

Specificity and multiplicity in the recognition of individuals: implications for the evolution of social behaviour

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ABSTRACT

Recognition of conspecifics occurs when individuals classify sets of conspecifics based on sensory input from them and associate these sets with different responses. Classification of conspecifics can vary in specificity (the number of individuals included in a set) and multiplicity (the number of sets differentiated). In other words, the information transmitted varies in complexity. Although recognition of conspecifics has been reported in a wide variety of organisms, few reports have addressed the specificity or multiplicity of this capability. This review discusses examples of these patterns, the mechanisms that can produce them, and the evolution of these mechanisms. Individual recognition is one end of a spectrum of specificity, and binary classification of conspecifics is one end of a spectrum of multiplicity. In some cases, recognition requires no more than simple forms of learning, such as habituation, yet results in individually specific recognition. In other cases, recognition of individuals involves complex associations of multiple cues with multiple previous experiences in particular contexts. Complex mechanisms for recognition are expected to evolve only when simpler mechanisms do not provide sufficient specificity and multiplicity to obtain the available advantages. In particular, the evolution of cooperation and deception is always promoted by specificity and multiplicity in recognition. Nevertheless, there is only one demonstration that recognition of specific individuals contributes to cooperation in animals other than primates. Human capacities for individual recognition probably have a central role in the evolution of complex forms of human cooperation and deception. Although relatively little studied, this capability probably rivals cognitive abilities for language.

Key words: individual recognition, habituation, cooperation, aggression, evolution of learning, developmental plasticity, cognition.

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I. INTRODUCTION

Recognition requires that individuals respond differently to sets of conspecifics based on signals associated with them. As in every form of communication, the receiver's nervous system classifies sensory input and associates behavioural (or neural) outputs with different sensory inputs. For recognition of different sets of conspecifics, classes of sensory input can be either relatively specific (when a set includes only one or a few other individuals) or relatively general. In other words, recognition varies in its specificity. Furthermore, the classification can be either binary (when only two sets of individuals are recognized) or multiple. Recognition thus also varies in its multiplicity. The specificity and multiplicity of recognition can vary independently in different organisms and situations. This variation suggests that the mechanisms of recognition vary in complexity.

An ability to recognize other individuals of the same species has now been reported for a wide diversity of species. Nevertheless, few studies have considered the specificity or the multiplicity of this capability. As a result, basic questions about the mechanisms and the evolution of recognition remain unanswered.

Capabilities for recognition of conspecifics evolve as a result of the advantages of distinguishing sets of social partners and responding appropriately to each (Reeve, 1989; Johnstone, 1997; Tibbetts & Dale, 2007). The evidence reviewed below suggests that these capabilities might evolve just enough complexity to obtain the available advantages and no more. Complex capabilities would thus evolve only as a result of advantages from complex forms of recognition.

Humans of course have prodigious capabilities for recognizing each other. The complexity of this ability has received little attention, however, perhaps because it is taken for granted. A continuing thread of investigation has focused on psychological mechanisms for recognition of individual faces and how they relate to other mechanisms of categorization (Peterson & Rhodes, 2006; Calder *et al.*, 2011), a subject with clear relevance to the continuing interest in machine recognition of faces (Zhao *et al.*, 2003; Tsao & Livingstone, 2008). Yet there have been no attempts to determine how many people humans can recognize and no systematic studies of how humans classify each other with different degrees of specificity. This omission is surprising because the human capacity for recognizing other individuals, for conceptualizing the relationships between individuals, and for differentiating our behaviour on the basis of these relationships underlies most human social behaviour. Furthermore, it seems possible that the cognitive demands rival those for language.

Humans also tend to extend their assumptions about our abilities for recognizing each other to other species. The predilection for this extrapolation seems to be related to our intimacy with other species. There is thus a widespread conviction that our pets recognize us. People with an interest in natural history are often convinced that some individuals, such as mates, parents, and offspring, recognize each other. In recent decades, since intensive field studies of animal behaviour began, many biologists likewise extended their assumptions about human recognition to their non-human subjects. The scientific study of animal behaviour, especially the investigation of releasers, eventually led ethologists to experiment with individual recognition.

Among the first was William Thorpe, whose students focused on vocal recognition of mates, parents, and young in various species of seabirds. It had previously been established that birds could distinguish between individuals of their own and other species solely by their vocalizations, but these studies (reviewed below) showed that birds could often also use vocalizations to distinguish between different individuals within their own species. Soon afterwards Bruce Falls pioneered investigations of birdsong as a means of recognition by territorial neighbours. In this case, it had always seemed plausible that birds would learn to avoid areas from which they had been evicted by rivals. Falls asked whether birds might also recognize rivals solely by the individual differences in their songs. He and his students used playbacks of recordings to provide the first convincing evidence (reviewed below) that distinctive songs were sufficient for recognition of conspecific individuals. Subsequently similar experiments have been conducted with many other species.

Falls provided an operational definition for individual recognition in this context: 'individual recognition [occurs when] recipients discriminate among similar sounds of different individuals in the absence of other identifying cues' (Falls, 1982, p. 238). This definition emphasizes one aspect of individual recognition, discrimination of similar cues presented by different individuals, but it does not emphasize the ramifications of this kind of discrimination for a classification of conspecifics.

This review explores these ramifications. Section II introduces patterns of specificity and multiplicity in recognition of conspecifics by animals. It is not necessary to review all reports of individual recognition (see Tibbetts & Dale, 2007, and Johnston, 2008, for other recent reviews). Instead, the focus is on specificity and multiplicity of recognition in natural situations. Section III reviews the neural and behavioural mechanisms that can result in recognition of conspecifics. It is clear that simple neural

mechanisms are in some cases enough to produce recognition of conspecifics, even individually specific recognition. Section IV reviews evidence for the evolution of complex forms of recognition. It emphasizes the promotion of cooperation by greater specificity and multiplicity of recognition. To conclude there is a brief reflection on the evolution of this form of complex cognition.

II. SPECIFICITY AND MULTIPLICITY OF RECOGNITION

(1) Specificity of recognition

Many experimental studies of recognition show that animals discriminate between cues associated with two categories of conspecifics. If one of these categories happens to include a single individual, then the specificity necessary for individual recognition is satisfied. For instance, playbacks of vocalizations have demonstrated that some colonial seabirds can distinguish between a mate and other conspecifics (White, 1971; Brooke, 1978; Moseley, 1979; Wiley, Hatchwell & Davies, 1991; Aubin & Jouventin, 1998; Lengagne, Jouventin & Aubin, 1999; Aubin, Jouventin & Hildebrand, 2000; Lengagne *et al.*, 2000), and comparisons of responses to a mate and strangers suggest similar discriminations in other organisms as well (Mundinger, 1970; Caldwell, 1992; Rahman, Dunham & Govind, 2001).

Other binary classifications of conspecifics, however, do not have this specificity. For instance, individual specificity is less clear in studies of parent-offspring recognition. Playbacks or modifications of the appearance of young have demonstrated that parents can recognize their own young by auditory or visual cues (Miller & Emlen, 1974; Schommer & Tschanz, 1975; Beecher *et al.*, 1986; De Fanis & Jones, 1996; Aubin & Jouventin, 2002; Illmann *et al.*, 2002; Insley, Phillips & Charrier, 2003) or that young can recognize their parents (Beer, 1970; White, 1971; Leonard *et al.*, 1997; Aubin & Jouventin, 1998; Insley *et al.*, 2003; Charrier, Pitcher & Harcourt, 2009; Jacot, Reers & Forstmeier, 2009).

