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Social and non-social knowledge in vervet monkeys

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The social knowledge of East African vervet monkeys is striking. Within a local population the monkeys recognize individuals, and associate each individual with its particular group. Within groups, the monkeys recognize dominance relations, rank orders, and matrilineal kinship, and they remember who has behaved affinitively towards them in the past. Outside the social domain, however, vervets appear to know surprisingly little about other aspects of their environment. Although they do distinguish the different alarm calls given by birds, vervets do not seem to recognize the fresh tracks of a python, or indirect evidence that a leopard is nearby. Similarly, although cooperation and reciprocity seem common in social interactions, comparable behaviour has apparently not evolved to deal with ecological problems. Results support the view that primate intelligence has evolved mainly to solve social problems. As a result, vervet monkeys make excellent primatologists but poor naturalists.

INTRODUCTION

We think of ourselves as relatively intelligent creatures for at least two reasons. First, humans not only learn rapidly when taught, they also acquire information without active instruction, by observing objects and events in the world around them. Secondly, human intelligence is not domain-specific, and knowledge acquired in one domain can readily be applied to another. Thus, a principle derived from a social problem can easily be applied to a logically similar problem involving objects.

Comparing human intelligence with the intelligence of non-human primates is difficult, because primate intelligence has thus far been measured almost exclusively by performance on learning tests. Comparatively little is known about the knowledge that monkeys and apes acquire naturally, in the absence of human intervention. More importantly, animal intelligence is generally tested only in one domain, using biologically arbitrary objects as stimuli. Most of the problems confronting non-human primates under natural conditions, however, are ones that derive from competitive and cooperative interactions with conspecifics. There is reason to believe that primates may reveal greater intelligence when dealing with each other rather than with irrelevant objects. In this paper, we examine what free-ranging vervet monkeys have learned, without human intervention, about their environment. We do so by means of observations and experiments that attempt to compare primate performance in social and non-social domains.

Primates tested in the laboratory, with objects, often face problems that are logically similar to the social problems confronting primates in the wild. Despite this similarity, however, the performance of primates in these two settings often seems to differ strikingly. To cite just one example, McGonigle & Chalmers (1977) and Gillan (1981) demonstrated transitive inference in captive squirrel monkeys and chimpanzees, respectively, but were able to do so only after considerable training with paired stimuli. In contrast, field observations suggest that, even from a very young age, monkeys are readily able to deduce a dominance hierarchy among conspecifics from their observation of dyadic interactions (Cheney 1978; Seyfarth 1981; Datta 1983; Gouzoules *et al.* 1984). Observations and experiments have also suggested that primates regularly classify individuals on the basis of kinship or close association (for example, Bachmann & Kummer 1980; Cheney & Seyfarth 1982*a*; Judge 1982; Smuts 1985). Moreover, numerous examples from field studies (admittedly anecdotal) suggest that primates can predict the consequences of their own actions on others, and understand enough about the behaviour and motives of others to be capable of deceit, and other subtle forms of manipulation (for example, Goodall *et al.* 1979; de Waal 1982; Kummer 1982; Cheney & Seyfarth 1984). Such observations are both intriguing and frustrating, because they suggest the existence in the wild of striking mental abilities that, with some notable exceptions (Woodruff & Premack 1979; Premack & Premack 1982), have not been documented or duplicated in the laboratory.

Because of the qualitative differences in field and laboratory stimuli, one possible explanation for the animals' differing performance suggests that primate intelligence is relatively domain-specific. This hypothesis argues that group life has exerted strong selective pressure on the ability of primates to form complex associations, make transitive inferences, and predict the behaviour of fellow group members. Thus abilities that seem to emerge only with human training in captivity may readily occur in primates under natural conditions, but mainly in the social domain (Jolly 1966; Chance & Jolly 1970; Humphrey 1976; Kummer 1971, 1982; see also Rozin 1976). Similarly, when captive chimpanzees solve technological problems that require foresight and an understanding of the consequences of past decisions (Dohl 1968), they may be demonstrating abilities for which they have been preadapted as a result of the need to make equally strategic decisions about each other (de Waal 1982).

This domain-specific hypothesis posits that natural selection may have acted to favour complex abilities in the social domain that are, for some reason, less easily extended or generalized to other spheres. The hypothesis does not, however, specify exactly how elaborate a monkey's social knowledge is, or what processes underlie it, nor does it claim that social knowledge can never be extended to other spheres. It argues simply that certain problems are solved more easily in the social domain as compared with other areas.

