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3 Recognition of Individuals: Specificity and Multiplicity

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1 ABSTRACT

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3 This review focuses on specificity and multiplicity in the
4 classification of other members of the same species. Individual
5 recognition is one end of a spectrum of specificity in the
6 classification of conspecifics. In addition, recognition varies from
7 binary to more complex classifications of conspecifics. Specificity
8 and multiplicity might evolve both for differentiation of rivals in
9 competitive situations and for differentiation of partners in
10 affiliative situations. Failure of recognition in some cases indicates
11 possible compromises in the recognition of conspecifics. In other
12 cases, simple forms of learning, such as habituation, can result in
13 highly specific recognition. In still other cases, recognition of
14 individuals involves complex associations of multiple cues with
15 multiple previous experiences, although, like other forms of
16 associative learning, it is probably always dependent to some degree
17 on context. Complex mechanisms for recognition should evolve
18 only when simpler rules of thumb cannot provide sufficient
19 specificity and multiplicity in social interactions. Such conditions
20 arise particularly in conjunction with cooperation between
21 individuals. Human capacities for individual recognition, although
22 little studied, probably rival the cognitive demands of language and

- 1 probably have a central role in the evolution of complex forms of
- 2 human cooperation.
- 3

1 INTRODUCTION

2

3 An ability to recognize other individuals of the same species
4 with various degrees of specificity has been confirmed
5 experimentally in a number of species. Nevertheless, important
6 questions about the mechanisms and evolution of recognition
7 remain unanswered. This review identifies some of these questions
8 by focusing on the specificity and multiplicity of recognition.

9 Recognition is a classification of conspecifics, a classification that
10 can include either relatively specific sets of conspecifics (in some
11 cases, single individuals) or relatively general ones. Furthermore,
12 the classification can be either binary (a single individual and all
13 others) or multiple. The behavioral mechanisms that produce
14 specificity and multiplicity in recognition evolve as a result of the
15 advantages of differentiated social behavior, including management
16 of competition, preferential treatment of kin, and cooperation.
17 Consequently, we suggest, the mechanisms of recognition are often
18 just complex enough to obtain these advantages.

19 Humans of course have prodigious capabilities for recognizing
20 each other. These abilities receive relatively little attention, perhaps
21 because they are taken for granted. A number of studies have
22 focused on psychological mechanisms for recognition of individual

1 faces and how they relate to other mechanisms of categorization
2 (Gauthier et al. 1999; Leder and Bruce 2000; Gauthier and
3 Logothetis 2000; Tanaka and Farah 1993), a subject with clear
4 relevance to the current interest in machine recognition of faces
5 (Zhao et al. 2003). Yet there have been no attempts to determine
6 how many people humans can recognize nor how this ability is
7 related to recognition of less specific sets of humans. This omission
8 is surprising because the human capacity for recognizing other
9 individuals, for conceptualizing the relationships between
10 individuals, and for differentiating their behavior on the basis of
11 these relationships underlies most human social behavior. It seems
12 possible that the cognitive demands rival those for language.

13 Falls (1982: 238) provided an operational definition for
14 individual recognition in his pioneering studies of birdsong:
15 “individual recognition [occurs when] recipients discriminate among
16 similar sounds of different individuals in the absence of other
17 identifying cues”. This definition emphasizes discrimination by
18 means of similar cues presented by different individuals in one
19 sensory modality. Falls and his students provided the first clear
20 evidence that similar vocalizations were sufficient for recognition of
21 conspecific individuals by birds (Brooks and Falls 1975a; Falls and
22 Brooks 1975; Brooks and Falls 1975b; Weeden and Falls 1959). This

1 definition leaves open questions about the specificity of
2 classification of other individuals, the mechanism of discrimination,
3 and the interactions of different cues in recognition. Our goal here
4 is to examine these questions.

5

6 SPECIFICITY AND MULTIPLICITY OF RECOGNITION

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8 A less restrictive definition of individual recognition requires
9 only that an individual respond differently to at least one other
10 individual in natural situations. The primary emphasis here is on
11 specificity. At least one individual must evoke responses unlike
12 those evoked by all others. A further issue is the number of
13 individuals differentiated, or the multiplicity of recognition. A
14 secondary emphasis is on natural situations. We first examine
15 specificity and multiplicity of recognition in natural situations and
16 then turn to the neural and behavioral mechanisms and the
17 evolution of these capabilities.

18

19 Specificity of recognition

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21 Many experimental studies of recognition show that subjects
22 differentiate two categories of conspecifics. For instance, playbacks

1 of vocalizations have demonstrated that some colonial seabirds can
2 distinguish between a mate and other conspecifics (Aubin and P.
3 Jouventin 1998; Aubin et al. 2000; Brooke, M. de L. 1978; Lengagne
4 et al. 1999; Lengagne et al. 2000; Moseley 1979; White 1971) and
5 comparisons of responses to a mate and strangers suggest similar
6 discriminations in other organisms as well (Caldwell 1992;
7 Munding 1970; Rahman et al. 2001). In addition, playbacks or
8 modifications of the appearance of young have demonstrated that
9 parents can recognize their own young by auditory or visual cues
10 (Aubin and Jouventin 2002; Beecher et al. 1986; De Fanis and Jones
11 1996; Illmann et al. 2002; Insley et al. 2003; Miller and Emlen 1974;
12 Schommer and Tschanz 1975) or that young can recognize their
13 parents (Aubin and P. Jouventin 1998; Beer 1970; Charrier et al.
14 2003; Insley et al. 2003; Leonard et al. 1997; White 1971). These
15 studies have all demonstrated that subjects distinguish two
16 categories of conspecifics. In some of these cases, when subjects
17 each have a single mate or a single offspring, the smaller of the two
18 categories includes only a single individual.

19 In many of these cases of binary recognition, the smaller
20 category includes several individuals, several young or two parents,
21 all of which evoke similar responses. In the experiments just cited,
22 parents with multiple young distinguish their own offspring from

1 others, but no evidence suggests that they differentiate each
2 individual offspring. Conversely, young animals often respond
3 selectively to their parents, without indications that the two parents
4 evoke different responses. A similar situation arises in social
5 insects. Each colony develops a distinctive odor, which is used to
6 exclude individuals from other colonies of the same species as well
7 as to exclude other species (Breed et al. 1995; Langen et al. 2000;
8 1998), although no evidence indicates recognition of individual
9 nestmates. These cases do not qualify as individual recognition by
10 our criterion of specificity.