These studies have all demonstrated that subjects distinguish two categories of conspecifics. In some of these cases, when subjects each have a single mate or a single offspring, one of the two categories includes only a single individual. In other cases, the smaller category includes several individuals, several young or two parents, all of which evoke similar responses. In all cases of parental recognition of multiple offspring, parents have been shown to be capable of distinguishing their own offspring from others, but no evidence suggests that they differentiate among multiple offspring. Even when each parent cares preferentially for only a portion of a brood, responses to playbacks suggest that they recognize two categories of young, those they feed preferentially and all others (Draganoiu *et al.*, 2006; Müller & Manser, 2008). Likewise, young animals often respond selectively to their parents (or preferential attendants), but there are no indications that multiple adults evoke different responses.

Studies of animals' responses to rivals encompass a variety of situations. Often they demonstrate a binary discrimination of familiar and unfamiliar conspecifics, but conclusions about individual specificity in recognition of rivals are usually uncertain. Many investigations of territorial behaviour have compared responses to vocalizations from neighbours and strangers (Weeden & Falls, 1959; Emlen, 1971; Brooks & Falls, 1975*a, b*; Stoddard, Beecher & Horning, 1990). Other experiments have compared responses to the odours or sight of familiar and strange individuals (Barash, 1974; Temeles, 1994; Leiser & Itzkowitz, 1999; Langen, Triplet & Nonacs, 2000; Husak, 2004). These experiments have shown that individuals respond differently towards these two sets of conspecifics, but they do not show the specificity of individual recognition. When animals' responses to rivals are studied in a laboratory, it is often possible to limit familiar rivals to a single individual, so that discrimination between familiar and unfamiliar rivals automatically has the specificity of individual recognition (Johnston & Bullock, 2001; Lai & Johnston, 2002; Lai *et al.*, 2004; Petrusis, Weidner & Johnston, 2004). In natural circumstances individuals might have more than one familiar rival, so that a discrimination between familiar and strange rivals might not involve the specificity of individual recognition.

A similar situation arises in social insects. In some species, each colony develops a distinctive odour, which is used to exclude individuals from other colonies of the same species as well as to exclude other species (Breed *et al.*, 1995, 1998; Langen *et al.*, 2000). Visual cues can also serve this purpose. Paper wasps use distinctive patterns on their cuticles to discriminate between nestmates and strangers (Tibbetts, 2002; Tibbetts & Curtis, 2007). None of these experiments, however, indicates recognition of individual nestmates. Once again experiments can sometimes limit familiar nestmates to a single individual. For instance, in some ants individuals use odour to discriminate between familiar and unfamiliar dominant individuals, and two founding queens show less aggression when they have had previous interactions with each than otherwise (D'Ettore & Heinze, 2005; Dreier, Van Zweden & D'Ettore, 2007). As in similar cases above, it is not clear that familiar rivals in natural circumstances would always be limited to a single individual.

Another parallel appears in group-living birds. In at least one species members of a group are known to respond less aggressively to vocalizations from other members of their group than to similar vocalizations from outsiders (Wiley & Wiley, 1977; Price, 1999), again without evidence for differentiation of individuals within groups. A similar situation occurs in a group-living bat (Boughman & Wilkinson, 1998).

Discrimination between more and less familiar conspecifics is probably widespread among animals. This ability probably often extends to recognition of familiar members of an individual's social group. Probably all sensory modalities can serve for this discrimination in a wide variety of animals. Nevertheless, in most cases there is no evidence that individuals differentiate conspecifics within sets of familiar

or unfamiliar rivals. A complicating factor is that familiarity with other conspecific individuals presumably varies nearly continuously. If so every individual must have one other that is most familiar. Nevertheless, there is no information for any species about its just-discriminable difference in familiarity. This information would allow us to estimate the sizes of sets of more and less familiar individuals. It remains uncertain whether discrimination of bins along a continuum of familiarity would ever attain the specificity of individual recognition.

Binary classifications of conspecifics, such as those demonstrated by nearly all experimental studies of recognition, reveal two fundamental features of recognition. First, recognition is a categorization of conspecifics into at least two sets of other individuals. Along with other kinds of categorization, it is one of the basic operations of any organism's nervous system and the foundation for more complex cognitive capabilities. Second, binary classifications of conspecifics vary in specificity over a wide scope. One of the two categories might include only a single other individual and the second all others, or the two categories might each include many other individuals. Along this continuum, there are differentiated responses to one sex, one age-class, parents, young, members of the same group, or any other category with one or more conspecifics. Even when one of two sets of conspecifics includes only a single other individual, it remains doubtful that this form of categorization parallels our own ability to recognize each other.

Classification of conspecifics might involve nested categories of progressively greater specificity. The narrowest of these categories might include single individuals, but some broader categories might include individuals that are not further differentiated. Recent studies of primates, for instance, indicate that at least some primates can differentiate both individuals and groups of kin (Cheney & Seyfarth, 1999; Bergman *et al.*, 2003; Wittig *et al.*, 2007a, b). It is not known, however, that all individuals associated with a category of kinship are further differentiated by their individual attributes. Even when baboons respond more strongly to cross-family than to within-family reversals of rank (Bergman *et al.*, 2003), it is hard to be sure that subjects do not associate some individuals only with categories of rank or kinship.

Such gradations of specificity no doubt characterize human recognition as well, although we rarely think about it. Assuming my experience is not unusual, professors are a good example. We routinely recognize students with different levels of specificity. For some we know names and other specific details or associations (recognition with individual specificity). For others we only know that they attend our lectures or did so in the past. Some we might identify as members of other groups. Some appear familiar but have no other associations for us. This variation in the specificity of categories recurs as a general feature of the classification of objects. Similar variation presumably occurs in the classification of conspecifics by any animal, although their classification is not necessarily the same as our classifications of their social partners. And the complexity

they achieve in recognizing conspecifics may or may not reach the complexity achieved by humans.

(2) Multiplicity of recognition

Parallels with human individual recognition increase when it is possible to demonstrate recognition of multiple individual conspecifics in similar situations. Multiplicity of recognition has its own inherent interest also, because the increased complexity of classification requires more complex neural mechanisms. Multiplicity, like specificity, thus increases the cognitive demands of recognition. There are two situations in which this capability seems likely to occur: recognition of multiple rivals and recognition of partners within a social group.

(a) Recognition of multiple rivals

A few studies have tried to determine whether or not territorial birds recognize their neighbours individually. Rather than including playbacks of a neighbour's and a stranger's songs at one place in a subject's territory, the procedure is elaborated to include an individual neighbour's vocalizations on both a boundary shared with that particular neighbour (a correct boundary) and one not so shared (an incorrect boundary). For comparisons these experiments include a second presentation at each boundary, sometimes a stranger's vocalizations (Falls & Brooks, 1975; Stoddard *et al.*, 1991) and sometimes the opposite neighbour's (Wiley & Wiley, 1977; Godard, 1991; Godard & Wiley, 1995). In the first case there is evidence for individual recognition of neighbours if the subject behaves differently to the neighbour's vocalizations at the two boundaries, but equally to strangers. In the second case, evidence consists of weaker responses to each neighbour at the correct boundary and stronger at the incorrect one. Recognition of individuals is indicated if the relative intensity of responses evoked by the same two vocalizations, one from each of two neighbours, reverse as the presentations are shifted from one boundary to the other.

The design of such 'cross-neighbour' experiments is complex. Because each subject receives four presentations (two at each boundary), separated by time to allow the subject to resume normal behaviour, there are possibilities for an effect of order of presentation (Wiley & Wiley, 1977). Consequently, whether presentations of a neighbour's songs at an incorrect boundary are paired with another neighbour's songs or with a stranger's might make a difference. Stoddard *et al.* (1991), for instance, found differences in the behaviour of song sparrows *Melospiza melodia* toward a particular neighbour in the two locations when its vocalizations were paired with strangers' but not when paired with another neighbour's. He concluded that the former procedure was a more sensitive test for individual recognition of neighbours (Stoddard *et al.*, 1991; Stoddard, 1996). This increased sensitivity might instead result from the greater salience of a stranger's song in general. Presentation of a stranger's songs might call the subject's attention to the site and thus increase the difference in responses to a particular neighbour

in the two locations. If so it might be best to present a stranger's songs before the neighbour's at both locations, rather than randomizing the order of presentation.

