Review TRENDS in Neurosciences Vol.24 No.10 October 2001

Self-referent phenotype matching: theoretical considerations and empirical evidence

Mark E. Hauber and Paul W. Sherman

In most birds and mammals, young are raised in family groups. The phenotypes of nestmates and parents are thus reliable cues for recognition of conspecifics and kin. However, in some species, young develop alone, or in broods of mixed relatedness (e.g. because of multiple paternity or maternity), or among heterospecifics or unrelated conspecifics (brood parasites). Under these circumstances, the best referent (model) for discriminating close from distant kin and heterospecifics from conspecifics might be one's own self. This recognition process is known as self-referent phenotype matching. Here we review recent experimental evidence of self-referencing and suggest that behavioral neuroscience can provide new tools and insights into how it works (its proximate mechanistic and ontogenetic bases) and why it exists (its adaptive significance).

Imagine that you are in the garden of an English estate, watching the colorful, noisy and dynamic sexual displays of free-ranging male peacocks. The birds are banded and you know a good deal about them. Their sires were captured several years ago and penned with four peahens. Eggs were collected daily and hatched in an incubator. Chicks were ringed at hatching and reared in mixed groups of siblings and nonsiblings.

A year later, all the peafowl were released at the estate. Now that the captive-bred males are 2–3 years old, they are sexually mature, and you are mapping their display sites. Putting together the behavioral and pedigree data you are astonished to find that genetic relatives display closer to each other than to non-relatives, and that brothers also are nearest display-neighbors far more often than expected by chance.

This scenario describes an experiment that Marion Petrie and her colleagues[1] recently conducted at Whipsnade Park Estate. The results are intriguing, and they raise two important questions. First, why would a subordinate male display near his dominant brother instead of finding his own isolated display arena? The authors suggest that cooperative displays might increase the attractiveness of male groups to females. If so, the genetic benefits of helping closely related dominants to attract more mates could outweigh the subordinate males' own meager mating opportunities[2]. Thus the evolutionary reason peacocks display with relatives could be to increase their inclusive fitness[3].

Petrie *et al.*'s data also raise an interesting mechanistic question: how did siblings end up as neighbors when their rearing regimen had apparently scrambled relatedness? The most likely hypothesis is that males were attracted to others who most closely resembled themselves, for example in plumage, vocalizations or displays[4]. Assuming that there is a correlation between an individual's phenotype and his genotype, this 'self-referent phenotype matching' mechanism[5,6] could enable peacocks sired by the same father (i.e. full- and half-brothers) to recognize each other. Here we review recent theoretical and empirical studies of self-referencing, explore its possible mechanistic bases and point out some exciting research avenues that these discoveries have opened to neuroscientists.

Mark E. Hauber
e-mail: meh20@cornell.edu
Paul W. Sherman
e-mail: pws6@cornell.edu
Dept Neurobiology and Behavior, Seeley G. Mudd Hall, Cornell University, Ithaca, NY 14853-2702, USA.

Phenotype matching and learning

There are two general categories of kin-recognition mechanisms[7] (Fig. 1). Individuals might recognize as a relative any conspecific encountered in a location that predictably contains only kin (e.g. a nest, burrow or display site). Such site-specific behavior results in 'indirect' recognition. Alternatively, individuals might recognize relatives 'directly' based on their phenotype (e.g. a gland odor, contact call or plumage ornament).

Direct recognition systems involve two parties, an actor and a recipient. The recognition process can be partitioned conceptually into three component parts[8]: (1) production: the nature and development of phenotypic labels (cues) in recipients that actors use to recognize them; (2) perception: the sensory detection of labels by actors and subsequent phenotype matching – that is, comparison of the recipient's cues to a template (internal representation). The ontogeny of recognition templates is also part of this component; and (3) action: the nature and determinants of behavioral actions that will be performed (e.g. nepotism, inbreeding avoidance, species recognition), depending on the similarity between actors' templates and recipients' labels.

Here we focus on the perception component, specifically on recognition templates. Theoretically, these internal representations might be completely learned or completely unlearned (i.e. environmentally or genetically determined). In practice, all well-studied cases of template development involve both influences[8].

PII: S0166-2236(00)01916-0

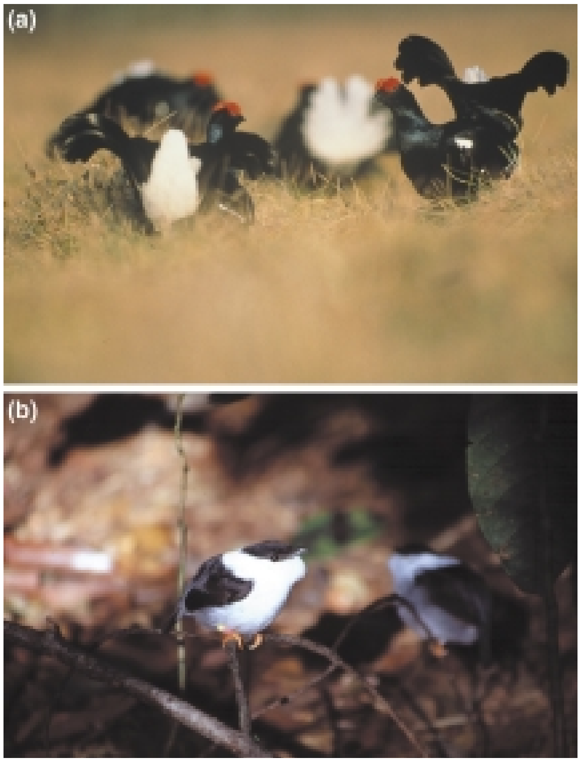

Fig. 1. Indirect and direct kin-recognition systems. (a) Adult male black grouse (*Tetrao tetrix*) display together to attract females during the breeding season. These social groups (leks) are composed of genetic relatives, probably because male grouse disperse short distances from their natal nests (indirect recognition), but males could also compare their own phenotypes to those of other males and display near the most similar ones (direct recognition). Photograph courtesy of David Tipling/VIREO. (b) White-bearded manakins (*Manacus manacus*) also attract females in leks, where related individuals group closer together than expected by chance. This association cannot be explained by natal philopatry (indirect recognition) and self-referencing based on plumage, voice or status is the most likely mechanism of kin recognition (direct recognition). Photograph courtesy of Tommi Lievonen/BIOTA.