11 The specificity of responses to conspecifics can vary along a
12 continuum of progressively larger classes of individuals.
13 Differentiated responses to single individuals are one end of this
14 continuum, with the greatest specificity. Responses to any
15 conspecific without further differentiation are the other end, with
16 the least specificity. In between are differentiated responses to one
17 sex, one age-class, parents, young, members of the same group, or
18 any other category of conspecifics. The specificity of responses
19 reflects the ability to categorize (or to classify) conspecifics.

20 A continuum of levels of specificity no doubt applies to
21 human recognition as well, although we rarely think about it. Any
22 university teacher confronts this continuum as a matter of course.

1 We continually recognize students with different levels of
2 specificity. For some we know names and other specific associations
3 (individual recognition in the strict sense above). For others we
4 only know that they attend our current lectures. Some appear
5 familiar but have no other associations for us. These capabilities are
6 related to capabilities for classification of objects and for object
7 recognition in general. Similar issues arise in recognition of
8 conspecifics by any animal.

9 In addition to the specificity of recognition is the question of
10 the multiplicity of individuals (or sets of individuals) recognized
11 with any level of specificity. The cases discussed above, both those
12 with strict individual recognition and those with recognition of
13 small sets of individuals such as parents or young, all provide
14 evidence for recognition of only one individual or one small set of
15 individuals. More complex recognition involves differentiated
16 responses to multiple other individuals. Multiplicity, like specificity,
17 increases the cognitive demands of recognition. There are two
18 situations in which this capability seems likely to occur: recognition
19 of multiple rivals and recognition of partners within a social group.
20
21 Recognition of multiple rivals

1 Almost any territorial animal must confront multiple rivals,
2 because they not only defend their territories against strangers but
3 also against more than one neighbor. The first experiments to
4 investigate territorial animals' responses to neighbors presented
5 vocalizations (or olfactory signals) associated with a neighbor and a
6 stranger (Barash 1974; Brooks and Falls 1975a; Emlen 1971; 1975b;
7 Stoddard et al. 1990; Weeden and Falls 1959). Such experiments
8 often produce evidence of differences in behavior toward neighbors
9 and strangers (Husak 2003; Langen et al. 2000; Leiser and Itzkowitz
10 1999; Temeles 1994). Although these experiments indicate an
11 ability to differentiate two sets of other individuals, like recognition
12 of progeny discussed above, they do not achieve the specificity of
13 individual recognition.

14 A few studies have elaborated this procedure by presenting an
15 individual neighbor's vocalizations on both the correct and an
16 incorrect boundary of the subject. A correct boundary is one
17 shared with that particular neighbor, and an incorrect boundary is
18 one not so shared. For comparisons these experiments include a
19 second presentation at each boundary, sometimes a stranger's
20 vocalizations (Falls and Brooks 1975; Stoddard et al. 1991) and
21 sometimes the opposite neighbor's (Godard and Wiley 1995; Godard
22 1991; Wiley and Wiley 1977). In the first case there is evidence for

1 individual recognition of neighbors if the subject behaves
2 differently to the neighbor's vocalizations at the two boundaries,
3 but equally to strangers'. In the second case, evidence would consist
4 of weaker response to each neighbor at the correct boundary and
5 stronger at the incorrect one. Recognition of individuals is
6 indicated if the relative intensity of responses evoked by the same
7 two vocalizations, one from each of two neighbors, reverse as the
8 presentations are shifted from one boundary to the other.

9 The design of such “cross-neighbor” experiments is complex.
10 Because each subject receives four presentations (two at each
11 boundary), separated by time to allow the subject to resume normal
12 behavior, there are possibilities for an effect of order of
13 presentation (Wiley and Wiley 1977). Consequently, whether
14 presentations of a neighbor’s songs at an incorrect boundary are
15 paired with another neighbor’s songs or with a stranger’s might
16 make a difference. Stoddard et al. (1991), for instance, found
17 differences in the behavior of song sparrows *Melospiza melodia*
18 toward a particular neighbor in the two locations when its
19 vocalizations were paired with strangers' but not when paired with
20 another neighbor's. He concluded that the former procedure was a
21 more sensitive test for individual recognition of neighbors
22 (Stoddard et al. 1991; Stoddard 1996).

1 This increased sensitivity might result from the greater
2 salience of a stranger's song in general. Presentation of a stranger's
3 songs might call the subject's attention to the site and thus increase
4 the difference in responses to a particular neighbor in the two
5 locations. It might indeed be best to present a stranger's songs
6 before the neighbor's at both locations, rather than randomizing the
7 order of presentation.

8 The alternative technique, pairing two neighbors' songs at two
9 boundaries, lacks the possible potentiation of responses by a
10 stranger's songs. It might thus provide a less sensitive test for
11 recognition of individual neighbors (a positive result might be more
12 likely). On the other hand, it would provide a more realistic test of
13 the ongoing ability of territorial animals to differentiate particular
14 neighbors and to track their locations.

15

16 Recognition of multiple members of a social group

17 In addition to any differentiation of multiple rivals,
18 individuals in social groups might also differentiate multiple
19 conspecifics by their affiliative relationships. Observers of groups of
20 animals often strongly suspect that their subjects can identify each
21 other. Nevertheless, experiments are necessary to confirm that
22 subjects respond to stable cues associated with individual partners

1 and not solely to their partners' immediate behavior or contexts. In
2 groups of vervet monkeys *Cercopithecus aethiops* and baboons
3 *Papio cynocephalus*, for instance, playbacks of recorded
4 vocalizations indicate capabilities for recognizing other individuals
5 by sound, in other words associating an individual's sounds with
6 previous social relationships (reviewed by Seyfarth and Cheney
7 2000). Some of these experiments provide evidence that females
8 categorize others into groups of matrilineally related kin, although
9 not necessarily as individuals within those groups (Cheney and
10 Seyfarth 1986; Cheney and Seyfarth 1999; Rendall et al. 1996). Two
11 studies demonstrate that vervets and macaques *Macaca fascicularis*
12 not only recognize their own infants by voice or photograph but,
13 within a social group, can associate any infant with its mother
14 (Cheney and Seyfarth 1980; Dasser 1988). These studies thus
15 provide evidence for high specificity and multiplicity in recognizing
16 members of the subject's group, although the limits of this
17 multiplicity remain unexplored.