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

Dominance hierarchies in social groups have also suggested individual recognition of rivals. However, linear hierarchies can form without any such recognition, simply as a result of intrinsic differences in threatening or fighting abilities, general experience with wins and losses, or status signals. Modifications of the appearance of individuals in dominance hierarchies provide evidence for differentiation between strangers and familiar opponents or between degrees of status signals (Guhl, 1968; Fugle *et al.*, 1984; Rohwer, 1985; Møller, 1987; Slotow, 1993; Wiley *et al.*, 1999), but they do not provide evidence for recognition of individual opponents or even relative dominance of particular opponents. Nevertheless, other evidence suggests that some fish and birds can differentiate sets of higher- and lower-ranking opponents among familiar individuals. Social inertia and bystander effects provide the strongest evidence for these categories of opponents (Wiley, 1990; Oliveira, McGregor & Latruffe, 1998; Wiley *et al.*, 1999; Peake *et al.*, 2001; Earley & Dugatkin, 2002), although the evidence so far does not establish that individual opponents are differentiated further. Evidence for recognition of individual opponents is stronger for primates, as discussed in the next section.

(b) Recognition of multiple partners in stable social groups

In addition to any differentiation of multiple rivals, individuals in social groups might also differentiate multiple conspecifics by their affiliative relationships. Observers of groups of animals are often convinced that their subjects can identify each other. Nevertheless, only experiments can confirm that subjects respond to stable features of individual partners and not solely to their partners' immediate behaviour or contexts. In groups of vervet monkeys *Cercopithecus aethiops* (now *Chlorocebus pygerythrus*) and chacma baboons *Papio ursinus*, for instance, playbacks of recorded vocalizations indicate capabilities for recognizing other individuals by sound, in other words associating others' vocalizations with previous social relationships (reviewed by Cheney & Seyfarth, 1990, 2007; Seyfarth & Cheney, 2000). Some of these experiments provide evidence that females categorize others into groups of matrilineally related kin (Cheney & Seyfarth, 1986; Rendall, 1996). In baboons, for instance, females respond more to combinations of vocalizations indicating reversals of rank between other unrelated individuals than to those confirming existing ranks (Cheney, Seyfarth & Silk, 1995). Females also look at nearby unrelated individuals when combinations of vocalizations

indicate that their respective relatives are engaged in an agonistic interaction (Cheney & Seyfarth, 1999). They respond more strongly to combinations indicating rank reversals across matriline than they do to those indicating reversals within matriline (Bergman *et al.*, 2003). In alliances and reconciliation, baboons also show an awareness of individuals' matrilineal relationships (Wittig *et al.*, 2007a, b). In all of these ways, baboons show that they can associate the vocalizations of individuals with expected social relationships and can classify individuals by their matriline. Similar studies demonstrate that vervets and macaques *Macaca fascicularis* not only recognize their own infants by voice or photograph but can also associate other infants with their mothers (Cheney & Seyfarth, 1980; Dasser, 1988). These studies thus provide evidence for high specificity and multiplicity in recognizing many members of the subject's group. Nevertheless, the limits of this multiplicity of individual recognition remain unexplored. We thus know that the baboons in any one troop are capable of recognizing some individuals some of the time, but not necessarily all individuals all of the time.

Presenting pictures of individuals to macaques and chimpanzees in captivity has also indicated recognition of individuals from the same troop (Rosenfeld & van Hoesen, 1979). Most of this research relies on matching to sample (the subject chooses a stimulus that most closely matches a target) (Parr, Winslow & Hopkins, 2000; Parr, 2003). This procedure has demonstrated expert abilities to categorize individuals. Nevertheless, it only indirectly supports an ability to differentiate multiple members of a social group. As with much of the research on human face recognition, this research focuses on the mechanisms for categorization of faces: the relative importance of features and configuration and the special mechanisms for recognition of faces as opposed to other forms of dedicated recognition (Tanaka & Farah, 1993; Gauthier, Behrmann, & Tarr, 1999; Gauthier & Logothetis, 2000; Leder & Bruce, 2000; Parr, 2003; Peterson & Rhodes, 2006; Tsao, Moeller & Freiwald, 2008; Wilmer *et al.*, 2010; Calder *et al.*, 2011).

In group-living birds, despite the presence of complex vocalizations, there is currently no experimental evidence for recognition of individual group members, although playbacks have shown recognition of group-specific vocalizations in birds (Wiley & Wiley, 1977; Nowicki, 1983; Farabaugh & Dooling, 1996; Price, 1999, 2003). Some highly social mammals also have complex individually specific calls, especially odontocete cetaceans. Aside from recognition of parents or offspring, so far no experiments have confirmed recognition of individuals within groups or group membership on the basis of these calls.

Aggregations of animals for breeding or feeding provide additional opportunities for recognition of multiple conspecifics. One possibility is differentiation of multiple neighbours in dense colonies of nesting birds, an ability that would resemble recognition of neighbours in species with large territories. In some colonial birds, individuals compete with established neighbours for nest material, but in other cases established neighbours appear to present no threat

to each other. Shearwaters that nest in burrows or cavities provide an example: there is no nest material and evictions of nesting birds by other established nesters are unrecorded (Mackin, 2005). In a colony of Audubon's shearwater *Puffinus lherminieri*, playbacks revealed lower responses to established neighbours' calls than to strangers' (Mackin, 2005), a capability similar to differentiation of neighbours and strangers by birds with large territories. Here again there is no evidence of more specific differentiation of individual neighbours.

III. FAILURE OF RECOGNITION

Ethologists often take it for granted that animals recognize each other. This impression is probably fostered by our tendencies to take recognition of other people for granted and to empathize with our subjects of study. In addition, it seems plausible that capabilities for complex learning in many birds and mammals might include individual recognition. This plausibility rests on an assumption that an aptitude for one kind of learning generalizes to other kinds. Although the generality or specialization of complex learning is a contentious issue (Shettleworth, 2000), studies of complex learning sometimes reveal special aptitudes that are not clearly related to general aptitudes for learning. Capabilities for spatial memory in food-caching birds provide an example (Kamil, Balda & Olson, 1994; Pravosudov & Clayton, 2002). Unlike the case of spatial memory, however, there have been few attempts to determine variation in or the limits of recognition.

Experiments that fail to demonstrate recognition, like all studies with negative results, are often difficult to interpret (Wiley & Wiley, 1977; Stoddard, 1996). An experiment might lack the statistical power to exclude alternatives to the null hypothesis. Even if statistical power is not a problem, evidence that animals fail to perform a task is never evidence that they cannot. A change in experimental conditions sometimes alters the result. Instead, just as comparisons of similar species have revealed differences in spatial memory, the best evidence that recognition has limitations comes from comparisons of species that differ in abilities to recognize conspecifics in similar situations.

Comparisons between closely related swallows have, for instance, established that species nesting solitarily do not recognize their own offspring, while those nesting in colonies do (Beecher *et al.*, 1986). Comparisons of gulls have shown that all species begin to recognize their own young at about the time the young leave the nests, although departure occurs soon after hatching in species that nest on the ground but not until fledging in species that nest on cliffs (Wooller, 1978). Penguins that raise their young in fixed nests use simpler cues for recognizing their single young than do penguins that breed in shifting colonies where fixed locations do not assist recognition (Jouventin & Aubin, 2002). Males of two species of baboon that differ almost 10-fold in mean size of troops also differ in abilities to recognize the calls of other

males. Gelada baboons *Theropithecus gelada*, unlike the chacma baboons discussed above, do not recognize all of the males in their troops, not even all of those with which they regularly interact (Bergman, 2010).

