Kin recognition mechanisms which to compare novel odors. Use their own smell as a standard against genetically related. Apparently, these rodents depending on whether they were genetically to odors of unfamiliar conspecifics that at maturity they responded differently toward, or avoid mating with, any conspecific they encounter in a location that predictably contains only relatives (e.g. a nest or burrow) – such site-specific behavior results in ‘indirect’ recognition. On the other hand, individuals might recognize relatives ‘directly’ by comparing their phenotypes with mental images (‘templates’) of kin formed during previous social encounters. For example, most birds and mammals learn characteristics of kin during early development, based on physical features of parents and siblings. Later on, they recognize individuals who resemble the remembered template closely enough as relatives. This works because parental care is obligatory in all mammals and most birds, because young are typically reared in groups, and because there is a correlation between phenotypic similarity and genotypic similarity. Therefore, phenotype matching mediated by social learning reliably results in kin discrimination.

However, in some circumstances, social learning predictably yields inadequate or misleading recognition templates (Box 1). For example, obligate brood parasites are reared by heterospecifics, thus learning phenotypes of nestmates or foster parents would result in species misidentification. Within species, multiple mating by females with different males potentially creates broods of mixed paternity (i.e. full- and half-siblings reared together) and multiple mating by males with different females might result in half-siblings that are reared apart (in different nests or dens). In these cases, individuals could conceivably discriminate conspecifics from heterospecifics or close kin from distant kin if they inspect and learn salient aspects of their own phenotype, and then match features of littermates or unfamiliar conspecifics to themselves. Circumstantial evidence of self-referent phenotype matching, which Dawkins called the ‘armpit effect’, exists for species satisfying several of these conditions; for example, multiple paternity (Belding’s ground squirrels and honey bees) and dispersal of juveniles (peacocks). However, in none of these cases was self-inspection proven experimentally nor social learning eliminated. Moreover, the existence of self-inspection as a mechanism facilitating nepotism has been doubted on the grounds that genes promoting such abilities are ‘outlaws’ if their selfish interests conflict with those of the rest of the genome. Presumably, the resulting intragenomic conflict would favor genes that suppress self-inspection. Indeed, under this hypothesis, genetic conflict should characterize and destroy not only self-referencing but also phenotype matching based on social learning of cues from any relatives. Alternatively, however, if genes encoding production and perception of self-recognition cues were well spread among chromosomes, the entire genome would benefit from their nepotism-promoting effects, thus maintaining phenotype matching, including the armpit effect. Mateo and Johnston’s new paper provides much needed empirical evidence regarding this controversy.

Golden hamsters are native to arid regions of Syria. Although little is known about their social behavior in nature, the home ranges of several males overlap with a female’s range. In captivity, females will mate with multiple males, thus resulting in mixed paternity of litters. Therefore, M. auratus apparently satisfy several conditions favoring self-inspection (Box 1). In addition, despite decades of inbreeding, females are known to discriminate between flank-gland odors of close and distant relatives, and between unfamiliar kin and familiar non-kin. However, these behaviors are consistent with both self-referent phenotype matching and social learning.

To disentangle the two mechanisms, Mateo and Johnston manipulated litter sizes and composition of simultaneously parturient mothers. They cross-fostered 18 female pups within 12 hours of birth, allowing each lactating female to rear three young: a biological son and daughter, and one foster daughter. When cross-fostered females were sexually mature (41–61 days), their responses to glass plates smeared with flank-gland odors of various conspecifics were quantified. The use of flank-gland odors minimized the possibility of early social learning (in utero or within 12 hr after birth) of siblings’ odors, because hamsters’ flank glands do not begin secreting until pups are >one month old.

Cross-fostered females approached plates containing odors of unfamiliar nonsiblings of both sexes significantly more quickly than odors of unfamiliar siblings (separated since birth) and of familiar nonsiblings (e.g. foster littermates that were reared together) (Fig. 1). Discrimination between odors of unfamiliar

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**Box 1. Circumstances favoring self-referent phenotype matching**

In parental species there are several ecological and social circumstances in which social associations are predictably inadequate or misleading indicators of relatedness, thus favoring self-referent phenotype matching to enhance nepotism and preclude inbreeding (after Ref. 4).