18 Presenting pictures of individuals to macaques and chimps in
19 captivity has also indicated recognition of individuals from the same
20 troop (Rosenfeld and van Hoesen, G. W. 1979). Most of this
21 research relies on matching to sample (the subject chooses a
22 stimulus that most closely matches a target) (Parr 2003; for

1 example, Parr et al. 2000). This procedure has demonstrated
2 expert abilities to categorize individuals. Nevertheless, it only
3 indirectly supports an ability to differentiate multiple members of a
4 social group. As with much of the research on human face
5 recognition, this research focuses on the mechanisms for
6 categorization of faces: the relative importance of features and
7 configuration and the possibility of special neural mechanisms for
8 recognition of faces as opposed to other forms of "expert"
9 recognition (Parr 2003; reviewed by Gauthier and Logothetis 2000).

10 In group-living birds, despite the presence of complex
11 vocalizations, there is currently no experimental evidence for
12 recognition of individual group members, although playbacks have
13 shown recognition of group-specific vocalizations in birds
14 (Farabaugh and Dooling 1996; Nowicki 1983; Price 1999; 2003; see
15 also Boughman and Wilkinson 1998). Some odontocete cetaceans
16 also have complex individually specific calls, but so far there is as
17 no experimental confirmation of individual or group recognition on
18 the basis of these calls.

19 Dominance hierarchies in social groups have suggested
20 individual recognition of rivals. However, linear hierarchies can
21 form without any such recognition, simply as a result of differences
22 in intrinsic fighting ability, general experience with wins and losses,

1 or status signals. Modifications of the appearance of individuals in
2 dominance hierarchies provide evidence for differentiation between
3 strangers and familiar opponents or between degrees of status
4 signals (Fugle et al. 1984; Guhl 1968; Møller 1987; Rohwer 1985;
5 Slotow et al. 1993; Wiley et al. 1999), but they do not provide
6 evidence for recognition of individual opponents or even relative
7 dominance of particular opponents. Nevertheless, there is other
8 evidence that at least some fish and birds can recognize sets of
9 higher- and lower-ranking opponents among familiar individuals,
10 although the evidence so far does not establish that individual
11 opponents are differentiated further. Social inertia and bystander
12 effects provide the strongest evidence for recognition of higher- and
13 lower-ranked sets of opponents (Early and Dugatkin 2002; Oliveira
14 et al. 1998; Peake et al. 2001; Wiley 1990; Wiley et al. 1999).

15 Aggregations of animals for breeding or feeding provide
16 additional opportunities for recognition of multiple conspecifics.
17 One possibility is differentiation of multiple neighbors in dense
18 colonies of nesting birds, an ability that would resemble recognition
19 of neighbors in species with large territories. In some colonial birds,
20 individuals compete with established neighbors for nest material,
21 but in other cases established neighbors appear to present no threat
22 to each other. Shearwaters that nest in burrows or cavities provide

1 an example: there is no nest material and evictions of nesting birds
2 by other established nesters are unrecorded (Mackin 2005). In a
3 colony of Audubon's shearwater *Puffinus lherminieri*, playbacks
4 revealed lower responses to established neighbors' calls than to
5 strangers' (Mackin 2005), a capability similar to differentiation of
6 neighbors and strangers by birds with large territories. So far there
7 is no evidence of more specific differentiation of individual
8 neighbors.

9

10 FAILURE OF RECOGNITION

11

12 There is a frequent conviction that animals of course
13 recognize each other. This impression is probably fostered by our
14 tendencies to take recognition of other people for granted and to
15 empathize with our subjects of study. A capability for complex
16 learning might incidentally include individual recognition, on the
17 assumption of generalized learning abilities. Furthermore, it is
18 often difficult to interpret experiments that fail to demonstrate
19 recognition (Stoddard 1996; Wiley and Wiley 1977). An experiment
20 might have lacked the statistical power to exclude alternatives to the
21 null hypothesis. Evidence that animals fail to perform is never
22 evidence that they cannot. A change in experimental conditions

1 can sometimes alter the result, as discussed above. Consequently,
2 careful comparisons offer the best evidence that some subjects do
3 not recognize conspecifics under conditions in which others do.

4 Comparisons between closely related swallows have, for
5 instance, established that species nesting solitarily do not recognize
6 their own offspring, while those nesting in colonies do (Beecher et
7 al. 1986). Comparisons of gulls have shown that all species begin to
8 recognize their own young at about the time the young leave the
9 nests, although departure occurs soon after hatching in species that
10 nest on the ground but not until fledging in species that nest on
11 cliffs (Wooller 1978). Penguins that raise their young in fixed nests
12 use simpler cues for recognizing their single young than do
13 penguins that breed in shifting colonies where fixed locations do not
14 assist recognition (Jouventin and Aubin 2002).

15 There have also been attempts to examine whether or not the
16 distinctiveness or complexity of birds' songs might affect
17 possibilities for individual recognition in territorial birds. A recent
18 such study (Wiley 2005) compared species that defend overlapping
19 territories of similar size in the understory of forests in eastern
20 North America. Male hooded warblers each sing about 6-10
21 different song patterns, which often include distinct individual
22 differences. As discussed above, differences in their responses to

1 playbacks of a neighbor's songs at opposite territorial boundaries
2 indicate that they can recognize the songs of individual neighbors.
3 The difference in their responses to neighbors' and strangers' songs
4 is even more pronounced. In nearly identical experiments, in
5 contrast, Acadian flycatchers *Empidonax virescens* do not respond
6 differently to neighbors' and strangers' songs (Wiley 2005). Unlike
7 the warblers, the flycatchers sing a single daytime pattern, which
8 has only subtle (although consistent) individual distinctions, and
9 even these distinctions are subject to degradation during
10 propagation in forests (Wiley 1991). In this case, the failure of the
11 flycatchers to recognize neighbors' songs, in comparable
12 experiments, coincides with a much more difficult discrimination.
13 Male red-eyed vireos *Vireo olivaceus* also defend territories in these
14 forests, although the territories are smaller than the flycatchers' or
15 warblers' and singing occurs mostly in the canopy rather than the
16 understory. Each male sings long bouts of brief but complex
17 phrases without immediate repetitions. Each has a repertoire of
18 about 40 different phrases, many of which are shared between
19 neighbors. In two experiments, again similar to those with the
20 warblers, Godard (1994) failed to show that males differentiated the
21 songs of individual neighbors.