There have also been attempts to examine whether or not the distinctiveness or complexity of birds' songs might affect possibilities for individual recognition in territorial birds. A recent such study (Wiley, 2005) compared species that defend overlapping territories of similar size in the understorey of forests in eastern North America. Male hooded warblers *Wilsonia citrina* each sing about 6–10 different song patterns, which often include distinct individual differences. As discussed above, differences in their responses to playbacks of a neighbour's songs at opposite territorial boundaries indicate that they can recognize the songs of individual neighbours. The difference in their responses to neighbours' and strangers' songs is even more pronounced. In nearly identical experiments in the same forest, by contrast, Acadian flycatchers *Empidonax virescens* do not respond differently to neighbours' and strangers' songs (Wiley, 2005). Unlike the warblers, the flycatchers sing a single pattern (aside from a somewhat different one at dawn), which has only subtle (although consistent) individual distinctions. As usual these distinctions are subject to degradation during propagation through the forest (Wiley, 1991). In this case, the failure of the flycatchers to recognize neighbours' songs, in experiments comparable to those with hooded warblers, coincides with a more difficult discrimination.

Male red-eyed vireos *Vireo olivaceus* also defend territories in these forests, although their territories are smaller than the flycatchers' or warblers' and their singing occurs mostly in the canopy rather than the understorey. Each male sings long bouts of brief but complex phrases without immediate repetitions. Each has a repertoire of about 40 different phrases, many of which are shared between neighbours. In two experiments, again similar to those with the warblers, Godard (1993a) failed to show that males differentiated the songs of individual neighbours.

Subtle distinctions and variable signals increase the difficulty of learning discriminations (Hearst, 1988; Miller & Escobar, 2003). The complex variability of vireos' songs and the near stereotypy of flycatchers' unlearned songs must make this task exceptionally difficult, especially in the acoustically complex environment of forests. The flycatchers, with their unlearned songs, perhaps cannot achieve sufficient individual distinctiveness in vocalizations to allow recognition in forests. The vireo appears to have evolved especially complex learned songs. Have the complex songs increased the difficulties of recognition? Or has the absence of an advantage for recognition permitted the evolution of such complexity in song? At least it is clear that recognition is not an automatic consequence of interacting with other individuals.

Differences in the timing of parents' recognition of offspring reinforce this conclusion, as seen in the comparisons of related species of gulls, swallows, and penguins mentioned above. As already mentioned, none of these cases is known to attain the specificity of individual recognition. Nevertheless,

they show that capabilities for recognition sometimes fail to evolve in circumstances in which it is clear that they might have. As discussed below, these limitations provide evidence that recognition is an adaptive feature of behaviour.

There is obviously a need for more investigation of the limits of conspecific recognition in a variety of species. The most informative studies would focus on comparisons of similar species in different environments, of different species in the same environment, or different situations for the same species.

IV. MECHANISMS OF RECOGNITION

(1) Association of multiple cues

Selective responses to cues from single individuals or small sets of individuals might result from a number of different neural or behavioural mechanisms. In many of the examples discussed so far, learning is presumably involved, but questions arise about the nature of this learning, its specificity, and its contexts.

These questions take on special importance in view of our convictions about human capabilities. Our abstract concept of another person sometimes attains great complexity, by associating many visual, auditory, and other cues in many contexts with many previous experiences. Yet we also have much less refined concepts of other people, based on associations of particular cues in particular contexts with particular experiences. As mentioned above, we sometimes recognize other people in a generic way, as a member of a set of individuals. Sometimes we recognize a person individually in the usual place but are uncertain when a chance encounter occurs elsewhere. Sometimes we are startled to see somebody new in a group of familiar people. Human capabilities for individual recognition perhaps never entirely transcend these constraints of familiarity, context, and imperfect specificity. It is thus worth considering the degree to which the mechanisms for recognition of conspecifics by animals involve associative learning, depend on context, and fail to achieve perfect specificity.

One approach is to use operant conditioning to study discrimination between cues from different conspecifics. These studies can reveal astonishing capabilities for discriminating between complex sets of signals from different individuals (Rosenfeld & van Hoesen, 1979; Stoddard *et al.*, 1992). Such studies reveal possibilities of perception and memory in optimal conditions. Yet animals can acquire discriminations in the laboratory that they do not necessarily make in natural situations. The operant conditions might not occur in natural situations, or, if they do, the variability of signals, the uncertainty of contingencies, and the distractions of other stimulation might prevent or attenuate the acquisition of discriminations in natural conditions. Animals in natural situations probably allocate their attention to a greater variety of tasks than do animals in laboratories and consequently fail to maximize performance

on any one task. Although conditioned discrimination can reveal the possibilities for recognition of conspecifics, it does not necessarily reveal the actualities in natural conditions.

An example of the relationship between conditioned discrimination and recognition is provided by laboratory studies of olfactory recognition by mammals. A number of studies have trained subjects to respond differently to odours from individual conspecifics (for example, Gheusi, 1997). In addition, animals often habituate specifically to the odours of a particular individual but retain responsiveness to those from another (for example, Mateo, 2002). Not all sources of odours produce such individual specificity in habituation. In some rodents, odours from urine do not have this specificity, although odours from various glands do (Johnston & Bullock, 2001). An ability to discriminate between olfactory cues from different individuals does not confirm that the subjects spontaneously associate the odours of individuals with any other previous experience with those individuals, as would be required for individual recognition in natural situations.

To investigate this latter possibility, Johnston & Bullock (2001) habituated male golden hamsters *Mesocricetus auratus* to one source of pheromones from females (either odours from the flank gland or from vaginal secretions) and then tested them for cross-habituation to the other source of pheromones from the same females. Habituation generalized to the second source of pheromones from the same female only when a male had had previous social interactions with her. The males had thus spontaneously associated the two odours from any one female in the course of normal social interactions. In somewhat similar experiments with Belding's ground squirrels *Spermophilus beldingi*, however, it was unclear that interactions with an individual affected cross-habituation (Mateo, 2006).

Male hamsters also associate individually specific odours with rivals (Petrucci *et al.*, 2004). Males that have lost a fight with a rival scent-mark less in response to the odours of that male than to those of unfamiliar males, even though the unfamiliar males had also won a fight with another male. Tests for avoidance in a Y-maze confirmed that losers avoided familiar winners (Lai & Johnston, 2002). Losers of fights thus developed conditioned avoidance of stimuli associated specifically with their opponents.

These tests of responses to conspecific odours show that individual hamsters spontaneously associate multiple cues from the same individual in the course of routine interactions. The use of habituation to test for associations among cues, however, leaves open the question of how the subjects differ in their behaviour towards individual conspecifics other than by persistence in sniffing. Yet the demonstration that association of odours is facilitated by social interactions with a female (even when separated by a screen) provides the best evidence that different odours are associated with an individual rather than simply with each other.

(2) Context-dependent associations

True recognition, suggest Bee & Gerhardt (2002), requires independence from context. They provide evidence that

recognition of individual neighbours by bullfrogs (*Rana catesbeiana*) meets this criterion. In their experiments, males along the edge of a lake were habituated to calls presented at an appropriate distance along the edge. The males were then tested for generalization of habituation after a change in either the fundamental frequency of the call (within the natural range of variation among individuals) or the location of the call (the opposite direction along the edge of the lake). The subjects' responses recovered most strongly when both cues changed together, less when either cue alone changed, and least of all when neither cue changed. Nevertheless the recovery was not statistically significant when location alone changed, although it was when frequency changed. By accepting the null hypothesis of no recovery following change of location, they concluded that recognition depended on the frequency of a call independent of its location. The overall pattern of recovery, however, suggests the alternative possibility: independent habituation to the two cues, frequency and location.