A familiar example is human incest avoidance[9]. Arranged marriages between children that grew up together, even if they are not genetic relatives, are more likely to fail than marriages between individuals that were not raised together (e.g. Refs 10,11). Apparently children are born with a genetic program (i.e. a darwinian algorithm[12]) that causes them to learn the individuals with whom they were reared and to treat them as siblings, irrespective of the actual fraction of alleles they share. Later on, the youngsters are not attracted (sexually) to their 'siblings', presumably because of a long evolutionary history of deleterious genetic consequences associated with incest. This is ironic because, in some cultures, the reason parents adopt a foster child in the first place is to provide a suitable and desirable marriage partner for their own offspring[10].

Most other mammals, birds and some social insects also learn characteristics of relatives during early development[8,13,14]. Recognition templates are based on physical or chemical features of individuals encountered in unambiguous social circumstances, such as the natal nest or burrow. Later on, actors recognize and preferentially treat recipients who resemble the template closely enough. This process is termed 'phenotype matching'[5,6,15,16].

Fig. 2. Golden hamsters (*Mesocricetus auratus*) learn the odor cues of their relatives as pups from their mothers and litter mates. However, they are also able to discriminate odors of genetic relatives even if they had been cross-fostered into litters <12 hours after birth (i.e. no social cues of relatives are available during ontogeny), suggesting that they also use their own odor as a referent to evaluate olfactory recognition cues (direct recognition). Photograph courtesy of N. Kountoupes/Cornell News Services.

Direct recognition by phenotype matching has been documented in wild baboons[17], captive chimpanzees[18] and several other mammals[5,19–21] (Fig. 2). In birds, a well-known example is sexual imprinting[22,23], in which an individual's mate choices as an adult are determined by the resemblance of the phenotypic cues of suitors (e.g. visual, auditory, etc.) to those learned from its parents or siblings during early ontogeny (e.g. Refs 24,25). Learning based on phenotypes of social associates is a reliable mechanism for kin recognition because (1) parental care is obligatory in all mammals and most birds, (2) young are typically reared in sibling groups, and (3) phenotypic similarity correlates with genotypic similarity[8]. Therefore, phenotype matching mediated by social learning reliably results in kin discrimination.

However, there are some circumstances in which social learning alone would predictably yield inadequate or misleading kin recognition templates (Box 1). For example, if females mate with more than one male during a single period of receptivity, as occurs in many passerine birds and some mammals[26], individuals reared together can have different sires, so full- and half-siblings grow up side by side. Conversely, polygynous mating by males with different females can result in paternal half-siblings that are reared apart (e.g. in different nests or dens). Intraspecific parasitism also creates broods of mixed relatedness. If the host and parasitic females both mated with the same male, the brood will contain full- and half-siblings because of mixed maternity, but if the host and parasitic females mated with different males, the brood will contain full-siblings and non-siblings that result from mixed maternity and

Box 1. Ecological and social circumstances in which social associations are predictably inadequate or misleading indicators of relatedness

In these circumstances, self-referent phenotype matching should be favored to facilitate species recognition, enhance nepotism and preclude inbreeding[a–c].

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

Inter-brood aggregation
Communal and cooperative breeding
Nest usurpation
Brood parasitism
Post hatch brood amalgamation
Adoption/kidnapping

Dispersal
Siblings from different generations disperse, first meeting as adults
Large or widely spread social group with overlapping generations

References

[a] Holmes, W.G. and Sherman, P.W. (1982) The ontogeny of kin recognition in two species of ground squirrels. *Amer. Zool.* 22, 491–517

[b] Sherman, P.W. (1991) Multiple mating and kin recognition by self-inspection. *Ethol. Sociobiol.* 12, 377–386

[c] Hauber, M.E. and Sherman, P.W. (2000) The armpit effect in hamster kin recognition. *Trends Ecol. Evol.* 15, 349–350

paternity[5]. Interspecific parasitism also creates mixed broods, in this case of conspecifics and heterospecifics. If young parasites learned only the phenotypes of their nestling associates or foster parents they would be doomed to species misidentification[27]. Finally, in some birds such as megapodes[28], chicks require no direct parental care and they hatch asynchronously, so juveniles might not interact with a conspecific until months or even years after hatching.

In all these cases, individuals might still be able to discriminate close from distant kin, or heterospecifics from conspecifics if they inspected and learned salient aspects of their own phenotype, and then matched the appropriate features of nestmates or other similar-aged individuals encountered near home to themselves. Holmes and Sherman[5], Lacy and Sherman[6] and Sherman[29] termed this process 'self-referent phenotype matching'; Dawkins[30] euphemistically called it the 'armpit effect'.