1 Subtle distinctions and variable signals increase the difficulty
2 of learning discriminations (Hearst 1988; Miller and Escobar 2002).
3 The complex variability of vireos' songs and the near stereotypy of
4 flycatchers' unlearned songs must make this task exceptionally
5 difficult, especially in the acoustically complex environment of
6 forests. The flycatchers, with their unlearned songs, perhaps cannot
7 achieve sufficient individual distinctiveness in vocalizations to allow
8 recognition in forests. The vireo appears to have evolved especially
9 complex learned songs. Have the complex songs increased the
10 difficulties of recognition? Or has the absence of an advantage for
11 recognition permitted the evolution of such complexity in song?

12

13 ASSOCIATION OF MULTIPLE CUES

14 Although it is clear that some animals in more or less natural
15 situations respond selectively to cues from single individuals or
16 small sets of individuals, we are left with questions about the
17 mechanisms of recognition. What kind of learning is required? Do
18 the contexts matter?

19 These questions take on special relevance in view of our
20 convictions about human capabilities. Our abstract concepts of
21 other individuals sometimes associate many visual, auditory, and
22 other cues in many contexts with many previous experiences. Yet

1 we also have much less specific concepts, based on associations of
2 particular cues in particular contexts with particular experiences.
3 We might recognize that a certain tall male sits in a certain part of
4 the room in our Tuesday class but not know anything else about
5 him or recognize him elsewhere. Sometimes we recognize other
6 people in a generic way, as one member of a set of individuals. We
7 might recognize a female we pass in the street as someone in our
8 class but not know anything else about her. Sometimes we
9 recognize a person individually in the usual place but are uncertain
10 when a chance encounter occurs elsewhere. Sometimes we do not
11 yet know everybody in our class individually but nevertheless are
12 startled to see somebody new there. Human abilities for individual
13 recognition perhaps never entirely transcend these constraints of
14 habituation, context, and imperfect specificity. It is thus worth
15 considering the degree to which recognition of conspecifics by
16 animals involves habituation as well as associative learning, depends
17 on context, and fails to achieve perfect specificity.

18 One approach is to use operant conditioning to examine
19 discrimination between cues from different conspecifics. Animals'
20 capabilities for discriminating between complex sets of signals from
21 different individuals can be astonishing (Rosenfeld and van Hoesen,
22 G. W. 1979; Stoddard et al. 1992). Such studies reveal possibilities

1 of perception and memory in optimal conditions. Yet animals can
2 acquire discriminations in the laboratory that they do not
3 necessarily make in natural situations. The operant conditions
4 might not occur in natural situations, or, if they do, the variability
5 of signals, the uncertainty of contingencies, and the distractions of
6 other stimulation might prevent or attenuate the acquisition of
7 discriminations in natural conditions. Animals in natural situations
8 probably allocate their attention to a greater variety of tasks than
9 do animals in laboratories and consequently fail to maximize
10 performance on any one task. Although conditioned discrimination
11 can reveal the possibilities for recognition of conspecifics, it does
12 not necessarily reveal the actualities in natural conditions.

13 An example of the relationship between conditioned
14 discrimination and recognition is provided by laboratory studies of
15 olfactory recognition by mammals. A number of studies have
16 trained subjects to respond differently to odors from individual
17 conspecifics (for example, Gheusi et al. 1997). In addition, animals
18 often habituate specifically to the odors of a particular individual
19 but regain responsiveness to those from another (for example,
20 Mateo 2002). Not all sources of odors produce such individual
21 specificity in habituation. In some rodents, odors from urine do not
22 have this specificity, although odors from various glands do

1 (Johnston and Bullock 2001). An ability to discriminate between
2 olfactory cues from different individuals does not confirm that the
3 subjects spontaneously associate the odors of individuals with any
4 other previous experience with those individuals, as would be
5 required for individual recognition in natural situations.

6 To investigate this latter possibility, Johnston and Bullock
7 (Johnston and Bullock 2001) habituated male hamsters to one
8 source of pheromones from females (odors from the flank gland or
9 from vaginal secretions) and then tested them for cross-habituation
10 to the other source of pheromones from the same females.

11 Habituation generalized to the second source of pheromones from
12 the same female only when a male had had previous social
13 interactions with her. The males had thus spontaneously associated
14 the two odors from any one female in the course of normal social
15 interactions. In somewhat similar experiments with Belding's
16 ground squirrels *Spermophilus beldingi*, however, it was unclear
17 that interactions with an individual affected cross-habituation
18 (Mateo 2006).

19 Male hamsters also associate individually specific odors with
20 other males with which they have interacted (Petrulis et al. 2004).
21 Males that have lost a fight with a rival scent-mark less in response
22 to the odors of that male than to those of unfamiliar males, even

1 though the unfamiliar males had also won a fight with a another
2 male. Tests for avoidance in a Y-maze confirmed that losers avoided
3 familiar winners (Lai and Johnston 2002). Losers of fights thus
4 developed conditioned avoidance of stimuli associated specifically
5 with their opponents.

6 These tests of responses to conspecific odors show that
7 individual hamsters spontaneously associate multiple cues from the
8 same individual in the course of routine interactions. The use of
9 habituation to test for associations between cues leaves open the
10 question of how (or even if) the subjects differ otherwise in their
11 behavior toward individual conspecifics. Yet the demonstration that
12 association of odors is facilitated by social interactions with a female
13 (even when separated by a screen) provides the best evidence that
14 different odors are associated with an individual rather than simply
15 with each other.