An alternative view argues that the contrast in ability between social and non-social behaviour derives not from any fundamental difference in ability between the two domains, but from the animals' lack of motivation to perform under laboratory conditions. Research on captive primates has been plagued by motivational problems, and it has often been difficult to distinguish between a lack of ability and a lack of incentive to perform the task at hand (for example, Terrace *et al.* 1979).

We have begun an investigation of these hypotheses by presenting free-ranging vervet monkeys with logically similar problems involving 'social' and 'non-social' stimuli. Although our field experiments are less precisely controlled than laboratory tests, they have at least two advantages. First, problems of motivation and human training are circumvented. Second, free-ranging primates daily encounter similar social and non-social problems, thus permitting a direct test of performance in the two domains. Third, our subjects regularly deal with objects in the external world that may be either relevant or irrelevant to their survival. It is therefore possible to compare social knowledge both with non-social knowledge of biologically relevant objects and with non-social knowledge of objects that are apparently unrelated to the animals' survival.

At the outset, two points should be emphasized. First, throughout the paper we draw a distinction between the performance of primates in the 'social' and 'non-social' domains. While we believe that this distinction is a real and heuristically important one, we recognize that the boundary between these spheres of activity is ill-defined. Secondly, in evaluating observations and experiments, we make no claims about the mechanisms underlying performance. Our experiments define knowledge operationally; they measure only the responses that particular stimuli evoke, and not the processes (mental or otherwise) that underlie such responses. Many of the results we describe could, for example, result either from relatively simple associative learning or from more complex cognitive processes. Our aim is not to argue for one of these alternatives. Instead, we use experiments to determine which of two stimuli is more salient, and to suggest that animals form some sorts of associations more readily than others.

1. Study site and subjects

Experiments were conducted on three free-ranging groups of vervet monkeys in Amboseli National Park, Kenya. Vervet monkeys live in stable social groups consisting of a number of adult males, adult females, and their juvenile and infant offspring (Cheney *et al.* 1985). As in most Old World monkeys, female vervets remain in their natal group throughout their lives, maintaining close bonds with maternal kin. Males, in contrast, emigrate to neighbouring groups at sexual maturity, often in the company of brothers or natal group peers (Cheney & Seyfarth 1983). Within each group, males and females can be ranked in linear dominance hierarchies that predict the outcome of competitive interactions over food, water and social partners. Offspring acquire dominance ranks immediately below those of their mothers, such that all members of a family typically share adjacent ranks (Cheney 1983*a*).

2. Relevant aspects of other species' behaviour

Vervets in Amboseli are preyed upon by leopards, a number of small carnivores, two species of eagle, baboons and pythons (Cheney & Seyfarth 1981). Predation is a major cause of mortality (Cheney *et al.* 1981, 1985). The monkeys give acoustically distinct alarm calls to different predators, and experiments have shown that each of these alarms evokes qualitatively different escape responses (Seyfarth *et al.* 1980). Calls given to leopards, for example, cause monkeys to run into trees, while calls given to eagles cause monkeys to look up in the air. The monkeys' alarm calls therefore function to designate different types of danger in the external world.

Vervets are not the only species to give alarm calls to predators, however, and it would seem advantageous for the monkeys to distinguish among alarm calls given by other species. We investigated the vervets' knowledge of other species' alarm calls through playback experiments with three different calls of the superb starling (*Spreo superbus*). Starlings give two acoustically distinct alarm calls to predators, neither of which bears any acoustic resemblance to the vervets' own alarms. One starling alarm – a harsh, noisy call – is given to various terrestrial predators (including vervets), all of which prey on starlings or their eggs but only some of which prey on vervets. The second alarm – a clear, rising tone – is given to many species of hawks and eagles, two of which prey on vervets.

In conducting playback experiments of starling alarm calls, we followed the same protocol previously used in tests of the vervet's own alarm calls (Seyfarth *et al.* 1980). First, we hid a loudspeaker near a group of one to five vervets ($\bar{x} = 17.4$ m; s.d., 5.3). The monkeys were then filmed for 10 s, to establish the probability that they would show a given response in the absence of any call. We then played one of the starlings' calls, and continued to film the monkeys' responses for another 10 s. Three starling calls were used: their ground predator alarm call, their aerial predator alarm call, and, as a control, their song. Individual monkeys generally appeared only once in all trials, and successive experiments on the members of a given social group were always separated by at least 48 h. Results are presented in figure 1.

