sufficiently stable over time to serve as the basis for a group-member label (Albone, 1984; Hepper, 1987).

Genetic Component

Perhaps the clearest evidence that minor genetic differences may result in detectable differences in olfactory phenotypes is provided by

studies with house mice (*Mus musculus*) of known genotypes. Females derived from wild populations discriminate between odors of soiled bedding material from males heterozygous for one of the various recessive *t* alleles (+/*t*) and those from males homozygous for the wild-type allele (+/+) (Lenington and Egid, 1985). Urinary and whole-body odors of inbred mice that are genetically identical except for the major histocompatibility complex (MHC) can also be distinguished by conspecifics (Yamaguchi *et al.*, 1981; Beauchamp *et al.*, 1986).

If phenotypic signatures are indeed genetically influenced, they should remain relatively invariant over the individual's lifetime, and the signatures of close kin would be more similar than those of unrelated animals. Resemblance among relatives might therefore be discernible to conspecifics even when likely environmental influences (e.g., diet) are held constant. As a test of this hypothesis, my colleague and I have recently conducted a series of experiments with spiny mice (*Acomys cahirinus*).

Littermate full siblings, individually isolated for 8 full days following weaning, showed no evidence of recognizing one another when reunited (Porter and Wyrick, 1979). In contrast, littermates that were separated for 9 days but housed with another sibling from their same litter during that time subsequently displayed discriminative interactions (Porter *et al.*, 1983). It is unlikely that the latter animals were responding to a common maternal label (see above), as they had no contact with their mother for 9 days prior to the beginning of the recognition tests. Rather, they presumably detected a genetically mediated resemblance between the individual signature of their cagemate sibling and those of "unfamiliar" (separated) siblings.

Whereas the above study indicates that spiny mice recognize similarity among their own full siblings, an additional (unpublished) experiment investigated the possibility that sibling resemblance might also be perceived by conspecifics that are not themselves close kin of the stimulus animals. All experimental animals were born in the laboratory breeding colony and maintained under identical conditions, including being fed the same commercially produced diet. At weaning, pups from different litters were housed together in pairs for 10 days. Following this treatment period, four unfamiliar and unrelated animals (one from each of four different pairs) were placed together into an observation terrarium. In each instance they composed two distinct pairs in which the individuals had been housed with each other's full sibling during the treatment period. That is, the animals making up each of these pairs were familiar with each other's sibling but had no prior contact with one another or with the remaining

Table I.   Summary of Experimental Manipulations to Test Recognition of Full Siblings of Familiar Nonkin

	Litter			
	A	B	C	D
Pups (housed together with parents until weaning)	A-1/A-2	B-1/B-2	C-1/C-2	D-1/D-2

Treatment pairs (2 unrelated animals housed together for 10 days prior to testing)

	A-1	A-2	B-1	B-2
	C-1	C-2	D-1	D-2

Test groups (4 animals housed together during 5-day observation period)[a]

Group 1		A-1 ⌐‾‾⌐ C-2	B-1 ⌐‾‾⌐ D-2
Group 2[a]		A-2 ⌐‾‾⌐ C-1	B-2 ⌐‾‾⌐ D-1

[a] Bracket indicates animals previously exposed to each other's full siblings.

two animals in the same observation cage. The experimental manipulation and composition of observation groups are summarized in Table I.

Over a 5-day test period, frequencies of dyadic huddling (involving bodily contact) were recorded during 36 time-sample observations per day. Further methodological details of the observation procedures are provided in previous publications (e.g., Porter and Matochik, 1983; Porter et al., 1981). In this manner, 14 groups containing four animals each were observed.

For every group of four animals there were two possible classes of dyadic huddles:

(1) sibling familiarity (SF)—two unfamiliar animals that had been housed with each other's sibling prior to testing (e.g., pairs A-1/C-2 and B-1/D-2 in observation group 1; Table I); and

(2) no sibling familiarity (NSF)—two unfamiliar animals with no prior contact with each other's siblings (e.g., pairs A-1/B-1, A-1/D-2, C-2/B-1, and C-2/D-2 in observation group 1; Table I).