16

17 CONTEXT-DEPENDENT ASSOCIATIONS

18

19 Context, in particular the locations of testing, often affect
20 learning. Furthermore, location is a feature of a stimulus that is
21 subject to habituation. Following habituation to a sound, a change
22 in location of the sound results in recovery of responses. Such

1 location-specific habituation occurs, for instance, in auditory
2 neurons in the brainstems of mammals (Kiang 1965). Less is known
3 about effects of location on habituation to olfactory signals.
4 Nevertheless, in the experiments with hamsters just discussed,
5 location might have influenced responses to odors. In all but one of
6 these experiments, males were exposed to females one at a time in
7 the males' home cages and subsequently tested in the same place for
8 cross-habituation to odors from one or both of the females. In the
9 one exception, males were exposed to soiled cages of females before
10 testing for cross-habituation to their odors in the males' home cages.
11 This situation is the only one that failed to provide evidence for
12 cross-habituation. It is possible that males associate juxtaposed
13 odors of females only when the males are in their home areas.

14 True recognition, suggest Bee and Gerhardt (2002), requires
15 independence from context. They provide evidence that recognition
16 of individual neighbors by bullfrogs (*Rana catesbeiana*) meets this
17 criterion. In their experiments, males along the edge of a reservoir
18 were habituated to calls presented at an appropriate distance along
19 the edge. The males were then tested for generalization of
20 habituation after a change in either the fundamental frequency of
21 the call (within the natural range of variation among individuals) or
22 the location of the call (the opposite direction along the edge of the

1 reservoir). The subjects' responses recovered most strongly when
2 both cues changed together, less when either cue alone changed,
3 and least of all when neither cue changed. Nevertheless the
4 recovery was not statistically significant when location alone
5 changed, although it was when frequency changed. By accepting
6 the null hypothesis of no recovery following change of location, they
7 concluded that recognition depended on the frequency of a call
8 independent of its location. The overall pattern of recovery,
9 however, suggests the alternative possibility: independent
10 habituation to the two cues, frequency and location.

11 In some cases, it is clear that recognition is strongly limited by
12 context. Birds whose flightless young remain in an easily located
13 nest often rely on location and ignore conflicting intrinsic cues
14 when identifying which young to feed (Beecher 1982; Wooller
15 1978). Nevertheless, even when parents recognize their own young
16 primarily by location, it seems likely that repeated exposure to their
17 young would result in some discrimination of intrinsic cues also.
18 Cross-fostering experiments, such as those used to investigate
19 parent-offspring recognition by birds, show that related species can
20 differ in whether or not parents use location in preference to
21 intrinsic cues to identify their young, but they do not show that

1 those species relying on location do not also develop some
2 recognition of intrinsic features of their young.

3 Probably all learning is to some extent dependent on context,
4 in the sense that discriminations are always weakened more or less
5 by shifts of context. At the same time, repeated exposure to
6 individually specific cues probably always results in some
7 discrimination. The pleiotropy of learning might assure enough
8 generality to prevent absolute restrictions by context. The relative
9 roles of contextual and intrinsic cues in recognition might well form
10 a continuum between extremes rarely if ever attained.

11 When identification depends strongly on context, this form of
12 recognition seems fundamentally different from our human
13 experience of individual recognition. We feel that our own
14 recognition of other humans depends on abstract concepts of each
15 individual, concepts absolutely independent of context. It is not
16 clear though that even human capabilities for individual recognition
17 ever achieve complete independence from context. Indeed, a review
18 of facial recognition by humans indicated that context was the
19 primary influence on accuracy of recognition (Shapiro and Penrod
20 1986).

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22 HABITUATION AND ASSOCIATIVE LEARNING

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The simplest neural mechanism for individual recognition requires nothing more than habituation to a frequent associate (Bee and Gerhardt 2001b; Falls and Brooks 1975; Wiley and Wiley 1977). Habituation seems to occur in all nervous systems (Buchwald and Humphrey 1972; Pinsker et al. 1970) with some remarkably predictable properties that result in simple discriminations between cues. Habituation is a progressive decrease in the intensity of response to a repeated stimulus (often following a transient increase in responsiveness as a result of sensitization or increased attention to the stimulus) and thus results in reduced responsiveness to this stimulus in comparison with others less frequently encountered (Groves and Thompson 1970; Petrinovich 1984; Petrinovich 1984; Thompson and Spencer 1966). Following habituation, a change in the features of the stimulus, including its location, results in some recovery of response, the magnitude of which depends on the magnitude of change. An interval without stimulation also results in some recovery of the response. Greater variability in the stimulation and longer intervals between presentations reduce the rate of habituation per presentation. A second intense stimulus, even in a different modality, results in immediate recovery of the response (dishabituation), but the effect of a dishabituating

1 stimulus itself habituates. Although some form of habituation might
2 occur in all nervous systems, habituation does not necessarily occur
3 at the same rate for every stimulus and sometimes it is difficult to
4 detect at all.

5 These features of habituation are all exemplified in many
6 experiments with repeated playbacks of songs within a bird's
7 territory (Lemon et al. 1981 and references cited therein; for
8 instance, Yasukawa 1981). In these experiments habituation of
9 responses to a repeated song often occurs within an hour. In
10 contrast, similar presentations just outside territories of Carolina
11 wren's *Thryothorus ludovicianus* produced no detectable
12 habituation for hours at a time (Simpson 1984).

13 When familiar individuals evoke less response than others,
14 individual recognition might involve no more than habituation to
15 cues encountered with different frequencies. This situation applies
16 to recognition of neighbors by territorial birds. As discussed above,
17 familiar neighbors in familiar locations (near correct boundaries)
18 evoke less response from subjects than do strangers or neighbors in
19 unfamiliar locations (incorrect boundaries).