In all science, the most convincing demonstration that a particular stimulus is responsible for a certain effect is to remove the stimulus and to observe failure of the anticipated effect. Therefore, not surprisingly, evidence for self-referencing as a mechanism by which organisms recognize relatives and heterospecifics has been largely circumstantial. This is undoubtedly because of the difficulty of eliminating all of an individual's experience with itself while still allowing the individual to develop along its 'normal' social ontogenetic trajectory. Recently these problems have been circumvented, at least partially, through novel experimental paradigms and careful field observations, combined with genetic techniques. Results have revealed evidence of self-referencing in a variety of species (Box 2)[74].

Phenotype matching and the nervous system: where do templates reside?

'Recognition' implies comparison of a cue with something already 'known' (i.e. held in the memory)[31]. However, in practice discrimination might not require neural processing. For example, many flowering plants discriminate against their own pollen, thereby preventing selfing, by matching molecules – protein products of a single highly polymorphic genetic locus[32]. 'Optimal outbreeding' is also promoted by acceptance of pollen from source plants that are neither too similar nor too dissimilar molecularly from the host plant's own pollen[33]. Larval tunicates (*Botryllus schlosseri*) often settle near and sometimes fuse with closely related larvae but not with nonrelatives. Here again the self-recognition cue is the presence of a shared protein-coding allele at a highly polymorphic recognition locus[34]. A more familiar example of self-referent phenotype matching is our immune system. Immune T cells must 'learn' the identity of other cells in their body in order to discriminate against pathogenic invaders and indigenous mutants, such as cancerous cells[35]. In all these cases and many others, the template against which recipients' cues are compared lies in the molecular make up of the actors' cells (e.g. cell-surface antigens, extra-cellular domains of cell-adhesion molecules, or other proteins embedded in cell membranes[36]) and does not depend on processing by the CNS.

However, many organisms recognize conspecifics or heterospecifics at a distance, as indicated by approach or avoidance behavior. Accomplishing long-distance recognition requires peripheral sensory systems and CNS processing. In the tripartite conceptualization of phenotype-matching mechanisms, the role of the CNS is to store the recognition template and compare it to the perceived cues. How the recognition template develops, exactly where it is stored, and how cue–template similarity is assessed[8,37] are the interesting, open questions.

Important advances in understanding the development of recognition templates have come from studies of avian song systems. In many songbirds, nestlings (both sexes) learn sexual vocalizations from social tutors, typically the male parent[16]. These templates enable later recognition of conspecific vocalizations via phenotype matching[15,38]. However, in some other species young males can recognize conspecific songs even though they were reared in isolation[39,40]. Although this usually is interpreted as evidence that the template is innate, it is possible that template formation actually involves self-referencing.

Box 2. Recent empirical evidence of self-referent phenotype matching in birds and mammals

Peacocks (*Pavo cristatus*)

Males that Petrie *et al.*[a] bred and raised in groups of mixed sex, maternity and paternity were released at Whipsnade Park where they preferentially displayed near brothers. These results cannot be because of (i) natal philopatry (because the birds were reared elsewhere) or (ii) social learning of nestmates' phenotypes (because kinship was scrambled during rearing, and unrelated males that were raised in the same pen did not display together). It is conceivable that (iii) microhabitat preferences are heritable and brothers ended up together because they had similar preferences. However, this seems unlikely because sons did not display near their sire's ex-display sites (i.e. young males did not share their father's site preferences). This leaves (iv) self-referent phenotype matching as the likely recognition mechanism.

Grouse [*Tetrao tetrix* (Fig. 1a) and *Lagopus lagopus scoticus*]

Analyses of DNA microsatellite markers indicate that male black grouse[b] and red grouse[c] that display near each other are more closely related than expected by chance. Although these studies did not investigate mechanisms of kin recognition experimentally, authors suggested a combination of (i) natal philopatry (limited dispersal from the natal site) and phenotype matching, either to the other chicks in their brood (ii) or to themselves (iv). The latter is more likely because siblings ceased interacting more than a year before males matured sexually and, before brood dissolution, chicks had juvenile phenotypes. Adult male plumage, displays, and vocalizations (i.e. possible phenotypic cues for arena–site choice) were not expressed until long after broods dissolved.

White-bearded manakins (*Manacus manacus*) (Fig. 1b)

Males display in groups (lek), and larger groups attract disproportionately more females. Shorey *et al.*[d] used DNA microsatellite markers to infer that males displaying on the same arena were related, and that close kin grouped together within arenas. The mechanism underlying kin clustering within manakin leks cannot be (i) natal philopatry (because females do not nest on arenas), (ii) social learning of nestmates' phenotypes (because the clutch size is only 1–2 eggs), or (iii) heritable microhabitat preferences (because the arenas are so small, usually <15 m × 15 m, that there are minimal microhabitat differences within them). Most likely (iv) males were attracted to individuals that resembled themselves phenotypically (e.g. in vocalizations, size, dominance) and therefore could be siblings.

Chacma baboons (*Papio cynocephalus*)

During the mating season, males and females form exclusive consortships. Alberts[e] reported that individuals who were born in the same troop <2 years apart were less likely to consort than pairs that differed more in age. Analyses of DNA microsatellites of consorting pairs revealed that paternal half-siblings exhibited lower levels of affiliative and sexual behaviors than nonkin (although half-sibs were not significantly less likely to consort than nonkin). This result cannot be attributed to (i) natal philopatry, (ii) social learning of littermates' phenotypes (because there is only one juvenile per litter), or (iii) similar microhabitat preferences of kin (because troops are so mobile). Most likely, (iv) males and females were repelled by opposite-sex individuals that were phenotypically similar to themselves for example in size, dominance, smell or vocalizations.