The observed frequencies of these two classes of pairings across all 14 groups of animals are presented in Table II. As outlined above, NSF pairings were twice as likely as SF pairings by chance alone. To correct for this 2:1 expected ratio, observed frequencies of NSF and SF dyadic huddles were multiplied by .75 and 1.5, respectively. The resulting corrected scores for SF vs. NSF dyadic huddles were then compared with

Table II. Frequency of Dyadic Huddles (Pairings) by SF and
           NSF Animals Across the 14 Observation Groups

	SF pairs	NSF pairs
$\overline{X}$ observed frequency	39.6	12.4
(SD)	(69.5)	(22.7)
$\overline{X}$ corrected frequency	59.4	9.3
Median (corrected)	18.8	2.3
	Wilcoxon's T = 15	
	N (minus ties) = 12	
	$p < .05$ (1-tailed)	

Wilcoxon's matched-pairs signed-ranks test, which revealed that SF pair-
ings were observed significantly more often than were NSF pairs. These
data indicate that *A. cahirinus* weanlings can detect phenotypic resem-
blance between familiar unrelated individuals and close kin (full siblings)
of those latter conspecifics, even under constant laboratory conditions.

    Additional support of genetically influenced signatures is provided
by Hepper (1987), who reported an inverse relationship between the de-
gree of relatedness and the duration of social investigation among labo-
ratory rats. The mean time of investigation increased linearly across the
following order of unfamiliar stimulus animals: full siblings (separated
shortly after birth), half-siblings, cousins, and unrelated conspecifics.
Similar results were obtained with different sets of stimulus rats. Hepper
(1987) concluded that the "identifier" (signature) is "possessed by kin in
direct proportion to their relatedness," rather than being an all-or-none
cue, with the proportion of individuals that possess the signature varying
across kin classes.

    Even though members of a kin class may share somewhat similar
signatures (as for Norway rats and spiny mice, discussed above), there
is sufficient phenotypic variability among close relatives to allow for in-
dividual discrimination. Weanling spiny mice huddle preferentially with
familiar littermate full siblings over other members of that same litter from
which they had been separated for 10 days prior to testing (Porter *et al.*,
1986). Such discriminative interactions between familiar and unfamiliar
siblings were not evident among animals rendered anosmic by intranasal
injections with zinc sulfate, indicating that individual recognition of full
siblings is mediated by olfactory cues. In related research, rats success-
fully distinguished between their full siblings by home-cage odors alone
(Hopp *et al.*, 1985). Both familiarity and relatedness were held constant

in this study; i.e., the experimental animals were all littermates that had been housed together from birth through the end of the test period.

These data suggest that olfactory phenotypes may be influenced by a number of interacting genes. According to this model, the overlapping genotypes of close kin result in a discernible resemblance in their odor signatures. Genotypic variability within a kin class could, nonetheless, serve as a basis for distinct individual odors.

It should be cautioned that differences in the odors of close kin despite the absence of identifiable environmental variability are not necessarily incontrovertible proof that such differences have a genetic basis. Subtle environmental factors might exert a marked influence on odor cues. Indeed, rats have been reported to discriminate between urine odors of two, presumably genetically identical, members of the same inbred strain. It was concluded that there may have been "individual differences in metabolic products" emanating from the stimulus animals or, more likely, that the urine samples were contaminated with feces, hair, food, or other substances (Brown *et al.*, 1987).

CONCLUSIONS

As argued above, sibling recognition in Muroid rodents is a consequence primarily of learned odor familiarization. Pups are reared in the presence of *kinship-correlated* odors (e.g., those associated with their mother or littermates) and subsequently discriminate conspecifics whose phenotypes match or approximate those familiar olfactory cues. Through this proximate mechanism, particular individuals (kin) to which an animal has been directly exposed, as well as others whose phenotypes resemble familiar olfactory signatures, may be recognized. Separate discussions of genetic and environmentally mediated *components* of odor signatures were adopted for heuristic purposes and do not imply that olfactory phenotypes per se can be readily dichotomized in this way. Ultimately, the odors that mediate social recognition no doubt develop through an intricate interplay of genotypic × environmental factors. Thus, maternal labels acquired by suckling pups may themselves reflect the mothers' unique genotypes (e.g., Gamboa *et al.*, 1986). Similarly, microorganisms contribute to the host's body odor by metabolizing a genetically influenced biochemical substrate.

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