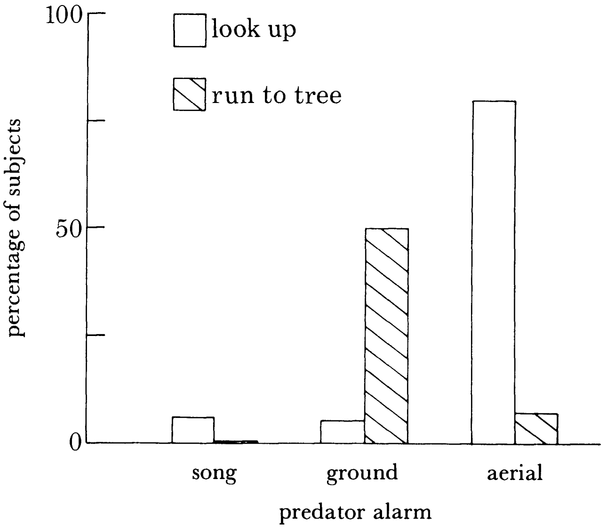

FIGURE 1. Responses of vervet monkeys to playback of three different starling vocalizations. Number of subjects for playback of song, terrestrial predator alarm, and avian predator alarm were 17, 18 and 15, respectively. Ground predator alarms evoked significantly more running to trees than either song ($\chi^2 = 11.4$, $p < 0.01$) or avian predator alarms ($\chi^2 = 7.3$, $p < 0.04$); avian predator alarms evoked significantly more looking up than either song ($\chi^2 = 18.2$, $p < 0.01$) or terrestrial predator alarms ($\chi^2 = 19.0$, $p < 0.01$).

Playback of the starling's ground predator alarm caused a significant number of monkeys to run into trees, while playback of the aerial predator alarm caused a significant number of vervets to look up. In contrast, the starling's song elicited little response. In this test, therefore, where the behaviour of another species was relevant to the vervets' survival, the monkeys' knowledge of another species' calls was similar to their knowledge of their own calls.

3. APPARENTLY IRRELEVANT ASPECTS OF OTHER SPECIES' BEHAVIOUR

The alarm calls of other species represent one end of a continuum of biologically relevant or irrelevant stimuli in the external world. It is perhaps not surprising that vervets discriminate between such alarm calls, since these calls are so obviously important to their survival. Can similar knowledge be demonstrated, however, for aspects of another species' behaviour that are apparently unrelated to the monkeys' survival? This seems an important question, because one striking feature of human intelligence is our inclination to accumulate information about the world that is not directly relevant to our survival. Can the same be said of vervet monkeys? Are vervets as good naturalists as they are primatologists?

To address this question one must first identify two comparable features of the monkeys' environment, one social and biologically relevant, the other non-social, and apparently irrelevant to the monkeys' survival. Then experiments must be designed to compare the monkeys' knowledge in these two domains. As a social, biologically relevant test, we asked the monkeys how much they knew about the ranging behaviour of other vervets. As a non-social, apparently irrelevant test we asked the monkeys how much they knew about the ranging behaviour of other species that neither compete nor interact with vervets in any obvious way.

Vervet monkeys aggressively defend their group's range against incursions by other groups. Females and juveniles are active participants in intergroup encounters, and give a distinctive vocalization when they spot the members of another group (Cheney 1981; Cheney & Seyfarth 1982*a*). In testing the vervets' knowledge of other groups' membership and ranges, subjects in one group were played the intergroup call of an animal from a neighbouring group, either from the true range of the vocalizer's group or from the range of another neighbouring group. In these paired trials, subjects responded with significantly more vigilance to calls played from the 'inappropriate' range than to calls played from the 'appropriate' range (Cheney & Seyfarth 1982*a*).

Subsequent experiments followed the same design, but used as stimuli the calls of other species. Vervets were played the calls of two species that are habitually found in or near water, the hippopotamus and the black-winged stilt (*Himantopus himantopus*). The hippopotamus's call is a territorial call, while the black-winged stilt's is a low-intensity alarm given to a wide variety of potentially disturbing species. These two species were chosen because neither competes nor interacts with vervets, and both are therefore of little biological importance to the monkeys. Nevertheless, each is a species that is so restricted to wet areas during the day that any indication of its presence in another habitat might be regarded, at least by humans, as anomalous. Black-winged stilts are never found away from water, and although hippos do emerge from water to feed on dry land, they do so only at night (Olivier & Laurie 1974).