Golden hamsters (*Mesocricetus auratus*) (Fig. 2)

In the lab, Mateo and Johnston[f] swapped pups between litters that were <12 hours old, leaving each female with three young: a biological son and daughter and a foster daughter. When the cross-fostered pups were sexually mature (41–61 days), their responses to flank-gland odors of various conspecifics were quantified. Test subjects discriminated odors of unfamiliar nonsiblings from odors of unfamiliar siblings (separated since birth) or familiar nonsiblings (foster littermates). Because the only social referents available to these females after they were >12 hours old were nonrelatives, they probably compared smells of unfamiliar conspecifics with their own flank-gland odors [i.e. (iv) self-referencing]. The protocol of this experiment ruled out (i) natal philopatry and (iii) heritable microhabitat preferences as recognition mechanisms. In addition, prenatal learning of littermates' phenotypes (ii) was unlikely because the production of flank-gland odors does not begin until >1 month after birth.

Arctic charr (*Salvenius alpinus*)

Individual charr that were reared in isolation were unable to discriminate between odor cues of siblings and nonsiblings when they were 15 months old[g]. Apparently, social learning from school-mates is important in forming the charr's recognition

In these species, males spontaneously sing rudimentary versions of their species-typical song[41–44], from which they could learn or perfect their template. Molecular tools are now available to determine whether an individual's experience with its own song results in sensitization or habituation at the neuronal level[45–47], which, in turn, could lead to subsequent discrimination of like (conspecific) and unlike (heterospecific) songs.

The neural processing of and behavioral responses to vocalizations (i.e. the perception and action components of recognition) have been associated with specific sites and pathways in the oscine forebrain. Lesioning or other disruptions of these areas eliminate abilities to discriminate among songs, without disrupting other auditory-related processing[44,48]. This implies that song templates are stored and accessed using these pathways and nuclei. For example, female canaries (*Serinus canaria*) exhibit sexually receptive postures in response to conspecific songs but not heterospecific songs. Lesions to the HVC (High Vocal Center) result in failure to discriminate behaviorally between songs of their own and different species[49]. In female zebra finches (*Taenopygia guttata*), lesioning another forebrain area, namely the cHV (caudal hyperstriatum ventrale, an auditory area), disrupts behavioral discrimination between conspecific and heterospecific templates. When Olsén *et al.*[h] reared juvenile charr in sibling groups for two years and then gave individuals a choice between water scented by an MHC-different sibling and an MHC-different nonsibling, the water scented by the sibling was preferred, confirming social learning (ii) of sibling odors. In addition, charr can use self-referencing because, when given a choice between water scented by a full sibling whose MHC genotype was identical to their own and water scented by a full sibling whose MHC genotype was different, the fish preferred water from MHC-identical siblings. Social learning (ii) cannot account for this result because test fish were reared in groups of siblings with variable MHC alleles. Natal philopatry (i) and similar microhabitat preferences (iii) also cannot account for the result. Apparently charr incorporate their own odors (iv) into their recognition template.

Brown-headed cowbirds (*Molothrus ater*) (Fig. 4)

In this obligate brood parasite, chicks are typically reared among heterospecifics so social learning would lead to species-recognition errors. Hauber *et al.*[i] hand-reared nestlings in visual isolation and dyed some of them black while leaving others undyed (gray). At fledging, the preferences of these birds for similarly and dissimilarly colored adult female cowbirds were assessed. In simultaneous choice trials, juveniles more quickly approached and preferentially associated with adults that were colored like themselves. This indicates self-referencing (iv) because manipulating the putative recognition cue (feather color) changed the color preference of dyed individuals relative to undyed controls. Alternative recognition mechanisms (i)–(iii) do not predict this outcome.

References

a Petrie, M. *et al.* (1999) Peacocks lek with relatives even in the absence of social and environmental cues. *Nature* 401, 155–157

b Höglund, J. *et al.* (1999) Microsatellite markers reveal the potential for kin selection on black grouse leks. *Proc. R. Soc. Lond B Biol. Sci.* 266, 813–816

c Piertney, S.B. *et al.* (1999) Spatial distribution of genetic relatedness in a moorland population of red grouse (*Lagopus lagopus scoticus*). *Biol. J. Linn. Soc.* 68, 317–331

d Shorey, L. *et al.* (2000) Fine-scale genetic structuring on *Manacus manacus* leks. *Nature* 408, 352–353

e Alberts, S.C. (1999) Paternal kin discrimination in wild baboons. *Proc. R. Soc. Lond. B Biol. Sci.* 266, 1501–1506

f Mateo, J.M. and Johnston, R.E. (2000) Kin recognition and the 'armpit effect:' evidence of self-referent phenotype matching. *Proc. R. Soc. Lond B Biol. Sci.* 267, 695–700

g Winberg, S. and Olsén, K.H. (1992) The influence of rearing conditions on the sibling odor preference of juvenile Arctic charr, *Salvelinus alpinus* L. *Anim. Behav.* 44, 157–164

h Olsén, K.H. *et al.* (1998) MHC and kin discrimination in juvenile Arctic charr, *Salvelinus alpinus* (L.). *Anim. Behav.* 56, 319–327

i Hauber, M.E. *et al.* (2000) Self-referent phenotype matching in a brood parasite: the armpit effect in brown-headed cowbirds (*Molothrus ater*). *Anim. Cogn.* 3, 113–117

songs[50]. Because female subjects continued to exhibit the species-specific behavioral responses even after surgery, these experiments imply a specific function for the manipulated brain nuclei in the perception rather than the action components of recognition. Whether the templates underlying this and other types of recognition are also stored in HVC or other song-circuit nuclei awaits investigation. Comparative analyses of female responses to conspecific and heterospecific songs are potentially illuminating, because although females of many species do not sing, they can nonetheless recognize conspecific songs without previous exposure[51,52]. Therefore, unlike males, the song-recognition template of these females develops without self-referencing to their own songs. The structural correlates of this sexual dimorphism (i.e. what is present in males but not in females) are ripe for investigation.