20 In a series of experiments with bullfrogs, Bee and Gerhardt
21 (2001) confirmed that decreased responses to neighbors fit all the
22 expectations of habituation. By repeatedly playing a synthesized

1 vocalization near calling males, they showed that responses
2 decreased over periods of tens of minutes. A temporary suspension
3 or a change to a slightly different dominant frequency resulted in a
4 partial recovery of responses. Furthermore, a change of location
5 also produced in a partial recovery of responses. Thus the
6 responses of bullfrogs seemed adequately explained by habituation
7 alone. If males' responses to natural neighbors' calls, with
8 presumably somewhat greater variability in timing and features, are
9 less than to strangers' and also recover when presented in novel
10 directions, habituation might provide a full explanation for this case
11 of individual recognition. Bee and Gerhardt pointed out that
12 recognition of familiar neighbors in other species might also result
13 from habituation, including habituation to the usual locations of
14 individuals.

15 Nevertheless, evidence suggests that associative learning is at
16 work during recognition of neighbors at least in some birds and
17 mammals. Realizing that the reduced responses to familiar
18 neighbors would make it difficult to differentiate between
19 habituation and associative learning, Richards (1979) took
20 advantage of a male eastern towhee *Pipilo erythrophthalmus* with
21 an extraordinary song. Its repertoire included a close match of a
22 Carolina wren's *Thryothorus ludovicianua* song. The neighbors of

1 this male responded to this unusual song, although less than to a
2 strange towhee's song, but other towhees ignored it completely as
3 they did actual wrens' songs. The neighbors must thus have
4 associated the unusual song with their familiar associate. Other
5 towhees without this experience continued to ignore the song. This
6 case of recognition thus excludes habituation because the neighbors
7 responded more strongly to the wrens' song than did other towhees.
8 More attention to the neighbors and associates of individuals with
9 abnormal features could reveal more about individual recognition.

10 Other results also indicate associative learning of territorial
11 neighbors. Song sparrows, for instance, when they cannot exactly
12 match a neighbor's songs, respond by selecting a song from their
13 own repertoires that matches a song in the neighbor's repertoire
14 (Beecher et al. 1996). Godard (1991) showed that the reduced
15 responsiveness by hooded warblers to their neighbors persisted
16 between breeding seasons, a period of about eight months, during
17 which they would not have heard their neighbors. Furthermore, a
18 hooded warbler increases aggression toward a neighbor near their
19 mutual boundary after playbacks that simulate an intrusion by the
20 neighbor into the subject's territory. A simulated intrusion by a
21 stranger does not affect responses to the neighbor near the mutual
22 boundary (Godard 1993, see further discussion below). In this case,

1 responses to a neighbor's songs in one context increase after
2 previous exposure to those songs in another context. Individual
3 recognition in this case must include associative learning in addition
4 to any effects of habituation.

5 Recognition of territorial neighbors that constantly change
6 locations and produce repertoires of songs presents formidable
7 problems of object constancy and classification. How the multiple
8 manifestations of any individuals' vocalizations (different variants
9 at the source, different locations, different times, different
10 modifications by degradation during transmission) all become
11 associated with a particular set of responses by another individual is
12 not obvious. It remains unknown whether individual recognition in
13 birds, for instance, fits any of the possibilities for classification
14 under investigation for humans (single or multiple dimensions,
15 exemplars or thresholds, preconceived prototypes or rules).

16 None of these results exclude a role for habituation in
17 recognition of neighbors, but they do indicate a role for associative
18 learning in some species. In some cases, it is probable that a
19 nervous system would first associate a stimulus with a consequence
20 and subsequently habituate to the stimulus. The neighbors of the
21 towhee with the unusual song must have associated the song with a
22 neighbor but then perhaps habituated to it in the course of many

1 inconsequential repetitions during the breeding season. Presumably
2 these neighbors would have responded more strongly to a strange
3 towhee's songs, in accordance with the results for many other
4 territorial birds. We do not know how they would have responded
5 to an unfamiliar wren's songs.

6 There is thus evidence for recognition of individual
7 conspecifics (or small sets of conspecifics) by associative learning,
8 by habituation, and by context alone. There is also evidence for the
9 association of multiple cues from individuals. In all cases, we lack a
10 full understanding of the role of context or location in recognition.
11 Although humans and at least some animals can achieve prodigious
12 feats of recognition in the course of normal social interactions, we
13 have much more to learn about the degree and nature of differences
14 between related species and between human and other animals'
15 capabilities. Nevertheless, it is apparent that recognition of
16 conspecifics varies among species not only in the degree of
17 specificity of recognition but also in the complexity of the cognitive
18 mechanisms for recognition.

19

20 OPTIMAL LEVELS OF RECOGNITION

21

1 Recognition of individuals is sufficiently complex that we
2 should consider it an adaptation evolved by natural selection and
3 thus should consider the conditions under which it is advantageous
4 for organisms. Furthermore, we should compare the evolutionary
5 consequences of the different possible mechanisms for this
6 recognition. The differences in capabilities for individual
7 recognition, described above, indicate that recognition of
8 individuals is not solely a pleiotropic consequence of generalized
9 learning.

10 Three prerequisites for the evolution of recognition seem
11 clear: (1) adequately differentiated features of individuals, (2)
12 neural capabilities for discriminating these features, and (3) net
13 evolutionary benefits for recognition. As even simple neural
14 mechanisms can achieve limited individual recognition, it seems
15 that all three of these prerequisites might occur in almost any
16 animal.

17

18 Evolution of specificity in recognition

19 When context alone provides enough specificity to direct
20 appropriate responses to individual conspecifics, as in the cliff-
21 nesting gulls and the solitary swallows discussed above, then the
22 additional cognitive capability for more complex forms of

1 recognition is unnecessary. Instead, animals can use a "rule of
2 thumb", a simple contextual rule when no more complicated rule is
3 necessary to achieve specificity. Such rules of thumb might be
4 learned or innate (independent of previous specific experience).

5 There are three kinds of advantages that might accrue from
6 recognizing individual (or small groups of) conspecifics: association
7 with kin, association for cooperation, and management of
8 competition. In each case we should consider the advantages of
9 both the complexity and the specificity of recognition. In many
10 cases more complex mechanisms might allow more specific
11 recognition.