Hippo and stilt calls were played to vervets either from the edge of a swamp or from a dry woodland area that contained no permanent water. All subjects were members of groups whose ranges bordered both types of area, and all had regularly heard the calls of both hippos and black-winged stilts when foraging near the swamp. Subjects were played hippo or stilt calls in paired trials, from either the swamp ('appropriate') or dry woodland ('inappropriate') habitat. Hippo calls were played at a mean distance of 91.9 m (s.d., 18.3) from the subjects, while stilt calls were played at a mean distance of 40.4 m (s.d., 11.2). As in previous experiments, these distances reflected the different calls' relative amplitudes. Order of presentation was systematically varied, and no individual appeared as a subject in more than one pair of trials. Because the calls were relatively long in duration, subjects were filmed for a total of 25 s following the onset of each call. Results are presented in figure 2.

Subjects responded to the playbacks either by looking in the direction of the loudspeaker or by apparently ignoring the call. In the case of hippo vocalizations, subjects generally showed little response to playback, regardless of the habitat from which the calls were played. In the case of stilt vocalizations, subjects typically responded to playback by looking in the direction of the loudspeaker, but with no significant difference in the duration of response in the dry or the wet habitat. There was some indication that the vervets recognized that the stilt's call was an alarm call: five of 18 subjects looked up and three subjects ran towards trees or stood bipedally when they heard the calls. Again, however, the monkeys did not respond more

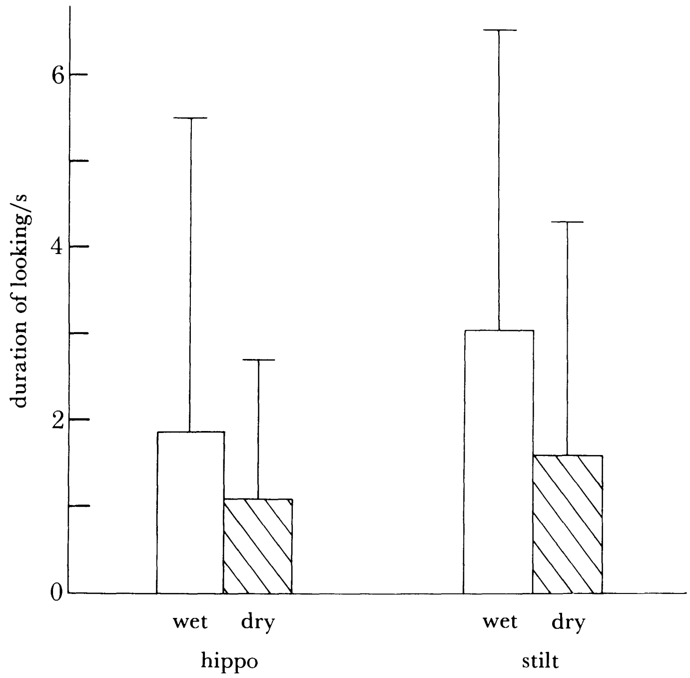

FIGURE 2. Duration of looking towards speaker (in seconds, measured at 18 frames per second) after playback of hippopotamus and black-winged stilt vocalizations from wet and dry habitats. Values shown are means and standard deviations. For hippo calls $n = 10$ subjects; for stilt calls $n = 18$ subjects. Duration of responses to calls played from different habitats did not differ significantly ($p > 0.10$).

strongly in one habitat than another. Vervets responded to both hippo and stilt calls as if they did not recognize that calls played from a dry habitat were anomalous.

These negative results, of course, cannot distinguish between the failure to recognize an anomaly and the failure to respond to one. It is entirely possible, for example, that vervets recognize that hippos belong near water, but that hippo calls played from a dry area simply fail to evoke any measurable response. Negative results *are* of interest, however, when contrasted with similar experiments that do evoke responses. Although vervets fail to respond to hippo or stilt calls coming from an inappropriate area, under comparable conditions they respond strongly to the calls of another vervet. The different performances are particularly striking given that the trials with conspecific calls asked subjects to assess the appropriate location of different *individuals*, whereas the hippo and stilt calls required only a gross understanding of the appropriate location of different *species*.

4. ASSOCIATIONS BETWEEN OTHER SPECIES

Previous playback experiments have demonstrated that vervets can associate the screams of particular juveniles with those juveniles' mothers (Cheney & Seyfarth 1982*a*). Vervets therefore seem capable of forming associations between other group members, based on observations of their social interactions. To test whether vervets can form similar associations outside the social domain, we tested their understanding of the relationships that exist among other species.