In the experiments with hamsters discussed above, location might have influenced responses to odours. In all but one of these experiments, males were exposed to females one at a time in the males' home cages and subsequently tested in the same place for cross-habituation to odours from one or both of the females. In the one exception, males were exposed to soiled cages of females before testing for cross-habituation to their odours in the males' home cages. This situation is the only one that failed to provide evidence for cross-habituation. It is possible that males associate juxtaposed odours of females only when the males are in their home areas.

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

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

Even habituation is affected by location. Following habituation to a sound, a change in its location results

in recovery of responses (Bee, 2001; Bee & Gerhardt, 2001). Such location-specific habituation occurs, for instance, in neurons in the brainstems of mammals. The experiments on hamsters' habituation to odours discussed previously show effects of location on habituation to olfactory signals.

When identification depends strongly on context, this form of recognition seems fundamentally different from our human experience of individual recognition. We feel that our own recognition of another human depends on an abstract concept of that individual, a concept that is absolutely independent of context. It is not clear though that even human capabilities for individual recognition ever achieve complete independence from context. Indeed, a review of facial recognition by humans indicated that context was the primary influence on accuracy of recognition (Shapiro & Penrod, 1986).

(3) Habituation and associative learning

The simplest neural mechanism for individual recognition requires nothing more than habituation to a frequent associate (Falls & Brooks, 1975; Wiley & Wiley, 1977; Bee & Gerhardt, 2001). Habituation seems to occur in all nervous systems (Pinsker *et al.*, 1970; Buchwald & Humphrey, 1972) with some remarkably predictable properties that can 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 (Thompson & Spencer, 1966; Groves & Thompson, 1970; Petrinovich, 1984). 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 stimulus itself habituates. Although some form of habituation might occur in all nervous systems, habituation does not necessarily occur at the same rate for every stimulus, and sometimes it is difficult to detect at all.

All of these features of habituation appear in many experiments with repeated playbacks of songs within a bird's territory (Lemon, Fieldes & Struger, 1981; Yasukawa, 1981). In these experiments habituation to songs repeated within a subject's territory often occurs within an hour. By contrast, similar presentations just outside subjects' territories in some cases produce no detectable habituation for hours at a time (Simpson, 1984). When familiar individuals evoke less response than others, individual recognition might involve no more than habituation to familiar cues, those encountered frequently, but not to unfamiliar cues. This situation could explain recognition of neighbours

by territorial individuals. As discussed above, territorial neighbours in familiar locations (near correct boundaries) evoke less response from subjects than do strangers or neighbours in unfamiliar locations (incorrect boundaries).

In a series of experiments with bullfrogs, Bee & Gerhardt (2001) showed that decreased responses to neighbours fit all the expectations of habituation. By repeatedly playing a synthesized vocalization near calling males, they showed that responses decreased over periods of tens of minutes. A temporary suspension or a change to a slightly different dominant frequency resulted in a partial recovery of responses. Furthermore, a change of location also produced a partial recovery of responses. Thus the responses of bullfrogs seemed adequately explained by habituation alone. If males' responses to natural neighbours' calls, which presumably include somewhat greater variability in timing and features than recorded calls, are less than to strangers' and also recover when presented in novel directions, habituation might provide a full explanation for this case of individual recognition. Bee & Gerhardt (2001) pointed out that recognition of familiar neighbours in other species might also result from habituation, including habituation to the usual locations of individuals.

Nevertheless, evidence suggests that associative learning is at work during recognition of neighbours at least in some birds and mammals. Realizing that the reduced responses to familiar neighbours would make it difficult to differentiate between habituation and associative learning, Richards (1979) took advantage of a male eastern towhee *Pipilo erythrophthalmus* with an extraordinary song. Its repertoire included a close match of a Carolina wren's *Thryothorus ludovicianus* song. The neighbours of this male responded to recordings of this unusual song, although less than to a strange towhee's song, but other towhees ignored it completely as they did actual wrens' songs. The neighbours must thus have associated the unusual song with their familiar rival. Other towhees without this experience continued to ignore the song. This case of recognition thus excludes habituation because neighbours responded more strongly to the wren's song than did other towhees. More attention to the neighbours and associates of individuals with abnormal features could reveal more about the mechanisms of individual recognition.

Other results also indicate associative learning of territorial neighbours. Song sparrows, for instance, when they cannot exactly match a neighbour's songs, respond by selecting a song from their own repertoires that matches a song in the neighbour's repertoire (Beecher, 1996). Hooded warblers' reduced responsiveness to their neighbours persists between breeding seasons, a period of about eight months, during which they would not have heard their neighbours (Godard, 1991). Furthermore, a hooded warbler increases aggression toward a neighbour near their mutual boundary after playbacks that simulate an intrusion by the neighbour into the subject's territory. A simulated intrusion by a stranger does not affect responses to the neighbour near the mutual boundary (Godard, 1993*b*; see further discussion below). In this case, responses to a neighbour's songs in one context

increase after previous exposure to those songs in another context. Individual recognition in this case must include associative learning in addition to any effects of habituation.

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

None of these results exclude a role for habituation in recognition of neighbours, but they do indicate a role for associative learning in some species. In some cases, it is probable that a nervous system would first associate a stimulus with a consequence and subsequently habituate to the stimulus. The neighbours of the towhee with the unusual song must have associated the song with a neighbour but then perhaps habituated to it in the course of many inconsequential repetitions during the breeding season. Presumably these neighbours would have responded more strongly to a strange towhee's songs, in accordance with the results for many other territorial birds. We do not know how they would have responded to an unfamiliar wren's songs.

(4) Conclusions

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

V. OPTIMAL LEVELS OF RECOGNITION

Although there is still much to learn about the specificity and multiplicity of recognition and the neural and behavioural mechanisms that produce it, it is clear that many animals can recognize individual conspecifics and in some cases this recognition is remarkably complex. This capability might evolve by natural selection as a result of advantages gained by organisms that can recognize conspecifics in particular

circumstances. Alternatively it might evolve as a pleiotropic consequence of a generalized advantage for learning. At issue is whether recognition of conspecifics is a specialized modular form of learning or an aspect of generalized abilities for learning. It thus provides a model for investigating the evolution of specialized or generalized cognition.

The evolution of individual recognition has interest for other reasons as well, because it has consequences for the evolution of other aspects of social behaviour. The possibilities for both competition and cooperation depend on capabilities for individual recognition. Furthermore, these possibilities differ depending on whether or not the mechanisms of recognition rely on associative learning or solely on habituation.

This section considers these issues. First, it focuses on the evolution of specialized capabilities for individual recognition. Second, it takes up the consequences of individual recognition for the evolution of complex forms of competition and cooperation.

(1) Evolution of specificity in recognition

The examples discussed above show that recognition of conspecifics does not always attain individual specificity nor more than binary multiplicity, even when human observers can do so. The gulls, swallows, and penguins already mentioned provide good examples. In each case, parents begin to recognize their offspring when the young leave the nest. In cliff-nesting gulls, young are confined to their nest until they can fly; in ground-nesting gulls, young abandon their nests to seek cover from predators, including other gulls, as soon as they can scramble on their own feet. In neither case is there evidence that parents recognize each of their young individually, nor achieve more than a binary classification of conspecific young. Recognition in this case occurs when and to the extent that there is a 'need to know'. The swallows provide a parallel example. Barn Swallows, which have solitary nests, do not develop recognition of offspring before the young leave the nest, whereas cliff swallows, which nest in dense colonies where there is always a chance that returning parents might mistake a neighbour's nest for their own, recognize the vocalizations of their young at an early stage. In both cases recognition is no more complex than needed and develops only when needed. We might expect gulls and swallows to develop more specific recognition of individual offspring once the young leave the nest and accompany their parents while foraging and roosting.