Neuroanatomical studies of male zebra finches indicate that they respond more strongly to playbacks of their own songs and other, similar songs than to more dissimilar vocalizations: expression of the immediate early gene ZENK was greater in the caudal part of the neostriatum (NCM) and in the cHV, but not in HVC, RA or area X when males were exposed to vocalizations that more closely resembled their own songs[53]. *In vivo* intracellular recordings indicated that identifiable, area X-projecting neurons in the HVC were probably sites of auditory discrimination in recognition of the birds' own songs. Singing by the subjects was not part of the experimental protocol, so the self-referencing that occurred must have involved comparison to an auditory template that does not depend on sound production.

However, auditory feedback from a male's own vocalizations is necessary for the production of adult crystallized songs in most songbirds[54]. This feedback probably occurs through a different neural pathway (i.e. the basal ganglia–forebrain pathway[55]), and singing practice is essential to proper song production[44,54]. Apparently, the birds continually and repeatedly compare accidental variants of their own song to the template.

Recently, it has become possible to localize brain regions associated with some of our own perceptual processes[56]. In an important review of the mechanistic bases of visually based self-recognition, Keenan *et al.*[57] suggested that "there may be a bias for the processing of 'self' within the right prefrontal cortex in humans and other primates" (p. 338). An interesting question is whether templates for other recognition modalities involved in self-recognition (e.g. olfactory or auditory cues) also reside in this brain area.

Self-referencing and the nervous system: template storing versus on-line processing

Is self-referencing a specialized form of phenotype matching, or is it a wholly different mechanism? The answer depends on whether a template is formed and used. In phenotype matching, cues or environmental predictors are learned. When an individual is subsequently called upon to make a behavioral discrimination, the referents from which those cues were learned might not be present. So, the individual must rely on its remembered template for the perception component of recognition. This is also a feasible mechanism for self-referencing: learning of one's own traits and comparison of this template to traits of subsequent social interactants.

However, self-referencing might rely on an alternative and equally plausible mechanism, which we term 'on-line processing.' Under this mechanism,

Fig. 3. Gray catbirds (*Dumatella carolinensis*) typically remove the odd-looking speckled egg of parasitic brown-headed cowbirds (*Molothrus ater*) from their otherwise uniformly green clutch. Photograph courtesy of Mark Hauber. Rejection of cowbird eggs is adaptive because the presence of an earlier hatching and intensively begging cowbird nestling, within a brood of yellow warbler (*Dendroica petechia*), reduces the survival of the offspring of most hosts. Photograph courtesy of A. Morris/VIREO.

no template is formed. Instead, individuals perform comparisons every time the situation warrants. On-line processing is possible because an individual's own phenotype is always available for comparison with others.

At present there is circumstantial evidence for both on-line processing and template formation. Consider two different darwinian algorithms underlying rejection of eggs of brood parasites. Gray catbirds (*Dumatella carolinensis*) typically remove odd-colored, mottled eggs from their clutch of solid green eggs[58] (Fig. 3). Rejection is adaptive because the mottled eggs belong to brown-headed cowbirds, and the presence of cowbirds chicks severely reduces catbird reproductive success[59]. However, when catbird clutches are experimentally manipulated during the laying period so that they contain all mottled eggs and then a single, green egg is added, the adults eject only the green egg[58]. Catbirds probably compare egg colors and reject 'odd' phenotypes. The reproductive cost of such an on-line comparison is that a catbird could reject its own eggs when they are the minority phenotype, which might happen if several cowbirds find and lay in the same catbird nest in quick succession.

Alternatively, catbirds might be more similar to reed warblers (*Acrocephalus scirpaceus*), a species that also recognizes and rejects parasitic eggs, but whose darwinian algorithm is different[58,60]. Females of the reed-warbler-specialist gens of the European cuckoo (*Cuculus canoris*) lay mimetic eggs. This has favored warblers that lay unique or previously uncommon (i.e. discriminable) egg patterns. However, the warblers also must recognize these novel eggs and treat them as their own. To do so, females inspect their first clutch closely and learn the characteristics of their own eggs. Comparisons to this remembered template enable females to reject foreign eggs in subsequent clutches[61]. Here, the cost of template formation is that if a cuckoo manages to slip an egg into a warbler's first clutch, the foreign egg will be incorporated into the host's recognition template and the bird will be doomed to accept cuckoo eggs for the rest of its life[62].

Phenotypes used for self-referencing, whether compared on-line or stored in memory, are themselves malleable constructs because individuals grow and change with age and experience. When there is a lengthy association between individuals whose characteristics change through time, continual on-line processing might enable both parties to keep up. This could be what enables us to consistently recognize similarities between our teenage offspring and ourselves in spite of the rapidity of their physiological and behavioral changes. Yet, people also can discriminate pictures of themselves from those of others throughout life, in spite of major changes in their facial phenotypes[56]. Mirrors are not necessary for such discriminations, so we apparently retain memories (templates) of how we looked in the past. However, this template must change together with an individual's changing phenotype, implicating a process of template updating[8].