Vervet monkeys regularly come into contact with Maasai tribesmen, who bring their cattle into the park to graze. Although the Maasai do not prey on vervets, they occasionally throw sticks or rocks at the monkeys, with the result that their approach causes increased vigilance and flight. Cows themselves pose no danger to the monkeys. Nevertheless, since cows never enter the park without Maasai, a cow alone potentially signals the approach of danger. To test whether monkeys have learned to associate cows with Maasai, we played the lowing vocalizations of either cows or wildebeest (*Connochaetes taurinus*, a common ungulate) to vervets in paired trials.

Calls were played to subjects from a mean distance of 72.3 m (s.d., 18.0). Each subject heard each type of call only once, with order of presentation varied. Because the calls were of relatively long duration, subjects were filmed for 25 s after the onset of each call type.

As figure 3 indicates, playback of cow vocalizations caused subjects to look towards the speaker for significantly longer durations than did playback of wildebeests' calls. This increased vigilance suggests that vervets associated cows with danger, and that they responded to the apparent approach of cows as they would to the approach of Maasai themselves.

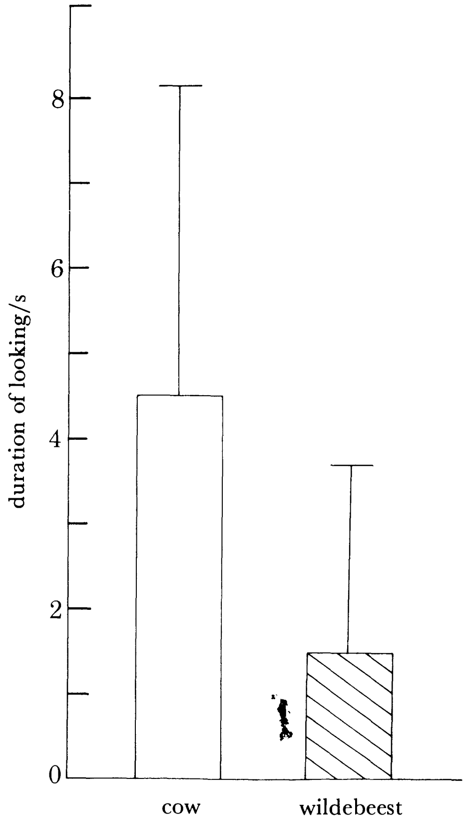

FIGURE 3. Duration of looking towards speaker after playback of wildebeest and cow vocalizations. Legend as in figure 2. Duration of responses was significantly longer after playback of cow vocalizations (two-tailed Wilcoxon test, $n = 19$, two ties, $T = 20.5$, $p < 0.05$).

5. SECONDARY CUES OF DANGER

When leopards make a kill, they frequently drag their prey into trees, where they can feed without harassment from other predators. This behaviour is peculiar to leopards, and local humans recognize that the sight of a fresh carcass in a tree denotes the proximity of a leopard. Each of the three vervet groups in our study has often seen leopards with carcasses in trees, and each time they have responded with prolonged alarm calls. We examined whether vervets knew enough about the behaviour of leopards to understand that a carcass in a tree in the *absence* of a leopard represented the same potential danger as did a leopard itself.

In conducting the experiment, we first procured a limp, stuffed carcass of a Thompson's gazelle, a species that is frequently preyed upon by leopards. This carcass was then placed in a tree, before dawn, approximately 50–75 m from the monkeys' sleeping trees. The carcass was positioned in such a way as to mimic its placement by a leopard (indeed, our attempt fooled at least one tour bus driver into thinking that a leopard was in the area). At first light, we observed the behaviour of the monkeys for a period of 2 h, noting at 5 min intervals the direction of gaze of as many group members as could be seen. In total, we presented the carcass to one group of baboons and four groups of vervets. One of these vervet groups had seen a leopard in a tree with a carcass only four days earlier, and had uttered prolonged alarm calls even when the leopard temporarily left the tree.

Despite all of the groups' experience with leopards and carcasses, neither baboons nor vervets alarm-called at the sight of the carcass alone. Moreover, there was no increased vigilance in the direction of the carcass over that which might have been expected by chance. In all cases, the monkeys behaved as if they did not recognize that a carcass in a tree denoted the proximity of a leopard.