The evolution of complexity in recognition is a special case of the evolution of learning in general. Learning in turn is a form of developmental plasticity. In the case of learning, an individual's behaviour (and presumably the structure and physiology of its nervous system) adjusts to changing situations in the course of its life. Perhaps all features of every organism, whether behavioural or not, have some degree of plasticity during development if for no other reason than the development (epigenesis) of any organism results from an interaction between the genes it inherits and the environment in which it lives. Some features of an organism

develop with remarkable predictability over the range of environmental variation ordinarily encountered by a species or population (or in experimental situations over even wider ranges). These features are often called 'innate' features of an organism, those that develop predictably regardless of relatively wide (but not indefinitely wide) environmental variation. Biologists also call these features 'canalized' to indicate that development proceeds on a predictable course despite relatively wide variation in environmental conditions. By contrast, the development of other features of an organism depend closely on specific features of the organism's environment or, in other words, its specific experience. The course of epigenesis is thus in some cases affected only by broadly general features of the environment and in other cases by highly specific features.

The nervous system shows this spectrum of epigenetic or developmental plasticity like other features of organisms. As a result some features of behaviour are 'innate', independent of environmental variation over a wide range of normal environments; others require complex associative learning as a result of particular kinds of experience. Between these extremes, however, there are features of behaviour that are neither innate nor learned in detail. Habituation, for example, produces a simple form of behavioural plasticity that occurs in an extremely wide range of animals and in response to nearly all forms of stimulation. Sensitization to repeated or continual stimulation is another widespread form of behavioural plasticity and often precedes habituation. Habituation results from an association of sensory input and motor output, not just adaptation of its sensory cells (another general feature of animals' nervous systems), and is thus a property of an animal's central nervous system (Marler & Hamilton, 1967; Kandel, 1977). Because it results in greater responsiveness to an unfamiliar stimulus than to a familiar one, it results in a simple form of discrimination.

Comparable features of related species often differ in their developmental plasticity (West-Eberhard, 2003). The degree of plasticity in development evolves by natural selection in accordance with the degree to which more canalized or more plastic development increases survival and reproduction. The advantages of canalization or plasticity presumably depend on the predictability of environmental conditions. When relevant environmental features do not change from generation to generation, then genes associated with canalized development are expected to spread in a population. The additional complexity to produce predictable responses to different environmental conditions is lost when it provides no advantage. When environmental conditions are not constant from one generation to the next, then genes associated with plasticity can spread in a population, as those organisms that can adjust to the current conditions each generation survive and reproduce more successfully.

When simpler mechanisms achieve the same advantages for survival or reproduction as complex ones, then accumulation of neutral mutations should prohibit the evolution of complexity and degrade developmental mechanisms to a simpler level. This degradation of complex

mechanisms to simpler ones with equal advantages would eventually result in organisms with sufficient complexity, and no more, for successful survival and reproduction in a particular environment. We should expect capabilities for recognition to evolve in this way. Recognition of offspring by gulls, swallows, and penguins, reviewed above, confirm this expectation of just enough complexity and no more.

A prediction that recognition should occur only when it is advantageous is also supported by two cases of facultative recognition, both involving territorial birds. Song sparrows in a resident population in Washington, which normally differentiate among their neighbours in responses to playbacks near boundaries, ceased doing so on an occasion when high mortality had caused territorial instability with increased numbers of new territories and shifts in boundaries (Stoddard *et al.*, 1991; Stoddard, 1996). Male Carolina wrens differentiate neighbours and strangers' songs in the spring, when nesting is beginning but territories are stable, but not in the autumn, when territorial boundaries are shifting as young birds establish new territories before winter arrives (Hyman, 2002).

Neff & Sherman (2002) make a somewhat similar argument about the evolution of learning. They emphasize that learned recognition should evolve only when it provides a more reliable cue for advantageous behaviour than an evolved genetic predisposition would. They thus focus on the advantages of plasticity as opposed to canalization of behaviour. The preceding argument extends their emphasis on natural selection of developmental mechanisms to include complexity as well. Neural and behaviour complexity in recognition evolves only when there is a 'need to know'. Otherwise complex developmental mechanisms do not evolve, or if they have previously evolved, they degrade to simpler ones.

Recognition of kin provides another example of this principle. Like recognition of offspring, recognition of other kin often lacks individual specificity. For instance, recognition of close kin by long-tailed tits *Aegithalos caudatus* depends on the development of calls resembling those of close associates early in life, normally their siblings and parents (Sharp *et al.*, 2005). In many mammals as well, spatial association is important for the development of kin recognition. For instance, in ground squirrels *Spermophilus* spp., recognition among female kin first appears as young animals emerge from their natal burrows and depends on both prior spatial association and genetic similarity (Holmes & Sherman, 1982; Holmes, 1995; Mateo, 2003). Rather than adjust their behaviour according to the degree of kinship with individual relatives, these animals appear to develop a binary classification of conspecifics as relatives and non-relatives.

In all of these cases, recognition develops only enough complexity and only in time for a 'need to know'. Despite some evidence that the ground squirrels might use some cues associated with genetic similarity, the overwhelming influence on the development of recognition is the association of offspring with a nest or burrow. Recognition of sets of offspring, parents, and siblings can all use this same 'rule of thumb'.

In some cases, these forms of recognition might require only habituation. Familiar individuals, normally kin, evoke less antagonistic and more affiliative behaviour than do unfamiliar individuals. To a degree that has not been determined, kin recognition by mammals might require no more developmental complexity than found in the nervous systems of a wide spectrum of animals. Habituation and sensitization of responses to familiar stimulation are enough for recognition of individual (or small sets of) conspecifics.

Greater specificity in recognition would have advantages whenever individuals move around or are otherwise likely to raise the possibility of confusion with others. Such conditions are likely when cohesive social groups include more than one lineage of relatives, as in some cetaceans and primates (Sayigh *et al.*, 1995; Janik, Sayigh & Wells, 2006; Cheney & Seyfarth, 2007). Greater multiplicity in recognition would have advantages whenever it pays to respond differently to many individual conspecifics. Such conditions are likely when individuals interact with other conspecifics in specialized ways. These possibilities arise in some cases of cooperation and competition.

(2) Individual recognition and the evolution of cooperation

Cooperation occurs between individuals when they both realize benefits greater than the costs of their interaction. It differs from mutualism, which occurs when both individuals benefit but there is no cost to their interaction. In other words, each realizes a greater benefit in the presence of the other, but it would pay for both do the same thing even if the other was absent. Cooperation also differs from situations that lack any contingency in the interaction of the two individuals. This distinction is important, because, when no physical necessity compels two individuals to interact, the possibility arises that one of them will fail to return the benefit after receiving it. Contingency thus creates the possibility of cheating. Some forms of cooperation are so intricate and intimate (for instance, some corals, lichens, mycorrhiza) that contingency seems to be missing. Yet the incipient stages of these forms of cooperation offer greater scope for contingency and thus cheating. Furthermore, many cases of collaboration and sharing by pairs or groups of birds and mammals, and especially humans, come with obvious risks of contingency. The goal here is to understand the importance of individual recognition in the evolution of cooperation with contingency.