12 The evolution of complex recognition depends on the
13 advantages of differentiating responses to particular classes of
14 individuals and the improvement in differentiation as a result of a
15 specialized mechanism for recognition. For instance, Neff and
16 Sherman (2002) emphasize that learned recognition should evolve
17 only when it provides a more reliable cue for advantageous
18 behavior than an evolved genetic predisposition. By extension,
19 recognition based on learned intrinsic cues should evolve only when
20 it provides a greater expected advantage than recognition based on
21 any simpler set of cues or any rule of thumb, innate or learned.

1 The assumption is that evolution yields the simplest mechanism to
2 produce the optimal specificity in behavior.

3 Recognition of kin, for instance, often lacks individual
4 specificity and instead relies on recognition of a set of other
5 individuals. In many cases, spatial association early in life is
6 sufficient for recognition of kin. Recognition of offspring by cliff-
7 nesting gulls and solitary swallows provide examples. Likewise in
8 ground squirrels, recognition among female kin first appears as
9 young animals emerge from their natal burrows and depends both
10 by spatial association and genetic similarity (Holmes 1995; Holmes
11 and Sherman 1982; Mateo 2003). Rather than adjust their
12 behavior according to the degree of kinship with relatives,
13 individuals appear to develop a threshold that separates relatives
14 and non-relatives. Furthermore, in some species, kin recognition
15 develops in the absence of indications that kinship affects behavior
16 in natural situations (Mateo 2002).

17 More specific recognition would have advantages whenever
18 relatives move around enough or are otherwise likely to raise the
19 possibility of confusion with others. Such conditions are likely when
20 cohesive social groups include more than one lineage of relatives, as
21 in some cetaceans and primates.

22

1 Individual recognition and the evolution of cooperation

2 A more complex possibility is cooperation between unrelated
3 conspecifics. An early proposal for the evolution of such
4 cooperation focused on reciprocity between individual partners
5 (Trivers 1971). The first quantitative confirmation of this
6 possibility introduced a specific form of reciprocity, tit-for-tat (first
7 cooperate, then match your partners' previous action) (Axelrod and
8 Hamilton 1981). Subsequently a number of other possibilities for
9 the persistence of cooperation have included modified tit-for-tat
10 (with occasional testing of partners for cooperation), pavlovian
11 tactics (a win-stay/lose-shift rule that requires behavior contingent
12 on both the actor's and the partner's previous action), indirect
13 reciprocation (each individual's status or standing depends on its
14 own actions and affects the actions of partners), punishment or
15 bribing of noncooperators, and recognition of other cooperators by
16 shared tags (Bowles and Gintis 2004; Nowak and Sigmund 2005;
17 Reeve and Keller 1997; Riolo et al. 2001). In addition, even
18 relatively nonspecific constraints on interactions such as long-term
19 spatial association can result in persistence of cooperation (Koella
20 2000; Mitteldorf and Wilson 2000; Nowak et al. 1994). Apparently,
21 any enduring interactions between individuals can foster
22 cooperation. If cooperation in a population depends on persistent

1 associations of interacting individuals, obligatory immobility in
2 sessile organisms and individual recognition in mobile ones serve
3 the same purpose.

4 Most of the literature on the evolution of cooperation has
5 focused on sufficient conditions for the persistence of cooperation.
6 Nevertheless, in all cases these conditions depend on the specificity
7 of interacting individuals' associations. If associations of interacting
8 individuals are the critical factor, it seems likely that recognition of
9 individual partners, the ability to associate individuals with
10 previous experience, would always promote the evolution of
11 cooperation. Even in the case of indirect reciprocity, individual
12 recognition of partners would prevent errors in judging the
13 standing or status of individuals. Likewise sessile organisms would
14 benefit from individual specificity in responses, in order to confine
15 cooperative behavior to those neighbors that in fact reciprocated.
16 Although cooperation without individual recognition might spread
17 or persist, individual specificity in directing cooperation with
18 partners would presumably do even better.

19 The specificity of recognition is crucial for these advantages of
20 cooperation. Differentiation of familiar and strange individuals, or
21 other sets of conspecifics, would not so easily promote reciprocation
22 by deterring defection. In groups of individuals with long-term

1 associations, the situation in which reciprocity often occurs, it is not
2 easy to demonstrate individual specificity in recognition. The
3 familiar case of vampire bats *Desmodus rotundus* provides an
4 example (Wilkinson 1990). During observations at their daytime
5 roosts, bats regurgitating food for another to eat were usually
6 (77/110 occasions) mothers feeding dependent offspring, but in
7 21/28 cases females fed other females with which they had high
8 indices of association at roosting trees (Wilkinson 1985a).

9 Preferences for locations within roosting trees or for familiar odors
10 could explain this strong pattern of feeding frequent associates.
11 Better evidence that prior association itself influences feeding comes
12 from an experiment with captive bats. The experimental group
13 included 3 and 4 adult females from each of two roosting groups
14 captured at locations 50 km apart. In this situation, regurgitations
15 of food to starved individuals almost always occurred between adult
16 females from the same original groups (12/13 occasions) (Wilkinson
17 1985a; Wilkinson 1984). This preference indicates some ability to
18 recognize familiar associates, but not necessarily recognition of
19 individuals, which would be necessary to identify cheaters within a
20 group. This experiment with captive animals also suggested that a
21 starved female was likely to receive food from an associate which
22 she had herself previously fed (Wilkinson 1984), but it is not clear

1 that this result reached statistical significance (in 6 trials with 8
2 possible reciprocators present, including the same individuals in
3 different trials, the expected number of reciprocators feeding was
4 2.7, while the observed number was 4). This captive group thus
5 provided evidence for a clear effect of familiarity on cooperation
6 but not necessarily for individual recognition. The natural situation
7 is further complicated by the persistence of matrilineal roosting
8 groups. Roosting groups include 8-12 adult females that remain
9 together for years (Wilkinson 1984). Yearling females usually
10 remain in their natal groups, and an immigrant joins a group only
11 about once every two years on average (Wilkinson 1985b). Thus
12 preferences for locations (both for roosting trees and for locations
13 within them) and the resulting familiarity with particular
14 individuals might serve as rules of thumb for identifying kin, much
15 as among the ground squirrels, swallows, and cliff-nesting gulls
16 discussed above. Such rules of thumb if they promoted interactions
17 among close relatives might explain the evolution of cooperation by
18 kin selection. Cooperation between unrelated individuals might also
19 evolve in this situation, as a consequence of the long-term stability
20 of roosting groups, but there would be no deterrent to cheating
21 unless bats could recognize individuals within groups.