As a further test of monkeys' knowledge of secondary cues of danger, we tested the vervets' recognition of python tracks. Pythons are a frequent predator on vervet monkeys (Cheney *et al.* 1981), and when vervets encounter a python, they give alarm calls to it and closely monitor its movements through the area (Seyfarth *et al.* 1980). Pythons lay distinct, wide, straight tracks which cannot be mistaken for those of any other species, and which are easily recognized by local humans. It is possible to determine the freshness of a python track by noting both the clarity of its outline and whether or not other species have walked across it. Indeed, on many occasions when we have encountered a fresh track we have subsequently been able to find the python in a nearby bush. Vervets in the three study groups have often watched and alarm-called at a python as it laid down a track and then disappeared into nearby bushes. Do vervets therefore recognize that a fresh python track represents potential danger?

To investigate this issue we relied upon both observation and experiments. Over a five-month period, we noted eight separate occasions when a python laid down a track in the dust and then disappeared into a nearby bush when there were no monkeys in the area. We then waited until the monkeys approached the area, and recorded their behaviour. In no case did any individual show vigilance or change its behaviour when it approached and crossed the track. Indeed, on two occasions at least one individual subsequently entered the bush where the track led, encountered the snake, and alarm-called at it. Five subsequent replications of these conditions were made by laying down an artificial python track in an area which the monkeys were approaching. Again, the animals showed no increased vigilance towards the track, and behaved as if they did not recognize that the track signalled danger.

In the preceding experiments, vervets performed well when the secondary cues of danger were auditory stimuli like alarm calls, but performed poorly when the secondary cues were visual stimuli like carcasses or tracks. There are at least two explanations for these results. First, auditory cues may be more salient than visual ones. Auditory signals have a more rapid onset time, and it has been shown that rats are more likely to associate sudden events with other sudden events, and gradual events with other gradual events (Testa 1974). Thus it may be easier for vervets to associate (and respond to) secondary cues of imminent danger when these cues are in the auditory modality. This explanation is limited, however, because it fails to explain why, in the first instance, natural selection has favoured different abilities in the visual and auditory domains.

Alternatively, it may be argued that the vervets' use of communication has evolved mainly to solve social problems, and that this has both shaped and limited their use of signals outside the social domain. Consider, for example, differences in the way primates use auditory and visual signals during social interactions. Vervets use vocal signals both in the presence and absence of visual contact. If animals are foraging in dense bush, a vocalization can tell them that another group is approaching, or that a snake has been seen nearby, without any supporting visual information (Cheney & Seyfarth 1982*b*).

In contrast, although vervets make extensive use of visual signals when communicating with each other, such signals are limited to occasions when animals are in sight of one another. Vervets do not, for example, make use of each other' tracks when foraging or monitoring incursions by neighbouring groups, nor do they visually mark aspects of their physical environment to denote their rank or group membership. As a result, their lack of attentiveness towards the visual cues of predators may be related to their limited use of visual signals as secondary cues in their social interactions. Conversely, the monkeys' regular use of auditory signals to designate objects and events may facilitate their use of auditory signals as representational cues when dealing with other species.

6. Cooperation and reciprocity

Cooperative alliances among humans are characterized by the exchange of goods or services between individuals. Significantly, such exchange is not limited to any particular domain. Exchange may involve actions (for example, reciprocal support in an aggressive coalition), individuals (the exchange of spouses between two villages), or material goods (the donation of money or food to cement an agreement). In contrast, while non-human primates frequently reciprocate past affinitive acts with future cooperation, the exchange of objects is rare (Chance 1961; Chance & Jolly 1970; Kummer 1971; Reynolds 1981).

A variety of studies has demonstrated that, in interactions involving both kin and non-kin, monkeys and apes may exchange grooming, alliances, and tolerance at food sites (for example, Packer 1977; Seyfarth 1977; Chapais & Schulman 1980; de Waal 1977, 1982). Primates seem both to remember past interactions and to adjust their cooperative acts depending on who has previously behaved affinitively towards them (Seyfarth & Cheney 1984). While monkeys and apes often reciprocate previous affinitive acts, however, such altruism rarely involves the use or exchange of objects. Primate tool use, which has received considerable attention because of its relevance to human evolution (for example, Beck 1974), is striking in part because it is relatively rare. By comparison, observers of primates are continually struck by their extraordinary ability to use other individuals as 'social tools' to achieve a particular result (for example, Kummer 1968; Chance & Jolly 1970). Similarly, although parties of baboons and chimpanzees often hunt and kill prey, there is little evidence that such hunts are truly cooperative, or that meat is genuinely shared (Kummer 1968; Altmann & Altmann 1970; Wrangham 1975; Busse 1978; Strum 1981; Teleki 1981).