An early proposal for the evolution of such cooperation focused on reciprocity between individual partners (Trivers, 1971). The first quantitative confirmation of this possibility indicated that a specific form of reciprocity, tit-for-tat (first cooperate, then match your partners' previous action), could spread in a population despite the presence of cheaters (Axelrod & Hamilton, 1981). Subsequently a number of other possibilities for the evolution of cooperation have included modified tit-for-tat (with preliminary testing of each partner for cooperation), pavlovian tactics (a win-stay/lose-shift rule that requires behaviour contingent on both the actor's and the partner's previous actions), shared rather

than reciprocated benefits, indirect reciprocation (when the actor's behaviour depends on the partner's interactions with others), punishment or bribing of noncooperators, and recognition of other cooperators by shared tags (Reeve & Keller, 1997; Riolo, Cohen & Axelrod, 2001; Bowles & Gintis, 2004; Nowak & Sigmund, 2005). In addition, persistent spatial association can promote the evolution of cooperation (Nowak, Bonhoeffer & May, 1994; Koella, 2000; Mitteldorf & Wilson, 2000).

The simulations that provide the theoretical basis for these conclusions make two fundamentally different assumptions about individuals' interactions. Some assume unstructured environments in which many individuals interact randomly. Others assume structured environments in which individuals only interact with a few partners. These two cases differ in the presence or absence of limitations on individuals' movements. In natural situations, these two extremes might intergrade.

For some sessile invertebrates, it is presumably nearly impossible for an individual to move to a new location. In less extreme cases, individuals sharing a safe location might face high costs of emigration, so that small groups of individuals would tend to remain together. A group might itself provide a degree of safety, in contrast to the risk of emigration. When individuals interact in small groups, some groups might include only cooperators by chance (Wilson, 1979).

These simulations also make two fundamentally different assumptions about the allocation of benefits. Some assume that benefits of cooperation are shared, and others that they are reciprocated. When benefits are reciprocated, for instance when partners feed or groom each other, the case resembles 'tit-for-tat'. In this case a cooperator with a defecting partner gets the sucker's payoff, a punishment for attempting to cooperate. By contrast, benefits from vigilance or confrontation of predators are shared among partners. As in the 'snow-drift game', a cooperator and a defecting partner each get reduced benefits. If the cost is low in relation to the shared benefit, then a cooperator with a defecting partner can still receive a net benefit and thus avoid a sucker's payoff. Consequently, when benefits of cooperation are shared between partners, rather than reciprocated, cooperation is more likely to evolve.

Some of these possibilities obviously require recognition of specific individuals. To play tit-for-tat, for instance, individuals must keep track of their previous interactions with partners. Specific recognition of multiple individuals is needed. Indirect reciprocation also requires specific recognition of at least some individuals, those with reputations as cooperators. Punishment of individuals that do not cooperate also requires recognition of individuals. Other possibilities, by contrast, do not need such cognitive capabilities. For instance, individuals might adjust their behaviour to their previous experience in general, rather than with each partner individually. These generalized pavlovian tactics or generalized reciprocity (win-stay/lose-shift) can result in the evolution of cooperation, although the outcome depends on initial conditions. Populations

starting with few pavlovian cooperators tend to stay that way, while those starting with many pavlovian cooperators evolve cooperation, despite the absence of individual recognition. Thus this situation might apply to the maintenance of cooperation rather than to its initial spread.

These investigations of the evolution of cooperation also differ in their basic goals. One thread has focused on identifying the simplest conditions for cooperation, without assumptions about the cognitive capacities of organisms. The other has focused on cognitive complexities that might set human cooperation apart from that of other organisms. The goal here, however, differs from both of these. It is the degree to which cognitive capabilities can promote the evolution of cooperation. This perspective changes the conclusions we reach.

For instance, although theory makes it clear that spatial constraints on individuals' interactions can alone result in the evolution of cooperation, in every such case the addition of individual recognition would make cooperation more likely. Even sessile organisms would benefit from individual specificity in responses, in order to restrict cooperation to those neighbours that in fact reciprocated. Shared benefits can promote the evolution of cooperation, even without individual recognition, but in every such case the addition of individual recognition would make cooperation more likely, because cooperators would be more likely to share mutually. Generalized pavlovian reciprocity can maintain cooperation, or in special cases promote its spread, but again a shift to individual recognition would make cooperation more likely. Even among humans, the ease of individual recognition in interactions between different ethnic groups might affect the probability of cooperation. In every case, capabilities for individual recognition promote the spread and maintenance of cooperation.

When our focus shifts in this way from the sufficient conditions for the evolution of cooperation to the optimal conditions, the specificity of recognition becomes critical. Discrimination of familiar and strange individuals, or other sets of conspecifics, might restrict interactions between individuals in much the same way that spatial constraints on interactions would. It would not, however, allow individuals to adjust their behaviour to particular partners, as required for tit-for-tat or indirect reciprocation. In these cases it is crucial to determine whether or not individuals achieve specificity of individual recognition.

In groups of individuals with long-term associations, a situation in which reciprocity often occurs, it is not easy to demonstrate individual specificity in recognition. The familiar case of vampire bats *Desmodus rotundus* provides an example (Wilkinson, 1990). At their daytime roosts, bats regurgitating food for another to eat are usually (77/110 occasions) mothers feeding dependent offspring, but in 21/28 other cases females fed other females. The donors and recipients in these cases also tended to associate with each other at these roosting trees (Wilkinson, 1985a). This strong pattern of feeding frequent associates could result from individuals' preferences for locations within roosts or

for other individuals with familiar odours. Better evidence that prior association itself influences feeding comes from an experiment with captive bats. An experimental group included adult females from each of two roosting groups 50 km apart (three and four individuals, respectively). In this situation, regurgitations of food to starved individuals almost always occurred between adult females from the same original groups (12/13 occasions) (Wilkinson, 1985*a*, 1984). This preference indicates some ability to recognize familiar associates, but not necessarily recognition of individuals. Only recognition of specific individuals would permit identification of cheaters within a group. This experiment also suggested that a starved female was likely to receive food from a bat she had herself previously fed (Wilkinson, 1984). Although this result does indicate recognition of specific partners, it is not clear that it reached statistical significance (in six trials with eight possible reciprocators present, including the same individuals in different trials, the expected number of reciprocating individuals was 2.7, while the observed number was 4). This captive group thus provided evidence for a clear effect of familiarity on cooperation but not necessarily for individual recognition.

The natural situation is further complicated by the persistence of matrilineal roosting groups. Roosting groups include 8–12 adult females that remain together for years (Wilkinson, 1984). Yearling females usually remain in their natal groups, and an immigrant joins a group only about once every 2 years on average (Wilkinson, 1985*b*). Thus preferences for locations (both for roosting trees and for locations within them) and the resulting familiarity with particular individuals might serve as rules of thumb for identifying kin, much as among the ground squirrels, solitary swallows, cliff-nesting gulls, and burrow-nesting penguins discussed above. Such rules of thumb, if they promoted interactions among close relatives, might explain the evolution of cooperation by kin selection. Cooperation between unrelated individuals might also evolve in this situation, as a consequence of the long-term stability of roosting groups, but there would be no deterrent to cheating unless bats could recognize individuals within groups.

The phenomenon of ‘dear enemies’ among territorial neighbours is another example of specificity in cooperation between unrelated individuals, even when persistent spatial association might be sufficient for the evolution of cooperation. If two established neighbours can agree on a boundary, they might reduce the time and energy spent in their interactions and thus both benefit by the additional time and energy to deal with interlopers, mates, or young. Although only a few studies seem to have considered the possibility, at least a few have reported that established neighbours (for instance, birds with neighbours returning from a previous season) are more successful in reproduction than are others with fewer returning and more new neighbours (Beletsky, 1989; Eason & Hannon, 1994; Grabowska-Zhang, Wilkin & Sheldon, 2012). Dear enemies are an example of true reciprocation, not sharing, because one individual receives no benefits if its partner does not participate.