1 The phenomenon of "dear enemies" among resident territorial
2 individuals provides an example of specificity in cooperation
3 between unrelated individuals even when persistent spatial
4 association might be sufficient for the evolution of cooperation. If
5 two established neighbors can agree on a boundary or other
6 division of a resource, they could reduce the time and energy spent
7 in their interactions and thus both benefit by the additional time
8 and energy for other interactions, with interlopers, mates, or young.
9 Although only a few studies seem to have considered the possibility,
10 at least a few report that established neighbors (for instance, birds
11 with neighbors returning from a previous season) are more
12 successful in reproduction than are others matched for age and
13 experience but with fewer returning and more new neighbors
14 (Beletsky and Orians 1989; Eason and Hannon 1994).

15 Does the capability for individual recognition contribute to
16 cooperation between neighbors? As described above, there is
17 evidence that hooded warblers can recognize their neighbors
18 individually. Godard (1993) tested the possibility that neighboring
19 hooded warblers use individual recognition to play tit-for-tat with
20 each other. Her experiment, mentioned briefly above, simulated a
21 deep intrusion by a neighbor into each subject's territory. The
22 subjects responded weakly to the neighbor near the boundary

1 before the intrusion, but strongly after the intrusion. Thus the
2 transgression of a neighbor resulted in increased aggression by the
3 subject soon afterwards. To control for the possibility that an
4 intrusion by any bird might arouse the subject, she included
5 simulated intrusions by a stranger, between presentations of the
6 neighbor's songs near the correct boundary. In this case, the
7 subject responded to the neighbor on both occasions relatively
8 weakly. The increased response to a neighbor after a simulated
9 intrusion was therefore specific to the intruding individual.
10 Individual recognition in this case permits a form of tit-for-tat
11 between individually recognized "dear enemies".

12 Predictions that individual recognition should appear when it
13 is advantageous are supported by two cases of facultative
14 recognition, both involving territorial birds. Song sparrows in a
15 resident population in Washington, which normally differentiate
16 among their neighbors in responses to playbacks near boundaries,
17 ceased doing so on an occasion when high mortality had caused
18 territorial instability with increased numbers of new territories and
19 shifts in boundaries (Stoddard et al. 1991; Stoddard 1996). Male
20 Carolina wrens differentiate neighbors and strangers' songs in the
21 spring, when breeding is beginning but territories are stable, but not

1 in the autumn, when young birds are establishing territories before
2 winter arrives (Hyman 2002).

3

4 Recognition during competition

5 Individual recognition might also have advantages in
6 exploiting competition. If an individual that loses (or wins) a
7 contest with another individual is likely to do the same in the
8 future, it would pay to recognize rivals to avoid unnecessary
9 contests (or to miss opportunities unnecessarily). When some
10 conspecifics pose a threat in competition for nest-sites or territories
11 and others do not, it can pay to focus attention on the "real
12 enemies", as in the case of recognition of neighbors by shearwaters
13 (Mackin 2005) or to adjust responses in relation to the level of
14 threat from different classes of opponents (Temeles 1994).

15 Recognition of rivals in some cases might not require
16 recognition of specific individuals. Instead, it would be sufficient to
17 recognize two groups of conspecifics, those higher and lower in
18 dominance. In this case, a rule of thumb might provide this level of
19 specificity. For example, status signals, especially those that reflect
20 the signalers' overall wins and losses, can produce a linear hierarchy
21 without a need for individual recognition of opponents. Social
22 inertia, as mentioned above, provides evidence that birds can

1 differentiate classes of higher- and lower-ranking opponents. When
2 some familiar opponents are treated with testosterone and others
3 are not, ranks do not change, although treatment with testosterone
4 results in higher rank among unfamiliar individuals (Wiley et al.
5 1999). Even in this case, there is little indication that individuals
6 recognize more specific classes of opponents. Linear hierarchies
7 require no more than recognition of relative ranks.

8 In some situations individuals might resist being recognized
9 individually or mimic another individual to promote confusion.

10 The widespread tendency of male songbirds to mimic the songs of
11 their established neighbors fits in this category. Younger or
12 otherwise less competitive males might mimic vocalizations of more
13 competitive neighbors, if minimizing aggression directed toward
14 strangers helps to establish a new territory or if mimicry of a
15 competitive male provides an advantage in attracting mates.

16 Another possibility is that young animals are selected to avoid
17 recognition if they could thereby avoid persecution by adults other
18 than their parents or even to obtain food from them. This situation
19 arises in dense colonies, where adults often attack young other than
20 their own. Nevertheless, young are also under selection to increase
21 their individuality in order to facilitate interactions with parents.

22 Young birds might achieve a compromise by combining convergent

1 appearance but distinctive voices, as sounds can usually be
2 presented or withheld as necessary. A similar situation arises in
3 broods with multiple paternity. Because males might discriminate
4 against young other than their own, it would presumably pay for
5 extra-pair young to blend with the paternal offspring. Early
6 development of individuality might inadvertently reveal paternity
7 as well. In short, individuality might be minimized whenever
8 individuals can avoid discrimination or exploit confusion by
9 conspecifics.

10

11 CONCLUSION

12

13 Recognition of individuals poses evolutionary as well as neural
14 and cognitive questions. We should not let our own remarkable
15 capabilities for individual recognition distract us from addressing
16 these questions in other animals. How complex is individual
17 recognition? What are the neural or cognitive mechanisms?
18 Under what conditions has it evolved and elaborated? This
19 review has suggested that the specificity and multiplicity of
20 recognition are adjusted by evolution for the task at hand. If the
21 cognitive mechanisms for recognition require energy and neural
22 structures that might also serve other purposes, then the

1 mechanisms for recognition should evolve to an optimal level of
2 complexity for each task. Greater specificity and multiplicity
3 would then evolve only when the advantages are correspondingly
4 great. The extraordinary capability of humans for individual
5 recognition might have evolved in conjunction with our similarly
6 extraordinary capabilities for manipulation and cooperation.

7
8
9

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