Reciprocity among monkeys and apes therefore appears to occur more commonly in the form of social interactions, such as grooming and alliances, than in the exchange of material goods (Chance 1961; Reynolds 1981). Before we conclude, however, that non-human primates differ from humans in restricting their cooperative acts mainly to the social domain, a number of caveats should be mentioned.

First, the relative rarity of food sharing among non-human primates may result at least partly from the fact that, with the exception of meat, the food of non-human primates is simply not worth sharing. Monkeys and apes feed mainly on leaves and fruit that are distributed in such a way that they are not easily monopolized by one individual. There may therefore be little benefit in acquiring food directly from another. Individuals may derive greater benefit through tolerance at a particular feeding site or fruiting tree, and indeed, grooming, copulation, and other affinitive behaviour do occasionally increase the frequency with which subordinate individuals are able to feed near dominant animals (Weisbard & Goy 1976). Second, while non-human primates seldom exchange material goods for future beneficial acts, such patterns of exchange do occur in other species. For example, in the courtship displays of many birds and insects, the male offers food to his mate (reviewed in Wittenberger 1981). Finally, while non-human primates do not provision each other with food, a number of species of carnivores bring food to a central den or gathering point, where young and other individuals are fed (reviewed in Wittenberger 1981).

Cooperative behaviour in some animal species, therefore, is occasionally characterized by the exchange of material goods. We do not know, however, whether such patterns of exchange are at all modifiable. While humans can readily substitute a behavioural altruistic act for a material one, such flexibility in the 'currency' of reciprocal acts has seldom been convincingly documented in other animals. More research is clearly needed before cooperation and reciprocity in non-human species are fully understood. For the moment, however, we may hypothesize that, as in other aspects of their behaviour, reciprocity in monkeys and apes appears to occur more often in the social than in the non-social domain.

7. Discussion

When interacting with each other, vervet monkeys are apparently able to form complex associations between individuals. Within a local population, vervets can both recognize individuals and associate them with particular groups. Within their own groups, the monkeys appear to understand dominance and matrilineal kinship relations, and also remember who has behaved affinitively toward them in the past.

Vervets seem less able, however, to form similar associations about non-social aspects of their environment, even when to do so would confer an obvious selective advantage. Although the monkeys do recognize and respond to the different predator alarm calls given by birds, they appear to ignore the visual or behavioural cues associated with some predators. They do not seem to recognize the relation between a python and its track, nor do they understand that a carcass in a tree indicates a leopard's proximity, even though they have had ample opportunities to learn such associations.

Similarly, although vervets and other primates exhibit many forms of cooperation and reciprocity in their social interactions, comparable behaviour using non-social currency (for example, food sharing) is relatively rare. Monkeys readily behave altruistically and form alliances to achieve social goals, but they seldom cooperate to find or exploit new types of food resources.

Finally, vervet monkeys are poor naturalists. They seem disinclined to collect information about their environment when that information is not directly relevant to their own survival. Vervets do not seem to know that hippos stay in water during the daytime, or that particular shorebirds do not occur in dry woodlands. These data are perhaps not surprising, but they do point out a potential difference between monkeys and human beings, who are naturally curious about much of their environment, and who engage in many activities that have little practical value to survival.

We believe that these results can help us to understand the intelligence of non-human primates, and to specify more precisely how the minds of monkeys and apes differ from our own. We also recognize that any interpretation is likely to be controversial. In the following section we therefore state our own hypothesis in its strongest form, then consider alternative explanations.

The primacy of social knowledge

It is now widely agreed that species-specific predispositions affect animal learning (Seligman & Hager 1972; Hinde & Stevenson-Hinde 1973; Johnston 1981). As a result of evolution in different habitats, the behaviour of different species depends not only on the logical structure of the problems they face, but also on the particular stimuli involved. We suggest that, among primates, evolution has acted with particular force in the social domain. As a result, while monkeys are able to form and make use of complex associations in their social interactions, the same sorts of associations are formed less readily when dealing with other species. Within the social group, the behaviour of monkeys suggests an understanding of causality, transitive inference, and the notion of reciprocity. Despite frequent opportunity and often strong selective pressure, however, comparable behaviour does not readily emerge in dealings with other animal species or with inanimate objects.

The special sensitivity of non-human primates to social events is not surprising. Human infants, after all, show special sensitivity to social as opposed to non-social visual stimuli (Sherrod 1981), to speech sounds as opposed to other auditory stimuli (Eimas *et al.* 1971), and to human interactions as opposed to other relations in their environment (see below). In a similar manner, non-human primates appear to exhibit their most subtle discriminations when dealing with conspecific faces, sounds, and social relations.