**Multiple mating**
- Full-siblings and maternal half-siblings are reared together
- Paternal half-siblings are reared apart

**Interbrood aggregation**
- Communal and cooperative breeding
- Posthatch brood amalgamation
- Adoption and kidnapping

**Parasitism**
- Intraspecific brood parasitism
- Interspecific brood parasitism

**Dispersal**
- Siblings from different generations disperse; their first meeting is as adults
- Large or widely spread social groups with overlapping generations
siblings and nonsiblings was confirmed by observations of other behaviors of cross-fostered females toward the plates, such as duration of investigation and frequency of flank-marking. Because the only social referents available to these females during development were nonrelatives, they apparently compared smells of unfamiliar conspecifics with their own flank-gland odors.

Interestingly, experimental females must also have incorporated odors from their foster family into their recognition template, because they investigated and marked plates containing flank-gland secretions of familiar nonsiblings as often as plates with secretions of unfamiliar siblings. To assess the relative importance of these cue sources, Mateo and Johnston compared females’ behavior toward secretions of their own unfamiliar sisters and unfamiliar sisters of their foster littersmates. The hamsters investigated the odors of unfamiliar biological sisters significantly longer, thus suggesting that a female’s own odors were weighted differently in her kin recognition template than those of her foster family.

Mateo and Johnston’s results constitute the best experimental evidence of self-referent phenotype matching. However, the data leave open the question of whether a hamster’s recognition template is learned (for example, by memorizing its own flank-gland odors) or is genetically determined (for example, owing to restrictive architectural design of perceptual filters) in its olfactory processing system. Distinguishing these possibilities requires attempting to ‘fool’ individuals by experimentally manipulating their phenotype and causing predictable recognition errors. Under the self-learning hypothesis, if a hamster’s own odor were altered experimentally (e.g. by changing its diet), it should treat similar smelling but unrelated, unfamiliar conspecifics like unfamiliar relatives.

Mateo and Johnston’s results do not directly address the function of kin recognition in nature. Captive hamsters flank mark in both territorial and mate-choice contexts, thus recognition might function to either minimize incest, maximize nepotism or both. Theoretically, self-referencing would be the more effective mechanism in forming templates used in nepotic contexts where individuals are attempting to discriminate close from distant kin, whereas social learning would be more effective in forming templates associated with mate choice, when additional referents (e.g. parents and siblings) are necessary to identify everyone to whom an individual is related. Thus, evidence of self-inspection in hamsters suggests that kin recognition probably facilitates nepotism (e.g. female cooperation in territory defense, communal nesting or food sharing).

In nature, self-referent phenotype matching might enable female hamsters to discriminate full- from half-sisters among nestmates and paternal half-sisters versus non-kin upon emergence from the natal burrow, as in Belding’s ground squirrels. Alternatively, the discriminations might be lab artifacts – errors in individuals’ recognition of their own odor, an ability which normally functions in some purely selfish context (e.g. maintenance of an exclusive territory). Under this interpretation, what appear to be fine-scale discriminations actually result from increasing errors with increasing relatedness (owing to greater odor similarity among closer kin; see Ref. 8). This raises the question of whether M. auratus frequently interact with maternal and paternal half-sisters in nature. If so, persistence of recognition mistakes is unlikely because, over time, selection would eliminate fitness-reducing errors; for example, by sharpening the recognition template (through inclusion of more chemical cues) or adjusting the rejection threshold more conservatively. The importance of evaluating the context and function of hamster kin discrimination in nature is re-emphasized.

In summary, Mateo and Johnston’s results clearly demonstrate the feasibility of self-referent phenotype matching. They also yield specific hypotheses about the social behavior of golden hamsters for testing in the field. This work, along with other studies implicating self-referencing, should galvanize the search for evidence of this intriguing but controversial kin-recognition mechanism among species in which social learning predictably is inadequate or misleading as a guide to relatedness.

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