Another example of template updating comes from experimental studies of juvenile cowbirds (Fig. 4). Manipulation of plumage colors revealed that fledglings pay attention to their own color when making decisions about social partners[27]. When young males molt into adult plumage during their first fall, their color changes from gray to shiny black[63]. Together with this drastic change in self-plumage, young males also begin to associate preferentially with older black-plumaged conspecific males rather than fledgling-like plumaged adult females[27,64]. This suggests that recognition by juvenile males probably involves on-line processing, although the formation of a new template upon molting also is possible. These alternatives could be tested via color manipulations and reversible lesioning of those brain areas, such as the dorsocaudal neostriatum, that are known to be involved in visual memory of social partners during filial imprinting[65].

Conclusions: blending nature and nurture

It is clear that self-referent phenotype matching is both widespread and adaptive. What we lack is knowledge of its mechanistic bases. For behavioral ecologists like us, neural recognition mechanisms remain 'black boxes'. We invite assistance in letting in some light! Our understanding of self-referencing would undoubtedly benefit from applications of both classical and new techniques in neurophysiology[39], temporary and permanent neural inactivation[53], high resolution structural[66] and functional magnetic resonance imaging (fMRI)[67], and gene regulation and other molecular mechanisms[68,69].

The tripartite construct of recognition systems (production, perception and action[8]) is a useful conceptual framework for guiding mechanistic research. However, no one yet knows how these components correspond to neural processes, or what the relationships, interdependence and possible physiological constraints are on each component[54]. For example, what is the physical manifestation of a 'template,' a 'darwinian algorithm' or a 'decision rule'? How do these concepts relate to neural, neurochemical and hormonal mechanisms? The tools of neuroscience can elucidate the mechanistic and developmental costs associated with specific recognition processes. This knowledge might then forge new links between neuroscientists and functional and evolutionary biologists, by enabling tests of cost–benefit models and derivation of evolutionarily stable alternative behavioral strategies.

Neuroscientists also might be able to solve two types of problems that have proven intractable to behaviorists. First, some experimental paradigms do not elicit clear behavioral responses to different classes of stimuli[70,71]. Although 'recognition' occurred, there was no detectable behavioral discrimination so the test yielded negative or inconclusive results. In such cases, the extent of neural activity [e.g. using positron emission tomography (PET) or fMRI to map the involved brain areas] and the types of neuronal responses (e.g. the firing patterns of neurons in specific brain areas) might reveal perception and processing differences between different classes of stimuli[57]. Similarly, differential activation of hormonal pathways, even in the absence of behavioral responses, could be used to elucidate whether self-referencing occurs[71,72].

Second, it is difficult to discriminate between genetic control and self-referencing by denying an individual experience with its own phenotype while still allowing normal development. For example, although predator avoidance by naïve fish fry following exposure to conspecific alarm substances ('schreckstoff') has been long thought to be under strict genetic control[73], it is also possible that young fish learn to respond to the alarm substance when it is released following injury to their own epidermis (e.g. by parasitic infection or mechanical abrasion). Reversible inactivation of olfaction or central processing of olfactory cues during early development could enable behavioral neuroscientists to discriminate between these alternatives.

Fig. 4. Brown-headed cowbirds (*Molothrus ater*) are obligate brood parasites, and nestlings are raised by heterospecifics. Social associations of juvenile cowbirds are affected by their own phenotype (e.g. plumage color): in choice tests, they preferred social partners that appeared similar to themselves. Photograph courtesy of R. Villani/VIREO.

Knowledge of whether learning and memory (recognition templates) are involved in recognition is essential to differentiate between phenotype matching and on-line self-referencing. As we have seen, self-referencing might turn out to be the mechanism of recognition in several contexts that had previously been thought to depend solely on genetic (innate) cues. Finally, we believe that understanding the generality of the proximate mechanisms involved in self-referencing will help bury the false dichotomy between ontogenies that are 'genetic' versus 'learned' (i.e. 'nature' versus 'nurture'). This is because, by definition, self-referencing involves both experience-dependent and -independent mechanisms.

Acknowledgements
We thank M.C.B. Andrade, T.J. DeVoogd, A. Gôth, J.M. Hernandez, R.E. Johnston, J.P. Keenan, A.C. Mason, J.M. Mateo, B.D. Neff, H.K. Reeve, S.I. Rothstein, K.E. Whitlock, Cornell's Animal Behavior Lunch Bunch, and the reviewers for useful commentary. Financial support was provided by a Howard Hughes Medical Institute Predoctoral Fellowship, the National Science Foundation, and the Agricultural Experiment Station at Cornell University.