Does a capability for recognizing specific individuals contribute to cooperation between territorial neighbours? There is one compelling case. As described above, evidence suggests that hooded warblers can recognize their different neighbours individually. Godard (1993*b*) tested the possibility that neighbouring hooded warblers use individual recognition to play tit-for-tat with each other. Her experiment, mentioned briefly above, simulated a deep intrusion by a neighbour into each subject’s territory. The subjects responded weakly to the neighbour near the boundary before the intrusion, but strongly after the intrusion. Thus the transgression of a neighbour resulted in increased aggression by the subject soon afterwards. To control for the possibility that an intrusion by any other bird might arouse the subject, she included simulated intrusions by a stranger. In this case, the subject responded to the neighbour relatively weakly both before and after the intrusion. The increased response to a neighbour after a simulated intrusion was therefore specific to the intruding individual. Individual recognition in this case permitted a form of tit-for-tat between individually recognized ‘dear enemies’.

Reciprocity in birds also occurs during defence of nests. An individual is more likely to assist in mobbing a predator in a neighbour’s territory when the neighbour has assisted in its own territory previously (Olendorf, Getty & Scribner, 2004; Krams *et al.*, 2008). In great tits *Parus major*, neighbours familiar with each other from the previous year are more likely to assist each other than are new neighbours, and birds nesting for the first time never assist their neighbours (Grabowska-Zhang, Sheldon & Hinde, 2012). Reciprocity in mobbing might thus depend on long-established familiarity of individuals with each other. Unlike in the ‘dear enemy’ relationships, birds participating in mobbing might themselves benefit directly by learning about potential predators or by mutually discouraging predators in the general vicinity of their own nests.

The multiplicity of recognition affects the possibilities for the evolution of complex forms of cooperation. Indirect reciprocity requires capabilities for tracking the behaviour of many individuals at once. Among primates, reciprocity often lacks immediate contingency. Nevertheless, reciprocity routinely occurs between partners with long-established familiarity (Cheney *et al.*, 2010; Cheney, 2011). The prevalence of this habit of reciprocity in primates remains uncertain for at least two reasons. First, it is difficult to establish the costs and benefits of the behaviour often involved, such as grooming, sharing surplus food, access to infants, and even routine alliance. Also problematic is the multiplicity of recognition in primate troops. Does recognition with individual specificity extend to all troop members at all times? If not, is reciprocity between individuals contingent on recognition? Certainly the development of long-term memories of other multiple individuals’ behaviour would promote indirect reciprocity.

Attempts to elicit cooperative behaviour in captive monkeys and apes have not always succeeded. In one of

the successful studies (Mendres & de Waal, 2000), the cooperating individuals were in continuous sight of each other during a shared task. The continuous spatial association of two individuals greatly simplifies the cognitive problem of monitoring a partner's behaviour. The laboratory setting thus does not reproduce the challenges for multiplicity in individual recognition and thus reciprocity in natural settings.

(3) Recognition during competition

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

Recognition of rivals in some cases might not require recognition of specific individuals. Instead, it would be sufficient to recognize two groups of conspecifics, those higher and lower in dominance. In this case, a rule of thumb might provide this level of specificity. For example, status signals or behaviour that reflects an individual's overall wins and losses can produce a linear hierarchy without a need for individual recognition of opponents. Social inertia, as mentioned above, provides evidence that birds can differentiate sets of higher- and lower-ranking opponents (Wiley *et al.*, 1999). Even in this case, unless coat-tail effects occur, there is no indication that individuals recognize more specific classes of opponents. Linear hierarchies require no more than recognition of two categories of relative ranks.

Piñon jays *Gymnorhinus cyanocephalus* appear to judge the relative dominance of unknown opponents by observing their interactions with known individuals (Bond, Kamil & Balda, 2004). Gradations in the behaviour of the observing individuals indicated that they had acquired quantitative estimates of the dominance of the unknown opponents, rather than an association of the newcomers with previously learned sets of higher- or lower-ranking opponents. It would, however, be necessary to rule out the possibility that the unknown opponents' behaviour did not provide direct quantitative cues for the observing individuals' initial reactions to them.

In some situations individuals might resist being recognized individually or mimic another individual to promote confusion. The widespread tendency of male songbirds to mimic the songs of their established neighbours fits in this category. Younger or otherwise less competitive males might mimic vocalizations of more competitive neighbours, if mimicry minimized interactions with an established neighbour or with strange rivals, or if mimicry of a competitive male provided an advantage in attracting mates. Another possibility is that young animals are selected to avoid recognition if they could thereby avoid persecution by adults other than their parents or even to obtain food from them.

This situation arises in dense colonies, where adults often attack young other than their own. Nevertheless, young are also under selection to increase their individuality in order to facilitate interactions with parents. Young birds might achieve a compromise by combining convergent appearance but distinctive voices, as sounds can usually be presented or withheld as necessary. A similar situation arises in broods with multiple paternity. Because males might discriminate against young other than their own, it would presumably pay for extra-pair young to blend with the paternal offspring. Premature development of individuality might inadvertently reveal paternity as well. In general it would pay to minimize individuality whenever individuals can avoid discrimination or exploit confusion by conspecifics.

(4) Conclusions

Available evidence suggests that the specificity and multiplicity of recognition are adjusted by natural selection for the task at hand. If the cognitive mechanisms for recognition require structures other than those that also serve other purposes, then the mechanisms for recognition should evolve an optimal level of complexity for each task. In some cases minimizing individuality has advantages. In other cases, discrimination of familiar and unfamiliar conspecifics suffices. Greater specificity and multiplicity in recognition evolves when their advantages are correspondingly great. Such advantages are particularly likely in complex forms of cooperation. The extraordinary capability of humans for individual recognition might thus have evolved in conjunction with our similarly extraordinary capabilities for deception and cooperation.

VI. CONCLUSIONS

(1) Recognition of conspecifics consists of a classification of individuals that can vary in specificity (the number of individuals included in a set) and multiplicity (the number of sets differentiated).

(2) Few studies of recognition have addressed the specificity and multiplicity of the classification of other individuals.

(3) Some reports of individual recognition have demonstrated individual specificity, but others have only shown discrimination of familiar and unfamiliar individuals.

(4) Recognition of multiple individuals has so far been documented in animals other than primates only for territorial neighbours of passerine birds.

(5) Dominance hierarchies do not require individual recognition, and social inertia requires only an ability to differentiate sets of high- and low-ranking individuals.

(6) Although primates provide the best evidence for high specificity and multiplicity in recognition of social partners, the limits of these capabilities remain unexplored.

(7) Comparison of species with similar social behaviour in similar habitats has revealed that they can differ markedly in their abilities for individual recognition.

(8) The mechanisms of individual recognition can include the association of multiple features of the same individual.

(9) The recognition of individuals, like other forms of associative learning, often depends on context, and in some cases context provides the only cues for recognition.

(10) In some cases habituation is sufficient to produce individual recognition, but recognition of multiple individuals can require associative learning.

(11) Capabilities for associative learning, a form of phenotypic plasticity, should evolve sufficient complexity, and no more, for successful survival and reproduction in a particular environment.

(12) In confirmation of this expectation, complex capabilities for specificity and multiplicity of recognition are narrowly associated with corresponding advantages.

(13) The evolution of cooperation does not require individual specificity of recognition but is, nevertheless, always promoted by this capability.

(14) Among animals other than primates, only in the case of territorial neighbours of birds has individual recognition been demonstrated in cooperative interactions.

(15) The extraordinary capability of humans for individual recognition might have evolved in conjunction with our similarly extraordinary capabilities for deception and cooperation.

(16) The cognitive challenge of individual recognition in humans, although largely unexplored, might rival that of language.

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