Because primate intelligence has evolved mainly to solve social problems, monkeys often show surprising gaps in their knowledge of the non-social world. For example, in social interactions visual cues are not used to represent objects or individuals in the absence of face-to-face encounters. Auditory cues, in contrast, often function during social behaviour to designate objects in the absence of visual information. These differences are reflected in the non-social domain, where monkeys are 'prepared' (Seligman 1970) to recognize auditory cues that are secondary indicators of predators, but appear 'unprepared' to associate visual cues with danger. Differences in the monkeys' use of visual and auditory information when dealing with other species may therefore result from the different way they communicate in these modalities when dealing with their own species.

Alternative arguments

(*a*) *Differences between apes and monkeys*

Some of our generalizations about domain-specific performance may be less applicable to apes than to monkeys (Premack 1976), since apes do appear to make occasional use of visual symbols in their social interactions. Free-ranging chimpanzees, for example, make sleeping nests each night, and, when the members of one group make incursions into the range of another, they have been observed to make aggressive displays upon encountering their neighbours' empty nests (Goodall *et al.* 1979). The captive chimpanzee Vicki was able to sort pictures of animate and inanimate objects into distinct categories without previous training (Hayes & Nissen 1971). Whether or not a monkey would be capable of similar classification is not known, because the relevant experiments have not yet been conducted.

(*b*) *The importance of ecological factors*

The food exploited by non-human primates, particularly ripe fruit, is both spatially and temporally dispersed. Field data on many species, especially orangutans and chimpanzees, indicate that primates frequently range over large areas, and that they remember the locations and phenological patterns of both water and a variety of plant foods (Clutton-Brock 1977; Rodman 1977; Wrangham 1977; Sigg 1980; Sigg & Stolba 1981). As a result, it has been argued that ecological pressures have played a major role in the evolution of primate intelligence (for example, Clutton-Brock & Harvey 1980; Milton 1981).

This hypothesis emphasizes that the distinction we have drawn between social and non-social knowledge is not a simple one. Primate memory has no doubt evolved as a result of the need to remember both the location of spatially dispersed food resources and previous social encounters. The point is not to oppose one unifactorial ecological argument against an equally unifactorial social one, but to gain a better understanding of precisely how ecological and social factors have combined to give non-human primates an intelligence that appears simultaneously to be superior to that of other mammals and inferior to our own.

Although ecological factors are undoubtedly important, primates do not appear to manipulate objects in their environment to solve ecological problems with as much sophistication as they manipulate each other to solve social problems (see above). The challenge of exploiting widely dispersed and ephemeral food items may thus have led to increased intelligence not simply because food collection itself becomes more difficult, but also because ecological complexity sets the stage for increasingly complex social competition.

Social knowledge and non-social knowledge in human infants

In the past, many students of human development believed that infants' knowledge of the social and non-social world developed at similar rates (for example, Piaget 1963). Recent studies question this view, and suggest that an understanding of certain concepts may appear at an earlier age when the stimuli involved are animate (especially other people) than when they are inanimate. For example, Hood & Bloom (1978) examined the development of children's expressions of causality, using two- and three-year-olds as subjects. Previous work had indicated that causal understanding develops slowly, and is often not apparent until age seven or eight (Piaget 1963). Hood & Bloom, in contrast, found that children readily discussed the intentions and motivations of people in causal terms. They did not, however, talk about causal events involving objects (see also references in Gelman & Spelke 1981; Hoffmann 1981). In a study of naming behaviour in children 17–22 months old, MacNamara (1982, p. 30) concluded: '...by the time the child comes to learn language, he has already learned that objects in certain categories are important as individuals, those in other categories are merely exemplars of the category. Person is the preeminent category of the first sort'.

These results, together with those presented above, suggest that there is, in both human and non-human primates, an evolutionary predisposition which makes it easier for organisms to understand relations among conspecifics than to understand similar relations among things. Compared with humans, non-human primates exhibit this predisposition in an extreme form: they show sophisticated cognitive skills when dealing with each other, but exhibit such skills less readily in their interactions with objects. Among humans the predisposition is more subtle, but nevertheless may appear in the earliest years of childhood, when infants exhibit remarkable social skills while at the same time remaining ignorant of much of the world around them. For a few brief years, children reveal the results of selection acting on the primate brain: selection that has made them particularly sensitive to the emotions, behaviour and social relations of their conspecifics.

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