References

1 Petrie, M. *et al.* (1999) Peacocks lek with relatives even in the absence of social and environmental cues. *Nature* 401, 155–157
2 Kokko, H. and Lindstrom, J. (1996) Kin selection and the evolution of leks: whose success do young males maximize? *Proc. R. Soc. Lond. B Biol. Sci.* 263, 919–923
3 Hamilton, W.D. (1964) The evolution of social behavior I–II. *J. Theor. Biol.* 7, 1–52
4 Sherman, P.W. (1999) Birds of a feather lek together. *Nature* 401, 119–120
5 Holmes, W.G. and Sherman, P.W. (1982) The ontogeny of kin recognition in two species of ground squirrels. *Amer. Zool.* 22, 491–517
6 Lacy, R.C. and Sherman, P.W. (1983) Kin recognition by phenotype matching. *Am. Nat.* 121, 489–512
7 Waldman, B. *et al.* (1988) Problems of kin recognition. *Trends Ecol. Evol.* 3, 8–13
8 Sherman, P.W. *et al.* (1997) Recognition systems. In *Behavioural Ecology* (4th edn) (Krebs, J.R. and Davies, N.B. eds), pp. 69–96, Blackwell Science
9 Bevc, I. and Silverman, I. (2000) Early separation and sibling incest: A test of the revised Westermarck theory. *Evol. Hum. Behav.* 21, 151–161
10 Wolf, A.P. (1968) Adopt a daughter-in-law, marry a sister: a Chinese solution to the problem of incest taboo. *Am. Anthropol.* 70, 864–874
11 Shepher, J. (1978) Reflections on the origin of the human pair-bond. *J. Soc. Biol. Struct.* 1, 253–264
12 Cosmides, L. and Tooby, J. (1987) From evolution to behavior: evolutionary psychology as the missing link. In *The Latest on the Best: Essays on Evolution and Optimality* (Dupre, J., ed.), pp. 277–306, MIT Press
13 Kendrick, K.M. *et al.* (1998) Mothers determine sexual preferences. *Nature* 395, 229–230
14 Hatchwell, B.J. *et al.* (2001) Kin discrimination in cooperatively breeding long-tailed tits. *Proc. R. Soc. Lond. B Biol. Sci.* 268, 885–890
15 Irwin, D.E. and Price, T. (1999) Sexual imprinting, learning and speciation. *Heredity* 82, 347–354
16 ten Cate, C. and Vos, D.R. (1999) Sexual imprinting and evolutionary processes in birds: a reassessment. *Adv. Study Behav.* 28, 1–31
17 Alberts, S.C. (1999) Paternal kin discrimination in wild baboons. *Proc. R. Soc. Lond. B Biol. Sci.* 266, 1501–1506

18 Parr, L.A. and de Waal, F.B.M. (1999) Visual kin recognition in chimpanzees. *Nature* 399, 647–648

19 Holmes, W.G. (1986) Identification of paternal half siblings by captive Belding's ground squirrels. *Anim. Behav.* 34, 321–327

20 Hauser, M.D. *et al.* (1995) Self-recognition in primates: phylogeny and the salience of species-typical features. *Proc. Natl. Acad. Sci. U. S. A.* 92, 10811–10814

21 Heth, G. *et al.* (1998) Kin recognition in golden hamsters: evidence for phenotype matching. *Anim. Behav.* 56, 409–417

22 ten Cate, C. *et al.* (1993) Sexual imprinting and song learning: two of one kind? *Neth. J. Zool.* 43, 34–45

23 Laland, K.N. (1994) On the evolutionary consequences of sexual imprinting. *Evolution* 48, 477–489

24 Bateson, P.P.G. (1978) Sexual imprinting and optimal outbreeding. *Nature* 273, 659–660

25 Clayton, N.S. (1990) The effects of cross-fostering on assortative mating between zebra finch subspecies. *Anim. Behav.* 40, 1102–1110

26 Birkhead, T.R. (2000) *Promiscuity. An Evolutionary History of Sperm Competition and Sexual Conflict*, Faber & Faber

27 Hauber, M.E. *et al.* (2000) Self-referent phenotype matching in a brood parasite: the armpit effect in brown-headed cowbirds (*Molothrus ater*). *Anim. Cogn.* 3, 113–117

28 Göth, A. (2001) Innate predator-recognition in Australian brush-turkey (*Alectura lathami*, Megapodiidae) hatchlings. *Behavior* 138, 117–136

29 Sherman, P.W. (1991) Multiple mating and kin recognition by self-inspection. *Ethol. Sociobiol.* 12, 377–386

30 Dawkins, R. (1982) *The Extended Phenotype.* W.H. Freeman

31 Websters Unabridged Dictionary (1975) Collins

32 Kao, T-H. and McCubbin, A.G. (1996) How flowering plants discriminate between self and non-self pollen to prevent inbreeding. *Proc. Natl Acad. Sci. U. S. A.* 93, 12059–12065

33 Waser, N.M. (1993) Population structure, optimal outbreeding, and assortative mating in angiosperms. In *The Natural History of Inbreeding and Outbreeding* (Thornhill, N.W., ed.), pp. 173–199, University of Chicago Press

34 Grosberg, R.K. and Hart, M.W. (2000) Mate selection and the evolution of highly polymorphic self/nonself recognition genes. *Science* 289, 2111–2114

35 Penn, D.J. and Potts, W.K. (1999) The evolution of mating preferences and major histocompatibility complex genes. *Am. Nat.* 153, 145–164

36 Haig, D. (1996) Gestational drive and the green-bearded placenta. *Proc. Natl. Acad. Sci. U. S. A.* 93, 6547–6551

37 Reeve, H.K. (1989) The evolution of conspecific acceptance thresholds. *Am. Nat.* 133, 407–435

38 Depraz, V. *et al.* (2000) Early tutoring and adult reproductive behaviour in female domestic canary (*Serinus canaria*). *Anim. Cogn.* 3, 45–51

39 Whaling, C.S. *et al.* (1997) Acoustic and neural bases for innate recognition of song. *Proc. Natl Acad. Sci. U. S. A.* 94, 12694–12698

40 Soha, J.A. and Marler, P. (2000) A species-specific acoustic cue for selective song learning in the white-crowned sparrow. *Anim. Behav.* 60, 297–306

41 King, A.P. and West, M.J. (1977) Species identification in the North American cowbird: appropriate responses to abnormal song. *Science* 195, 1002–1004

42 O'Loghlen, A.L. and Rothstein, S.I. (1993) An extreme example of delayed vocal development – song learning in a population of wild brown-headed cowbirds. *Anim. Behav.* 46, 293–304

43 Marler, P. (1997) Three models of song learning: evidence from behavior. *J. Neurobiol.* 33, 501–516

44 DeVoogd, T.J. and Szekely, T. (1998) Causes of avian song: using neurobiology to integrate proximal and ultimate levels of analysis. In *Animal Cognition in Nature* (Pepperberg, I. *et al.*, eds), pp. 337–380, Academic Press

45 Mello, C.V. *et al.* (1992) Song presentation induces gene-expression in the songbird forebrain. *Proc. Natl. Acad. Sci. U. S. A.* 89, 6818–6822

46 Mello, C.V. *et al.* (1995) Repeated exposure to one song leads to a rapid and persistent decline in an immediate-early genes response to that song in zebra finch telencephalon. *J. Neurosci.* 15, 6919–6925

47 Mateo, J.M. and Johnston, R.E. (2001) Self-referencing in hamsters – reply. *Trends Ecol. Evol.* 16, 74–75

48 Scharff, C. *et al.* (1998) Conspecific and heterospecific song discrimination in male zebra finches with lesions in the anterior forebrain pathway. *J. Neurobiol.* 36, 81–90

49 Brenowitz, E.A. (1991) Altered perception of species-specific song by female birds after lesions of a forebrain nucleus. *Science* 251, 303–305

50 MacDougall-Shackleton, S.A. *et al.* (1998) Neural bases of song preferences in female zebra finches (*Taeniopygia guttata*). *NeuroReport* 9, 3047–3052

51 Dooling, R.J. and Searcy, M.H. (1980) Early perceptual selectivity in the swamp sparrow. *Dev. Psychobiol.* 13, 499–506

52 Braaten, R.F. and Reynolds, K. (1999) Auditory preference for conspecific song in isolation-reared zebra finches. *Anim. Behav.* 58, 105–111

53 Bolhuis, J.J. *et al.* (1999) Localized neuronal activation in the zebra finch brain is related to the strength of song learning. *Proc. Natl. Acad. Sci. U. S. A.* 97, 2282–2285

54 Leonardo, A. and Konishi, M. (1999) Decrystallization of adult birdsong by perturbation of auditory feedback. *Nature* 399, 466–470

55 Brainard, M.S. and Doupe, A.J. (2000) Interruption of a basal ganglia–forebrain circuit prevents plasticity of learned vocalizations. *Nature* 404, 762–766

56 Keenan, J.P. *et al.* (2001) Self-recognition and the right hemisphere. *Nature* 409, 305

57 Keenan, J.P. *et al.* (2000) Self-recognition and the right prefrontal cortex. *Trends Cogn. Sci.* 4, 338–344

58 Rothstein, S.I. (1975) Mechanisms of avian egg recognition: do birds know their own eggs? *Anim. Behav.* 26, 268–278

59 Lorenzana, J. and Sealy, S.G. (2001) Fitness costs and benefits of cowbird egg ejection by gray catbirds. *Behav. Ecol.* 12, 325–329

60 Davies, N.B. (2000) *Cuckoos, Cowbirds and Other Cheats*, Poyser

61 Lotem, A. *et al.* (1992) Rejection of cuckoo eggs in relation to host age – a possible evolutionary equilibrium. *Behav. Ecol.* 3, 128–132

62 Lotem, A. (1995) Learning to recognize nestlings is maladaptive for cuckoo, *Cuculus canoris*, hosts. *Nature* 362, 743–745

63 Farmer, C. and Holmgren, M.A. (2000) Sexual dichromatism in the plumage of juvenile brown-headed cowbirds. *J. Field Ornithol.* 71, 429–436

64 Freeberg, T.M. (1999) Spatial associations provide a context for social learning of courtship patterns in brown-headed cowbirds (*Molothrus ater*). *J. Comp. Psychol.* 113, 327–332

65 Bock, J. and Braun, K. (1999) Filial imprinting in domestic chicks is associated with spine pruning in the associative area, dorsocaudal neostriatum. *Eur. J. Neurosci.* 11, 2566–2570

66 Van der Linden, A. *et al.* (1998) Non invasive *in vivo* anatomical studies of the oscine brain by high resolution MRI microscopy. *J. Neurosci. Methods* 81, 45–52

67 Belin, P. *et al.* (2000) Voice-selective areas in human auditory cortex. *Nature* 403, 309–312

68 Clayton, D.F. (1997) Role of gene regulation in song circuit development and song learning. *J. Neurobiol.* 33, 549–571

69 Jarvis, E.D. *et al.* (2000) Behaviourally driven gene expression reveals song nuclei in hummingbird brain. *Nature* 406, 628–632

70 Johnsrude, I.S. *et al.* (1994) Effect of motivational context on conspecific song discrimination by brown-headed cowbirds (*Molothrus ater*). *J. Comp. Psychol.* 108, 172–178

71 MacDougall-Shackleton, S.A. *et al.* (2001) Physiological and behavioural responses of female mountain white-crowned sparrows to natal- and foreign-dialect songs. *Can. J. Zool.* 79, 325–333

72 Tchernichovski, O. *et al.* (1998) Context determines the sex appeal of male zebra finch song. *Anim. Behav.* 55, 1003–1010

73 Chivers, D.P. and Smith, R.J.F. (1998) Chemical alarm signalling in aquatic predator–prey systems: a review and prospectus. *Ecoscience* 5, 338–352

74 Hauber, M.E. and Sherman, P.W. (2000) The armpit effect in hamster kin recognition. *Trends Ecol. Evol.* 15, 349–350